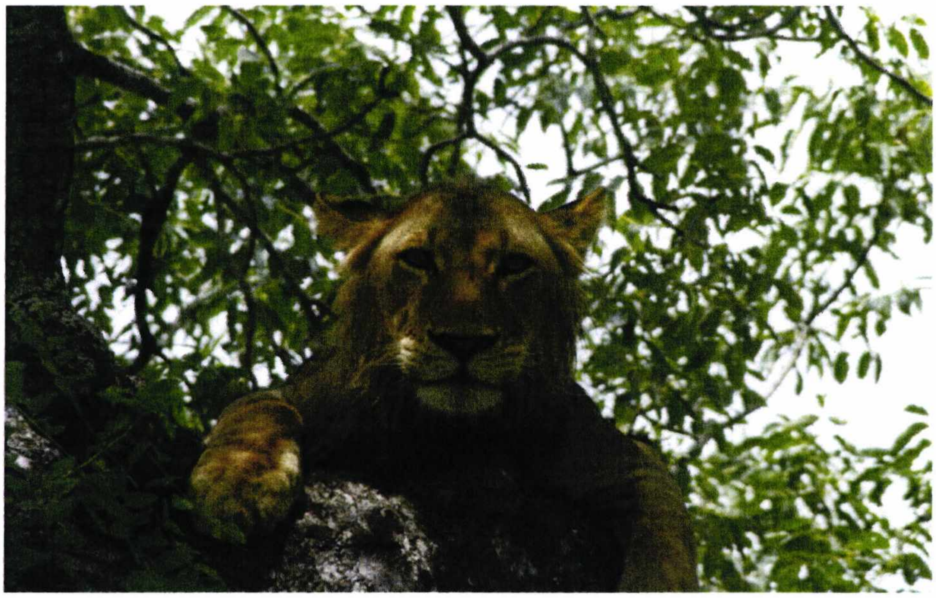
HUNTING FOR SUSTAINABILITY: Lion Conservation in Selous Game Reserve, Tanzania.



A thesis submitted to the University of Kent for the degree of Doctor of Philosophy in Biodiversity Management.

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2010

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DECLARATION

I, Henry Brink hereby declare that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated. The material contained in this thesis has not been previously submitted for a degree at the University of Kent or any other university.

Signed: Henry Brink

Date: 09/11/2010

Abstract

The Selous Game Reserve (SGR) in Tanzania, at 47,500km^2 is large, and is reliant on trophy hunting by tourists for revenue. The study of lions (*Panthera leo*) in SGR therefore offers the opportunity to investigate sustainable resource utilization as a tool in conservation. Using a combination of methods the lion population of SGR was estimated at 4300 (range 1700-6900), representing Africa's largest lion population. The north and west of the reserve had higher densities of lions. The population of an 800km^2 intensively studied area in northern SGR at Matambwe has remained relatively constant since 1997, but the adult sex ratio has decreased from roughly 1 male : 1.3 female in 1997 to 1 male : 3 females in 2009.

The ecology of the Matambwe lions of northern SGR was studied from 2006-2009, and lion distribution in this area was best explained by lean or dry season prey biomass. Two different methods were used to work out the lion carrying capacity. Environmental and anthropogenic factors that best explained lion distribution in northern SGR were distance to the reserve boundary and villages and soil type of an area.

The SGR is divided into 43 hunting blocks which are leased by companies. The management of trophy hunting in SGR and Tanzania is driven by a quota system set through educated guesswork by the government for each hunting block. Based on a study of lion hunting off-take, a reduction of the lion hunting quota to one lion 1000km^{-2} for SGR is suggested. Attempts to estimate the lion population per hunting block and then suggest a quota based on a figure below ten percent of the adult male population also leads to a reduction in the hunting quota.

The impact that length of block tenure by companies has on trophy hunting of lions in SGR was investigated. The blocks in SGR with the most lions shot 1000km^{-2} annually were the blocks that experienced the steepest declines in trophy offtake from 1996 to 2008 and tended to be under short-term tenure. These short-term blocks, however, brought in the greatest amount of revenue for the government.

The important factor in the long-term survival of the lion will be human attitudes and actions. Detailed interviews with key informants and general questionnaires highlighted many different possible ways to reform lion trophy hunting in SGR. Many of the necessary reforms are not new, yet there seems to be reluctance to embrace these reforms.

Acknowledgements

Starting the Selous Lion Project and the completion of this thesis would not be possible without the help, support, and kindness of many people. Firstly, I would like to thank and acknowledge my academic committee. Nigel Leader-Williams took a chance and accepted me as a student in 2006, and Peter Bennett took over in 2009 when Nigel moved to Cambridge. Bob Smith was always available with a friendly ear and useful advice. I have worked for and with Craig Packer since 2003, and am grateful for the many opportunities he has afforded me.

I am grateful for permission, support and constructive advice from the Tanzania Wildlife Research Institute (TAWIRI) and the Wildlife Division (WD) of the Ministry of Natural Resources and Tourism to carry out lion research in Selous Game Reserve. At TAWIRI, I value the friendship and assistance of Dennis Ikanda, Simon Mduma, Honari Maliti, Julius Keyyu, Neciphor Lesio, Herbert Ndunguru, and Angela Mwakatobe. At the WD, this project would not be possible without the help of Benson Kibonde, John Mbwiliza, Mr. Foya, Mr. Gwamaka, Gloria Bideberi, Jafari Omari, Obed Mbangwa, John Kaya, Nebbo Mwina, and Mama Tibanyenda. There are too many rangers and field personnel at Matambwe, Msolwa, Ilonga and Kingupira to thank adequately by name for their everyday kindnesses and help. The TAWIRI-Herta Messerli Foundation Veterinary Programme (Richard Hoare, Robert Fyumagwa, and Sian Brown) provided invaluable assistance in collaring the lions. Similarly Donald Mpanduji, of Sokoine University of Agriculture, was essential in removing collars at the end of the project. Fraser Smith also helped spot lions from his plane. I am extremely grateful for Pendo Samson's help in collecting data from Tanzanian newspapers.

The research has been made possible by grants from National Geographic (Grant # EC0274-06), IdeaWild, SIDA (Swedish International Development Cooperation Agency through Göran Spong), and Panthera. I am extremely grateful to Simon Dures for allowing us use of his car for over a year. Both Wildthings Safaris and Sable Mountain Lodge provided invaluable logistical and financial assistance.

I would also like to thank the following lodges, hunting and safari companies, and organisations for providing logistical support, sharing their knowledge of the Selous lions, and collecting lion data for us: Beho Beho Camp, Selous Impala Camp, Selous Safari Camp, Sand Rivers Camp, Lake Manze Camp, Kidai Rhino Project, Tanzania Wildlife Cooperation Ltd, Tanzania Big Game Safari Ltd, Miombo Safari Ltd, Wild Footprints Ltd, Kiboko Hunting Safaris Ltd, Masailand Hunting Company Ltd, Selous Mbega Camp, Rufiji River Camp, and Authentic Tanzania Safaris. Göran Spong shared his friendship and lion data from 1996-1999, which was an enormous help. Both Onesmo Jacob and Dennis Mchopa were legends when it came to collecting lion data in the Matambwe sector of Selous.

Dennis Ikanda, Bernard Kissui, Ifura Ukio, John Stewart, Ingela Janssen, Harunnah Lyimo, Haddas Kushnir, Meggan Craft and Iain Taylor, all fellow lion watchers and deserved of special thanks, and would understand better than most the tedium and joy involved in studying that most magnificient of beasts, the lion. I am extremely grateful to Margaret Kosmala for help with the SimSimba simulation model. Thanks also to Anna Estes, Anne Hilborn, Grant Hopcraft and Tiziana Lembo for good times and support in Arusha and Serengeti. The following DICE students made life more interesting and enjoyable at Kent: Enrico Di Minin, Steve Green, Kristian Metcalfe, Gail Campbell-Smith, Bruno Nhancale, Simon Tollington, and Winnie Kiiru. Kelly Moyes provided helpful advice on the thesis and was enjoyable company in Kent and Norfolk.

I am extremely grateful to numerous friends in Dar es Salaam, who helped in numerous little (and sometimes not so little) ways that made life much more bearable and fun: Roy & Zoe (& Roo); Jim & Tina (& Asgar); Woody & Hannah; Mike & Lucy (& Billy); and, Kathryn & Graham. The Premier Garden Bar, and its clientel of ancients, who have seen it all before, deserve special mention and thanks. Mustafa Silimu and Julius Mwakazembe helped immensely in Matambwe, and made things much more comfortable.

Lastly, I would like to thank my family, especially my parents, Hans and Marti, for their constant support and encouragement. I would also like to thank Peter Skinner for housing me during the write-up phase. This project is as much Kirsten's as mine, and I am intensely grateful and humbled by all she has done over the last four years. Thanks.

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1 General Introduction

1.1 INTRODUCTION

The year 2010 marks the International Year of Biodiversity and the global deadline for halting the loss of biodiversity. Biodiversity is still in decline and most governments will miss their 2010 targets (UNEP, 2010). Predator diversity studies are particularly relevant to conservation because they focus on the trophic group that is most extinction prone (Finke & Snyder, 2010). Although, large carnivores may be poor biodiversity surrogates (Dalerum *et al.*, 2008), they do require large areas to live (Carbone & Gittleman, 2002) and are sensitive to landscape fragmentation (Crooks, 2002). Due to detrimental conflicts with humans, these large carnivores are no longer found in much of their original range and are increasingly restricted in distribution to protected areas, or PAs (see Woodroffe & Ginsberg, 1998; Gittleman *et al.*, 2001; Caro, 2003).

Much of the world's terrestrial biodiversity and endangered species are found in tropical countries engaged in rapid industrialization and development (see Borgerhoff-Mulder & Coppolillo, 2005; Bradshaw *et al.*, 2009; Gardner *et al.*, 2010). Quite often PAs in these countries would offer greater short-term financial returns if utilized for mining, agriculture, timber production, or other industries, and are therefore expected to pay for their lack of industrial utilization, be it through game-viewing photographic tourism or some form of sustainable resource utilization, like trophy hunting (see Loveridge, *et al.*, 2006; Norton-Griffiths, 1998). In very poor countries, PAs may also be expected to contribute financially to the national economy and surrounding communities who bear the brunt of the human-wildlife conflict inherent with living near dangerous wild animals (Leader-Williams & Hutton, 2005). Proponents of trophy hunting emphasize that it allows for the use and conservation of areas that the photographic tourists would not visit (e.g. Hutton & Leader-Williams, 2003). Such PAs are generally classified internationally by IUCN in their Categories IV to VI (IUCN, 1994); and account for over 85% of PAs in Tanzania.

The Selous Game Reserve in Tanzania is Africa's largest and oldest PA (Baldus, 2009), supporting one of Africa's largest lion populations and is reliant on trophy hunting for revenue. The study of lions in Selous Game Reserve, Tanzania, therefore offers the opportunity to investigate sustainable resource utilization as a tool in conservation. The rest of this introductory chapter provides background information on sustainable resource utilization, Selous Game Reserve, lions, and ends with an outline of the thesis.

1.2 SUSTAINABLE RESOURCE UTILIZATION

1.2.1 Sustainable Resource Utilization and Hunting.

Sustainability is the capacity to endure. In ecology the word describes how biological systems remain diverse and productive over time. For humans, this translates into the potential for long-term maintenance of well-being, which is dependent on the natural world and responsible use of natural resources. As in any branch of natural resource utilization, the science of hunting revolves around sustainability (Milner-Gulland *et al.*, 2009); what is the effect of hunting on populations, and how can this be used to improve its management?

Much of the original work on the sustainability of hunting has been developed within the framework of fisheries science (Hilborn & Walters, 1991) and the underlying science is well understood. In fisheries the focus has been on modelling the impact of fishing on stock sizes and making recommendations to management to optimize yields over time (Clark, 1990). Conversely, managing hunting of wild populations on land is less hampered by a lack of data on population size and maximising commercial yields, and has had much more of a biological focus (Sinclair *et al.*, 2005). However, in both cases there is often an assumption that there is a management authority and that it can influence hunting rates and choose a sustainable level of hunting (Milner-Gulland *et al.*, 2009); nonetheless all management decisions will inevitably involve interplay between science, values and politics (Kellert & Clark, 1991).

1.2.2 What is Trophy Hunting?

Commercial forms of extractive use have developed as part of the choice in modern conservation paradigms (Hutton & Leader-Williams, 2003); tourist hunting is one such choice (see Table 1.1). However, the extractive use of wildlife remains contentious; with numerous examples of wildlife populations being detrimentally impacted when used commercially (Milner-Gulland & Mace, 1998); and, an on-going debate among conservationists over whether wildlife should or should not be killed to promote conservation (Hoyt, 1994). From a conservation standpoint, tourist hunting is useful only so long as it provides long-term protection of habitats and populations and, for this reason, hunting must be conducted on a sustainable basis (Caro *et al.*, 1998). In addition, it has been argued that extractive use (tourist hunting) must provide incentives for conservation, and importantly these incentives must be more equally shared among the people who bear the costs of living with wildlife (Hutton & Leader-Williams, 2003).

Table 1.1: What is tourist hunting? (adapted from Loveridge *et al.*, 2006)

Subsistence hunting	Undertaken to provide food for hunters and their dependents.
Market (or commercial) hunting	Undertaken to provide food to a consumer community for cash.
Recreational hunting	Undertaken primarily for leisure, as an activity that provides the participant with enjoyment.
Sport hunting	Prime motivation being the thrill of the chase.
Trophy hunting	Prime motivation being the acquiring of trophies.
Tourist hunting	Hunters that might be motivated by sport or trophies, but implies that the hunter is from outside the community where the hunting is taking place.

Hunting is often categorized into subsistence hunting, market hunting and recreational hunting, the differences being primarily motivational. The distinctions between the various types of hunting can be blurred, for example, in tourist hunting there is a commercial element to it, in that hunters are willing to pay large sums of money for it, and many components of the activity are saleable commodities. For simplicity, trophy hunting will be used to describe the hunting of lions in Selous Game Reserve in the rest of this thesis, although it could be rightly described as sport, tourist or recreational hunting.

There is a growing belief that the more cost-effective way to conserve biodiversity is for wealthy states to compensate local people for not damaging sensitive sites or species (James *et al.*, 1999). However, there is currently still no global commitment to financing the costs of conservation, nor the institutional capacity to distribute such payments (Loveridge *et al.*, 2006). Therefore, until there is, encouraging local sustainable use of natural resources through high return, arguably low impact activities, such as trophy hunting, may be preferable to more destructive alternatives, such as agriculture, subsistence hunting or logging, which tend to extirpate wildlife populations and destroy habitats.

1.2.3 Ethics of Trophy Hunting.

Trophy hunting is subject to considerable debate; with proponents citing the conservation and socioeconomic benefits of trophy hunting, in contrast opponents are concerned with issues of sustainability, and of ethics, animal welfare and animal rights

(Leader-Williams, 2009). The debates can be quite heated as antagonists lack any common ground and have differing moral starting positions. Indeed, some disputes on trophy hunting also touch on issues of race, class and gender – serving as a lightning rod for a host of different concerns (Dickson, 2009). Detailed discussion of the ethics of trophy hunting is beyond the scope of this section, but it is important to recognise that debate surrounds the subject and summarise some of the key points.

The animal welfare and rights arguments against trophy hunting hinges around the notion that if an animal is capable of feeling pain, it is wrong to cause them to suffer (Singer, 1995); and that certain animals have rights, and one of those rights is not to be killed (Regan, 1984). Regan (2001) describes those animals with a right to life as those that can perceive and remember, have desires and preferences, can act intentionally, and have a sense of the future. Less sound, but more widespread, is the argument that trophy hunting and other forms of recreational hunting are morally objectionable as the killing is done for fun (Dickson, 2009). Indeed, if those engaged in the hunt take pleasure specifically in the suffering caused to the animal, rather than in the activity as a whole, it would be a sick past-time and very difficult to justify.

Scruton (1998) argues that participants of fox-hunting take part to enjoy the activity as a whole, suggesting that fox-hunting displays the virtues of traditional social solidarity, respect for the hunted animal and concern for the countryside. These arguments could be applied to trophy hunting as a whole. The most common argument for recreational or trophy hunting focuses on the positive consequences for conservation, in particular that of income generated by trophy hunting being invested in conservation. Others still have argued that the 'good of the biotic community is the ultimate measure of moral value' (Callicott, 1980); thereby defending, and suggesting it may be a moral requirement in certain situations, to reduce the population size of an over-abundant species.

Trophy or big game hunting in Tanzania developed during the colonial period, and the rules and traditions of the activity were consciously elaborate to constitute this as a suitable recreation for the colonial elite (MacKenzie, 1988); most notably was the idea of the 'fair chase,' thereby making it ethically superior to the other forms of hunting, in particular subsistence or commercial hunting, practised by the territory's subjects. This past still has a bearing on attitudes and feeds resentment today. Trophy hunting is only affordable to the extremely wealthy. The larger successful hunting companies are all owned by whites or foreigners, and 99% of professional hunters are also either white or foreign. In fact, over 50% of the Selous is leased to one person from Europe. As a low ranking government official put it quite succinctly; "it is a pastime for wealthy foreigners, run by foreigners, for the benefit of other wealthy foreigners – what does it have to do with Tanzanians?" This, of course, does not reflect the official government view of trophy hunting as an important revenue earner and tool in wildlife conservation; where "hunting is an economically viable and sustainable use of wildlife that is consistent with the policy of high quality, yet low density tourism that can contribute significantly to the national economy" (MNRT, 2007).

1.2.4 Wildlife Management and Trophy Hunting in Tanzania.

Tanzania supports an abundance of wildlife, and has some 30% of its land area under wildlife protected status. The amount of land under different protected status is listed in Table 1.2. Management of the wildlife sector is split between management of National Parks by Tanzania National Parks (TANAPA), Forest Reserves by Forest and Beekeeping Division of the Ministry of Natural Resources and Tourism (MNRT), Ngorongoro by the Ngorongoro Conservation Area Authority (NCAA), and the rest of the areas by the Wildlife Division (WD) also of the MNRT. The key legislation allowing for wildlife management are the National Parks Ordinance of 1959, which covers wildlife within National Parks; Ngorongoro Conservation Area Ordinance of 1959; Forest Act of 2002 which covers Forest Reserves; and, the Wildlife Conservation Act of 1974. Overall legislation is now guided by the Wildlife Policy (MNRT, 2007) which confirms the government's overall right of ownership of wildlife: "In recognition of the importance of conservation of biological diversity to the livelihood of mankind, the state will retain the overall ownership of wildlife."

Table 1.2: Wildlife Protected Land (from Baldus, 2004)

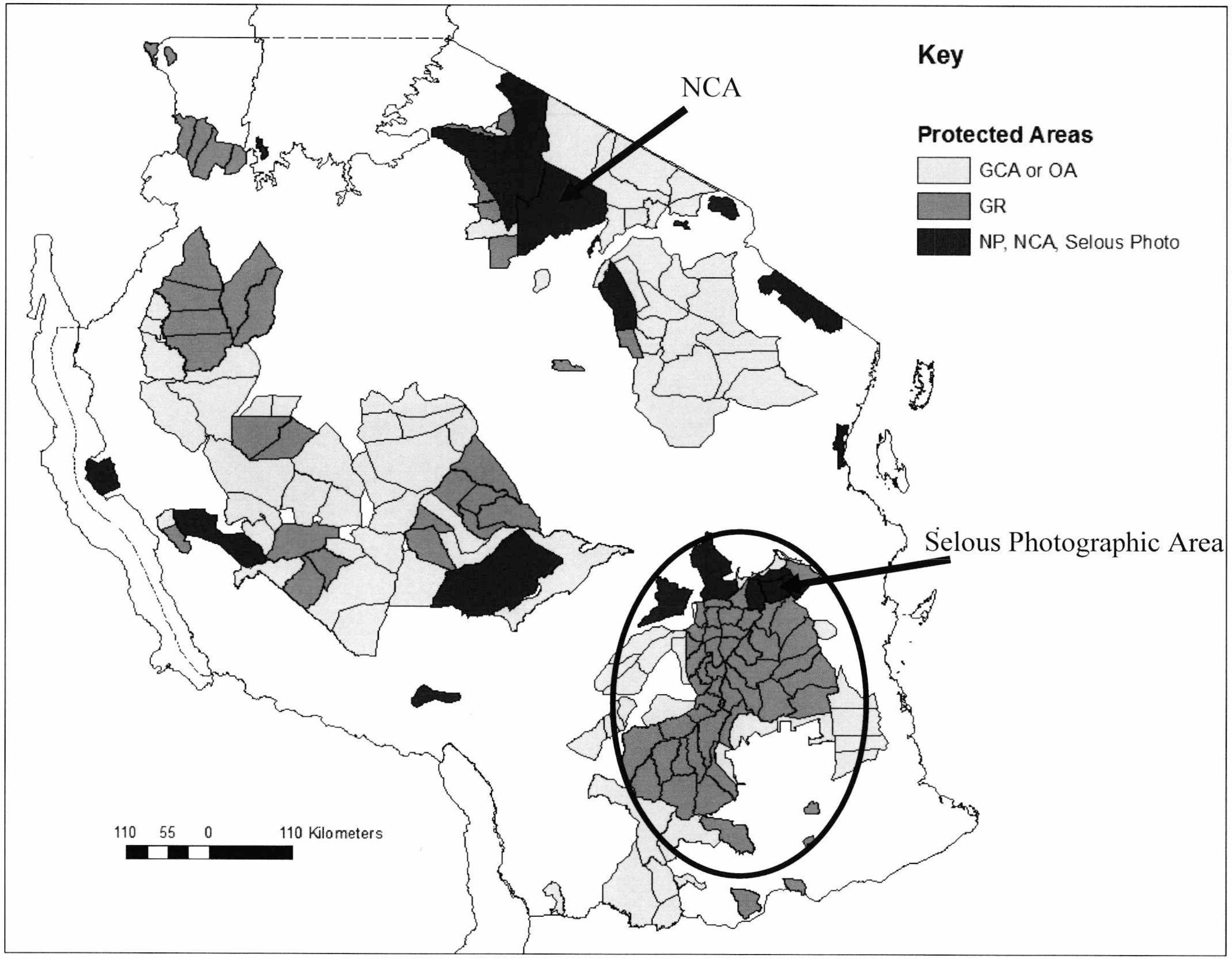
Category	Approximate Area (km^2)	Percentage of total area
National Parks	39,000	3%
Game Reserves	120,000	10%
Ngorongoro Conservation Area	8,300	1%
Forest Reserves	87,000	7%
Game Controlled Area	107,000	9%

In accordance with the Wildlife Conservation Act (1974), Tanzania's wildlife can be hunted through the issuance of a license by the Director of Wildlife. However, hunting cannot take place in any of the following: in any National Park (NP); in the Ngorongoro Conservation Area; or within one kilometre of the boundary of these areas. Hunting is permitted in Game Reserves (GR) and Game Control Areas (GCA). GRs are devoted to wildlife conservation and prohibit any permanent human settlements or grazing of livestock. In contrast, in GCAs, human settlement and the grazing of livestock are unrestricted, but hunting of wildlife is only permitted under licence. A total of 74 species of big game are listed under the Wildlife Conservation Act (1974) that may be shot on license by hunters who are not citizens or residents. Aside from a hunting ban between 1973 and 1978, Tanzania has been involved with tourist hunting since the 19^{th} century. In 2003, there were over 130 hunting concessions covering in excess of 200,000 km^2 that were leased to hunting outfitters/companies licensed to conduct tourist hunting, with hunting in the Selous Game Reserve representing 35% of tourist hunting in Tanzania (Baldus & Cauldwell, 2004).

Nicholson (2009) describes the inception, development and delineation of hunting blocks in and around Selous Game Reserve. Initially, in the 1920s and 1930s, it was largely a theoretical exercise with lines drawn on sparsely populated areas of the map with few or no defining features. In the 1950s and 1960s, the various Game Reserve boundaries were revised to conform to natural, visible features. But many boundary adjustments have been made since and it is only relatively recently that geographic coordinates have been recorded and GIS data developed for all hunting blocks (Baldus & Cauldwell, 2004).

Since the late-1990s many GCAs were designated as Wildlife Management Areas (WMA), and then as Open Areas (OA). The distinction between hunting blocks on GCAs, WMAs and OAs is not clear cut, (i.e. all allow for human settlement and wildlife to coexist, and hunting is only permitted under licence) but reflect when the blocks were set up. GCAs are the oldest, and most were set-up prior to the early 1990s. The WMAs reflect Tanzania's attempt to introduce community-based management of wildlife in the late 1990s, since then in 2004/5 new hunting blocks have been designated as OAs (for a detailed discussion see Nelson *et al.*, 2007, and Chapter 6). This has, however, meant that Tanzania has sets aside more land since 2003 in an extensive network of protected areas for wildlife conservation (see Figure 1.1): which are made up of NPs (38,365 km^2); GRs (102,049 km^2); and GCA, WMA or OA (202,959 km^2). There are now some ~160 hunting blocks or concessions covering over 305,000km^2 (Packer *et al.*, 2010). Hunting has become an even more important source of revenue for wildlife conservation in Tanzania.

Figure 1.1: Protected Areas of Tanzania.
Selous Game Reserve and surroundings ringed. GCA = Game Control Area; GR = Game Reserve; OA = Open Areas; NP = National Park; NCA = Ngorongoro Conservation Area.



1.2.5 Economics of Trophy Hunting in Tanzania.

Trophy hunting plays a growing and important role in the economy of Tanzania. In 1988, trophy hunting generated a direct revenue for the government of $1.25 million, this had increased to $5.34 million by 1992 (PAWM, 1996). As a whole for the Tanzanian economy (for the government and hunting outfitters combined), this went from $4.67 million in 1988 to $13.96 million in 1992 (PAWM, 1996). By 2001, the Wildlife Division accrued US$ 10 million from hunting annually, and the Tanzanian hunting industry as a whole generated approximately US$ 27 million (Baldus & Cauldwell, 2004). The latest figures available are for 2006, in which ~1500 tourist hunters earned the government around $20 million in fees, and 700,000 photographic tourists earned the government around $70 million (Tarimo, 2009). There are no recent estimates of what trophy hunting is worth to the wider economy. A review of the economic and conservation significance of trophy hunting across sub-Saharan Africa concludes that although South Africa generates the most revenue through trophy hunting, it occurs across a greater geographical area in Tanzania (Lindsey *et al.*, 2007a).

1.2.6 Lion Trophy Hunting in Africa, Tanzania and Selous.

In social species, especially carnivores, killing one individual can result in unanticipated disturbance or death of other individuals in the population (Tuyttens & Macdonald, 2000). Male lions enhance their reproductive success by killing rival male's offspring (infanticide). This brings newly acquired females into oestrus earlier than if they had successfully raised their offspring to maturity (Packer, 2000). Therefore, removal of territorial males by tourist hunting may result in the death of their offspring, killed by new males moving into the vacant territory; and if this occurs frequently, the impact on the population will be detrimental (Whitman *et al.*, 2004). However, it is important to note that lions have the capacity to recover rapidly from a drop in numbers. As seen in the recovery within six years of the Serengeti lion population after a third of the population had died in 1994 canine distemper outbreak (Packer *et al.*, 2005a); and seen in Ngorongoro Crater when the lion population crashed from 75-100 lions to 12 individuals in 1962, and recovered to over a 100 individuals by 1975 (Kissui & Packer, 2004).

In South Africa, it was noted that the sex-ratio of cubs was highly male biased after culling (Starfield *et al.*, 1981). A shift in the sex-ratio suggests that a population compensates for the removal of adult males by producing (or rearing) a higher percentage of male cubs. Creel & Creel (1997) noted a sex-ratio biased towards male cubs in the Selous Game Reserve, suggesting that this reflected a high turnover of pride males, perhaps due to hunting. Studies from Hwange National Park, Zimbabwe, found that tourist hunting in concessions around the Park removed 72% of the adult male lions from a study population covering 6000km^2 of the National park and reduced the proportion of males in the adult population from around 30% to 13%, or reduced the adult sex ratio from 1:3 to 1:6 in favour of adult females (Loveridge & Macdonald, 2002; Loveridge *et al.*, 2007). Reduction in male lion density resulted in males expanding their ranges to include more prides of females. Thereby, increasing the probability of males leaving the protection of the Park and themselves become vulnerable to trophy hunting. Similarly, Cooper (1991) in studies from Savuti, Botswana, where males were also rare as a result of trophy hunting, showed that females did not benefit from the protection of males and lost a higher proportion of their prey to spotted hyenas (*Crocuta crocuta*). Botswana put a moratorium on lion hunting in 2000 (lifted in 2005 and imposed again in 2009). While the above research in Zimbabwe led to reductions in the annual lion hunting quota.

Buffalo, lions and leopard are the main attraction for tourist hunting in Tanzania, with these three key species responsible for generating 24% of the total Wildlife Division (WD) income (Baldus, 2004). A lion is only available to hunt on a 21 day safari. The trophy/game fee of each lion shot was US$2000 in 2005. This has now increased to US$4900 in 2010. There has also been a doubling in all the other fees payable to the WD between 2004 and 2008 (see Table 1.3 which represent the minimum payable to the WD by a tourist).

Table 1.3: Fees Paid to the WD for a Lion by Tourist Hunter (2004-5 & 2008-9):

		2004-5	2008-9
Permit fee	Fee for a hunting safari of more than 7 days	$600	$1250
Conservation fee	Daily fee per tourist hunter	$100 x 21	$150 x 21
Observer fee	Daily fee per person accompanying a hunt	$50 x 21	$100 x 21
Trophy handling fee	Fee for a hunting safari of more than 7 days	$300	$500
Trophy/Game fee	For one lion	$2000	$4900
	Total	$6050	$11,900

Annually, approximately 250 lions are taken by tourist hunting in Tanzania, of which 75-90 are taken in Selous Game Reserve (Baldus, 2004). The trophy fees for lion are high, and therefore increasing the number of lion on quota greatly increases the quota value and is one of the easier means for the Wildlife Division to apply pressure on hunting companies to increase revenue as companies have to achieve 40% of their total quota. However, recent research using models parameterized with 40 years of Serengeti demographic data strongly suggest that tourist hunting of lions would be sustainable if only males above five years are hunted, as this would allow males the opportunity to remain resident in a pride long enough to rear a cohort of young (Whitman *et al.,* 2004). A relatively high off-take would be possible provided no young lions are removed and the quality of trophies would be much improved. These results imply that strict adherence to off-take of only old animals would make quotas for lion obsolete, and highlights the importance of being able to age lions in hunting situations. The Tanzania Hunters and Outfitters Association (TAHOA) accepts the notion of only hunting older male lions, and set a minimum age requirement of six years on lion trophies in 2004.

Nose colour serves as a good indication of a lion's age in the Serengeti ecosystem (Whitman *et al.*, 2004). The lion nose starts off pink, and becomes progressively freckled with age, with a six year old lion having over 60% black in their nose. Hunting companies have stated the difficulty of assessing nose colour in hunting situations, and questioned the validity of using Serengeti data across Tanzania. Other methods to age lions are suggested by Smuts *et al.* (1978), and include rate of closure of pulp chambers of canines and incremental cementum line build up on canine roots. A guide to aging lions for trophy hunters has since been produced (Whitman & Packer, 2007).

In the Selous, trophy quality, in particular skull length has been used as empirical evidence that lion hunting between 1995 and 2003 was sustainable (Cauldwell, 2004); that is, there was no significant decline in trophy quality over the period (see Figure 1.2). However, it should be noted that male lion skull lengths increase markedly from 8cm when they are born to 35cm when they are three years old, and then levels off (Smuts *et al.*, 1978; Smuts *et al.,* 1980). So all the Selous data is showing is that tourist hunting is predominantly taking males above three years of age, and therefore skull length is not a good indicator of sustainability.

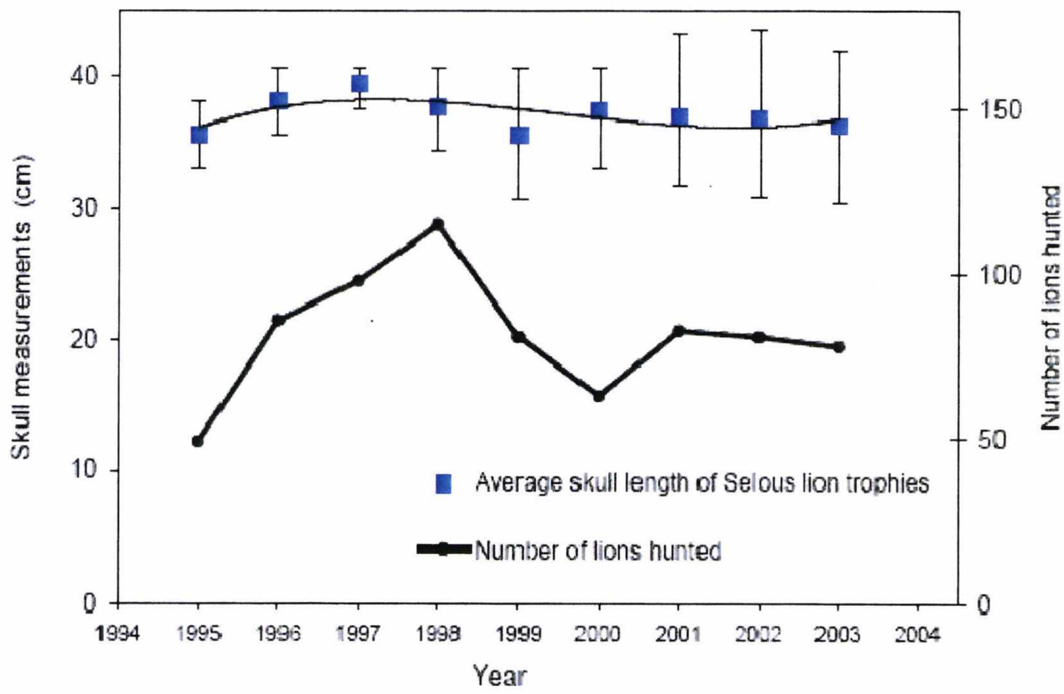


Figure 1.2: Skull length and number of lions hunted from 1995-2003 in Selous Game Reserve (from Cauldwell, 2004).

1.3 SELOUS GAME RESERVE

At 47,500km^2 the Selous Game Reserve is larger than Switzerland. Its origins date back to the German colonial period, when a small reserve was gazetted in 1896, in part of today's Game Reserve, making it Africa's oldest protected area (Baldus, 2009). By 1912, the number of reserves in the area had increased to four. After the First World War, mainland Tanzania (Tanganyika) became a League of Nation mandate administered by the British. In 1922, the British colonial government joined these reserves together and the resulting area was named the Selous Game Reserve in memory of Captain Frederick Courtney Selous, an early naturalist, hunter and author, who was shot in the area during the First World War (see Millais, 2006). The driving force behind setting up the Reserve was the protection of the wildlife in the area from hunters (both local and tourist), reducing levels of human-wildlife conflict (particularly with elephants) by moving people away from wildlife, and moving people to areas without trypanosomiasis-carrying tsetse flies (National Archives, Dar es Salaam).

During the 1920s, tourist hunters were given generous quotas (e.g. 268 animals of 39 species), which they could shoot in any area *except* the Game Reserves (Baldus & Cauldwell, 2004). During the 1930s and 1940s, tourist hunting was established as a viable industry, and continued to grow during the 1950s. After Tanzania's independence in 1961, the Selous Game Reserve was opened to tourist hunting for the first time in 1965. The Selous was divided into 47 hunting blocks in the 1960s, since then there has been numerous boundary adjustments, and it is only recently that geographic coordinates for the outer boundaries and hunting block boundaries have been traced on standard topographic maps (Cauldwell, 2004).

Baldus and Cauldwell (2004) provide a detailed account of the tourist hunting in Tanzania between 1970 and 2003, and a summary is included here. In a bid to nationalize the tourist hunting industry, a complete ban on tourist hunting was introduced in 1973. In 1978, under control of the newly formed Tanzania Wildlife Corporation (TAWICO), a government parastatal, tourist hunting was allowed again. However, due to the limited capacity of TAWICO, and the dire economic climate in Tanzania in the early 1980s it was difficult for outfitters to operate in the remote hunting blocks. In 1988, corruption and incompetent management by TAWICO was evident, and the management of hunting was removed from TAWICO and placed once again with the Wildlife Division. In 1988/89 the Tanzania Government launched a massive anti-poaching operation as a joint exercise between the Wildlife Division, Tanzania National Parks (TANAPA), the police and the army. As a result of this action, poaching in Tanzania, particularly in the Selous Game Reserve was reduced to comparatively low levels. This is highlighted in elephant population numbers during this period (see Seige & Baldus, 2000): in 1976, there were over 100,000 elephants in Selous; by 1989, there were less than 30,000 elephants due to poaching; the population has recovered to 60,000 in 2000. Since 1988 the tourist hunting industry has shown substantial growth. A number of changes were introduced, notably an increase in private sector hunting outfitters and some funds generated from the wildlife sector channelled to local communities. In addition, the fee structure was overhauled, with greater funds being retained by the Selous Game Reserve (since 1994, 50% of fees retained). However since 2004, the Selous Game Reserve has lost this retention scheme; all money goes to the central treasury and the Selous has to apply annually for a budget (Baldus, 2009).

The Selous is internationally designated as a World Heritage Site. As a large and inaccessible area infested with tsetse flies and underlain by poor soils, yet supporting one of Africa's largest big game populations, the Selous has developed a considerable reputation as a tourist hunting destination (Leader-Williams & Hutton, 2005). However, since 1988 two hunting blocks have been set aside for leases to non-consumptive tourism (i.e. photographic tourism), in 2003 two more hunting blocks were added to the photographic area. Currently, the photographic area comprises four blocks covering 2996 km^2 or six percent of Selous Game Reserve. There is some speculation of a further two blocks being added to the photographic area. It has been held as dogma that the Selous is too woody to offer decent game viewing for photographic tourists, too remote and inaccessible to allow for the volumes of tourists needed to make photographic tourism pay, and having a higher volume of visitors to the area would have a greater negative impact on the environment. The solution has therefore been low volume, high revenue generating tourist hunting (Baldus & Cauldwell, 2004; Leader-Williams & Hutton, 2005). Recent comparison between photographic and hunting tourism suggests that photographic tourism generates 1.8 times the income of hunting tourism per unit area, but also has 42 times the number of tourist per unit area (Cauldwell, 2004). As there has been some desire expressed to expand the photographic area, it is valid to ask whether the various hunting blocks are being utilized in the most effective manner for conservation and what other management options there are.

Between 1987 and 2003, GTZ (German Development Aid) helped rehabilitate Selous Game Reserve through the Selous Conservation Project (SCP). It is now seven years since that project ended, and there is a pervasive mood that things are getting worse in Selous again. For example, casual labourers (e.g. people building/maintaining the roads) had not been paid for five months in 2009; rangers had only received a fraction of their salaries for this period; and, rangers had not received their night allowances for patrols, so patrols were no longer going out (or there was no money to supply the patrols with food and equipment). The Selous has also been shown to be the source of recent shipments of ivory seized in the Far East (Wasser *et al.*, 2009).

1.4 LIONS

1.4.1 Nomenclature, Conservation Status and Distribution

Family:	Felidae
Genus:	*Panthera*
Species:	*leo*
Common Names:	African Lion (English); Lion d'Afrique (French); León (Spanish); Simba (Kiswahili)
Conservation Status:	Vulnerable; VU C2a(i) (Cat Specialist Group, 2001)

The lion formerly ranged throughout much of Africa to South-West Asia. Populations in Asian countries disappeared within the last 150 years; a small relict population (300 individuals) remains in the Gir Forest, India (Nowell and Jackson, 1996). The lion has a broad habitat tolerance, absent only from tropical rainforest and the interior of the Sahara desert (Nowell and Jackson, 1996). One hundred years ago, lions were found in all suitable habitats in Africa south of the Sahara (African Lion Working Group, 2004). Now, lions are increasingly rare outside of protected areas, with a declining population due to reductions in their prey base and habitat, and persecutions by humans (Nowell and Jackson, 1996). East and Southern Africa are home to the majority of the continent's lions, with Tanzania supporting between half and a quarter of the world's remaining free-ranging lions (Bauer & Merve, 2004; Chardonnet, 2002).

The African lion is listed under Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Lack of data on lion populations was used in the recent effort to upgrade the African lion from Appendix II to I at CITES; the following statement is of relevance to this study, "the fact that the largest population of free-ranging African lions in Tanzania, that in the Selous Game Reserve, has not been the subject of recent direct population survey and population estimate is of concern" (CITES CoP 13 Prop. 6, 2004).

1.4.2 Lion Ecology

The lion is the only social member of the big cats in which related females band together in prides (Schaller, 1972). Lion prides are territorial; they defend exclusive territories against other prides and often occupy the same range over several generations (Schaller, 1972). A pride comprises an average of 2-9 related females (range 1-18), their dependent cubs, sub-adults and a resident coalition of 1-6 males (Schaller, 1972; Bygott *et al.*, 1979; Packer *et al.*, 1990). Cubs of either sex are totally dependent on their mothers for food and protection till two years of age and females produce their first litter at around four years of age (Packer & Pusey, 1987); while males are considered sexually mature by three and half years old (although studies from woodland habitat have shown that lions may not become resident in prides, and therefore sexually active till they are five years old; Funston, 2003). Hence, in this study females and males are categorized as cubs till age two and as adults from then on.

The diet of the African lion constitutes a broad range of prey species that vary between habitats depending on the most common and locally available prey species. Medium (100-300kg) to large (average +400kg) prey is the most preferred range of species (Hayward & Kerley, 2005). Individual lions in a pride hunt cooperatively. Cooperative hunting was originally proposed as an evolutionary force for social living in lions (Schaller, 1972). However, work since then has shown that foraging requirements were not sufficient to explain the observed grouping pattern seen in lions (Packer *et al.*, 1990); instead, it is suggested that lions grouped to protect their young against infanticide. The need to maintain territory and females' reproductive success patterns all strongly influenced lion grouping behaviour. The most recent analysis of group living and territoriality in lions suggest that habitat heterogeneity could have enhanced the evolution of territoriality in lions because, as resource despots, larger prides out-compete smaller ones over high quality resource patches (Mosser & Packer, 2009).

Cohorts of young males leave their natal pride to enter a nomadic phase of life as a coalition before sexual maturity. A new male coalition gain residence in a new pride by evicting the existing coalition (Bygott *et al.*, 1979), and evicts or kills any cub less than two years old (Packer & Pusey, 1983). While male coalitions may comprise siblings or closely related males, unrelated male companions may also form coalitions, and larger male coalitions have a higher per-capita reproductive success (Bygott *et al.*, 1979; Packer & Pusey, 1982). Males engage in territorial patrols and defence of their cubs. Therefore, male presence is crucial for cub survival and successful recruitment of offspring. A coalition on average retains residence in a pride for at least two years, enough time to successfully raise their young; frequent replacement of resident males severely depress cub recruitment, and could have cascading effects leading to the overall population decline (Whitman *et al.*, 2004; Loveridge *et al.*, 2007).

1.4.3 Lions in Selous Game Reserve and Tanzania

The management of hunting in Selous Game Reserve (SGR) is driven by a quota system, whereby each hunting block is allocated a quota of animals to hunt. Project Managers, as Chief Park Wardens are known, suggest quotas for Game Reserves, with aerial survey data (where available) and recommendations from hunting outfitters and professional hunters taken into account (Severre, 1996). There is concern by many people that the lion quota are too high; in SGR on average only 52% of the lion quotas have been used since 1996 (Baldus & Cauldwell, 2004). Baldus (2004) also states in his study of lion conservation in Tanzania, "more practical lion research and monitoring is needed in Tanzania including lion numbers, illegal killings, human-lion conflict and hunting of lions."

Lion population numbers are difficult to estimate accurately. The current estimate for free-ranging lions in the world is only 16,500 to 50,000, with estimates for Tanzania ranging from 7000 to 18000 (Bauer & Merve, 2004; Chardonnet, 2002). The SGR and surrounding buffer zone (Selous ecosystem) may potentially hold the largest single population of lions in Africa. However, these numbers are largely based on 'best guesses.' A more accurate estimate of lion numbers is clearly needed, but even more urgent is a detailed study on the impact of human activity on lion population trends. Trophy hunting occurs in SGR, and the reserve is surrounded by a rapidly growing human population.

Lions have been intensively studied in the Serengeti National Park, Tanzania for 40 years (Schaller, 1972; Packer & Pusey, 1983; Packer *et al.* 1988; Scheel & Packer, 1995, Packer *et al.*, 2005). Increasingly the focus of lion research has been on conservation outside National Parks (Woodroffe & Frank, 2005; Hemson, 2004), as large carnivores inspire local opposition to conservation due to detrimental impacts on livestock and human safety (Wilson, 2004). Recent studies in Tanzania highlight that over 563 human fatalities occurred between 1989 and 2004 from lion attacks; of which two thirds occurred in districts neighbouring SGR (Packer *et al.*, 2005b). There has only been limited study of the Selous lions: a 1974 study of lion populations in eastern SGR (Rodgers, 1974), a study in 1992 of lion density in relation to hunting quotas and off-take (Creel & Creel, 1997), and a 1999 study in northern Selous (Spong, 2002; Spong *et al.*, 2002) serve as useful baseline studies.

Rodgers (1974) combined three methods to estimate lion density in eastern SGR (Kingupira) to get a density of 0.08 adult lions km^{-2}, while the two other studies in northern Selous (Matambwe) had densities of 0.13 adults km^{-2} (Creel & Creel, 1997) and 0.16 individuals km^{-2} (Spong, 2002). Higher prey densities in the northern Selous are thought to account for the difference in densities (Creel & Creel, 1997). The 1992 study of lion densities in relation to off-take concluded that tourist hunting took between 2.7% and 4.3% of the adult male population annually, and therefore was suggested as being sustainable; however, this only accounted for 28% of the annual hunting quota, and full utilization of the hunting quota would not be sustainable (Creel & Creel, 1997). Furthermore, studies of space use by lions in northern Selous (Matambwe) have shown that lions show a significant preference for riverine and short-grass habitat, and a significant avoidance of acacia woodland, which reflects prey abundance in each of the habitats (Spong, 2002). These prides had a mean core area (50% of the time) of $11.7 \pm 8.6km^2$ (mean $\pm$ SD), and a mean home-range (90% of the time) of $52.4 \pm 26.3km^2$ (Spong, 2002). However, recent work in Serengeti suggests that on the broad scale lions shifted their ranges according to seasonal movement of prey, but on a finer scale lions fed in areas with high prey 'catchability' (i.e. ambush zones; e.g. erosion embankments, points of access to water, and woodland edges) rather than high prey density (Hopcraft *et al.*, 2005). Current work in Serengeti using 40 years of data shows that although the pride occupying an area may change, areas that support large numbers of lions will continue to support large numbers of lions; furthermore, there are hotspot areas for lion reproductive success (i.e. areas with significantly more cubs being born and surviving to adulthood; Mosser, 2008).

1.5 OUTLINE OF THESIS

The thesis explores resource use as tool in conservation, by looking at whether the trophy hunting of lions is sustainable in Selous Game Reserve (SGR), Tanzania. Firstly, Chapter 2 explores the possibility of monitoring the lion population in SGR by comparing the results of several census techniques. The results of lion population monitoring are used to explain lion distribution and ecology under 'natural' conditions where there is no trophy hunting in Chapter 3. Data collected during this project have been used to show that trophy hunting in Tanzania has had a negative impact on lion populations (Packer *et al.*, 2009; Packer *et al.*, 2010; see Appendix 14). Therefore in Chapter 4 different methods are used to suggest a more sustainable lion trophy hunting quota for SGR, and the main drivers for unsustainable lion trophy hunting in SGR are explored in Chapter 5. In Chapter 6, the thesis explores the attitudes and perceptions in Tanzania (through newspapers) and in SGR (through questionnaires and interviews) to lion trophy hunting, as it is these attitudes that will largely determine the long-term success of the conservation of the African lion. The sustainability of lion trophy hunting in SGR and the potential conservation outcomes of these practices are the focus of my study. The thesis is presented as a collection of separate manuscripts and these are then discussed in general in Chapter 7.

Furthermore, other publications related to this thesis are listed below, and can be found in Appendix 14. My contribution to the publications is described on the next page.

Appendix 14.a: Packer, C., Kosmala, M., Cooley, H.S., Brink, H., Pintea, L., Garshelis, D., Purchase, G., Strauss, M., Swanson, A., Balme, G., Hunter, L. & Nowell, K. (2009) Sport Hunting, Predator Control and Conservation of Large Carnivores. PLoS One **4 (6)**: e5941.

Appendix 14.b: Packer, C., Brink, H., Kissui, B.M., Maliti, H., Kushnir, H., & Caro, T. (2010) Effects of trophy hunting on lion and leopard populations in Tanzania. *Conservation Biology*. In Press. (Should be published in 2011 in Volume 25, Pages 142-153).

My contribution to the published papers in Appendix 14 is as follows. I had a limited contribution to Appendix 14.a (Packer *et al.*, 2009) by providing data on lion and leopard (*Panthera pardus*) trophy hunting from Tanzania, although the analysis of these data helped highlight some of the population trends in these two species. The paper (Packer *et al.*, 2009) looks at sport or trophy hunting of lion and leopard across Africa, and American black bears (*Ursus americanus*) and cougars (*Felis concolor*) in North America; and concludes that infanticidal species and areas with the highest sport hunting intensity were more susceptible to population declines. On the other hand, my contribution to Appendix 14.b (Packer *et al.*, 2010) was pivotal. I collated the bulk of the hunting data, provided and collected some of the lion population data, helped analyse the data, and helped write the paper. Appendix 14.b looks at the effects of trophy hunting on lion and leopard populations in Tanzania. These effects are negative for lions and less clear cut for leopard.

2 Monitoring Lions in Selous Game Reserve.

2.1 ABSTRACT

The Selous Game Reserve in Tanzania probably contains Africa's largest population of lions (*Panthera leo*), making it a popular destination for trophy hunters and tourists. However, there is a lack of recent data on this lion population, and therefore a range of information was collected between 2006 and 2009 to address this problem. In August 2009, there were 112 lions in an 800 km^2 study area in the photographic tourism part of Selous, giving a density of 0.14 lions km^{-2}, or 1 lion 7 km^{-2}. The overall density has remained relatively constant over the three years of this study and as far back as 1997. However, the adult sex ratio has decreased from 1 male : 1.3 female in 1997 to 1 male : 3 females in 2009. Audio call-ups of buffalo distress calls were used to carry out rapid census of lions in three hunting sectors of Selous in the west, south and east of the reserve, and one photographic area in the north. Estimated lion adult densities varied from 0.02 to 0.10 km^{-2}; the northern and western areas had a higher density of adults. The lion population in Selous is estimated at 4300, with a range 1700-6900. This chapter stresses the need to calibrate the results of call-ups and the importance of long term projects for measuring population trends.

2.2 INTRODUCTION

Adaptive management and conservation of natural ecosystems requires effective monitoring of biodiversity, including regular surveys of wildlife abundance. Such surveys should both use cost-effective and efficient techniques, while also generating reliable estimates that can detect temporal and spatial trends in wildlife abundance (Danielsen *et al.*, 2009). These surveys are particularly important when managing an exploited species, as this increases the risk of reducing population size to levels at which exploitation is economically, or in extreme cases, biologically unviable (Adams, 2004; Milner-Gulland *et al.*, 2009). This situation is exemplified by the African lion (*Panthera leo*), as the trophy hunting of this species provides an important source of revenue for several conservation agencies seeking to fund their activities through sustainable utilisation. However, this species is particularly vulnerable to over-harvesting because infanticide by extra-group males is common (Whitman *et al.*, 2004; Caro *et al.*, 2009; Packer *et al.* 2009).

Perhaps the most important example of this need comes from the Selous Game Reserve (SGR), Tanzania, which contains the country's largest population of lions and where trophy hunting is the main source of conservation income (Baldus, 2004). Despite its importance for lion conservation, the population has not been surveyed recently and this has created a number of issues that relate to the hunting of this species. For example, lack of data on lion populations informed recent efforts to up-list the African lion from Appendix II to Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). More specifically, it was argued "that the largest population of free-ranging African lions in Tanzania, that in the Selous Game Reserve, has not been the subject of recent direct population survey and population estimate is of concern" (CITES CoP 13 Prop. 6, 2004). This is because there have only been three studies of lions in the Selous, one in the 1970s and two in the 1990s (Rodgers, 1974; Creel & Creel, 1997; Spong, 2002). Here, a study is described that addresses this problem by providing new data on the population status of lions in SGR.

Various methods have been used to count lions, such as roar counts (Rodgers, 1974), mark-resighting (Smuts, 1976), spoor transects (Stander, 1998), call-ups (Ogutu & Dublin, 1998), and individual identification (Pennycuick & Rudnai, 1970). Individual identification has been the preferred method for long-term research projects on lions (Schaller, 1972; Packer *et al.*, 2005a). However, individual identification may not be feasible when population estimates are required over large areas and/or are needed quickly, for example to set hunting quotas or understand human-wildlife conflict patterns (Lichtenfeld, 2005). To this end, a number of indirect measures have been developed to estimate relative lion abundances and the current preferred indirect method in East Africa is call-ups or playback response surveys (Ogutu *et al.*, 2005; Whitman *et al.*, 2006; Kiffner *et al.*, 2009). Therefore, in this study individual identification is used in a section of SGR and this is combined with call-up surveys to determine: (i) lion population trends based on individual identification from a study population that has been intensively studied from 1997-1999 and again from 2006-2009; (ii) if a rapid assessment of the Selous' hunted lion population using call-ups provides meaningful results.

2.3 METHODS

2.3.1 Study area:

Covering 47,500km^2, SGR is one of Africa's largest protected area, and supports one of six remaining populations of >1000 African lions and may support the largest lion population in Africa (Bauer & Merve, 2004). The SGR is internationally designated as a World Heritage Site. As a large and inaccessible area infested with tsetse flies and underlain by poor soils, yet supporting one of Africa's largest big game populations, the SGR has developed a considerable reputation as a premium trophy hunting destination (Leader-Williams & Hutton, 2005; Baldus, 2009). For this reason, the SGR was originally sub-divided into 47 hunting blocks in the 1960s (Leader-Williams *et al.*, 1996). More recently four northern blocks, covering six percent of SGR, have been set aside for photographic tourism, while the remainder continue as trophy hunting concessions (Figure 2.1). Within 800 km^2 of this photographic area of the Matambwe sector in northern SGR, latitude 7°35'S, longitude 38°10'E, an intensive study of lions took place from 2006-2009 (marked Study Area in Figure 2.1). A similar survey had taken place in the same area from 1997 to 1999 (Creel & Creel, 1997; Spong *et al.*, 2002). The intensive study area comprises a mosaic of wooded savanna, miombo and *Combretum* thickets. Four other areas of roughly 100km^2 were less intensively surveyed using call-ups in 2009 (marked Call-up Areas in Figure 2.1).

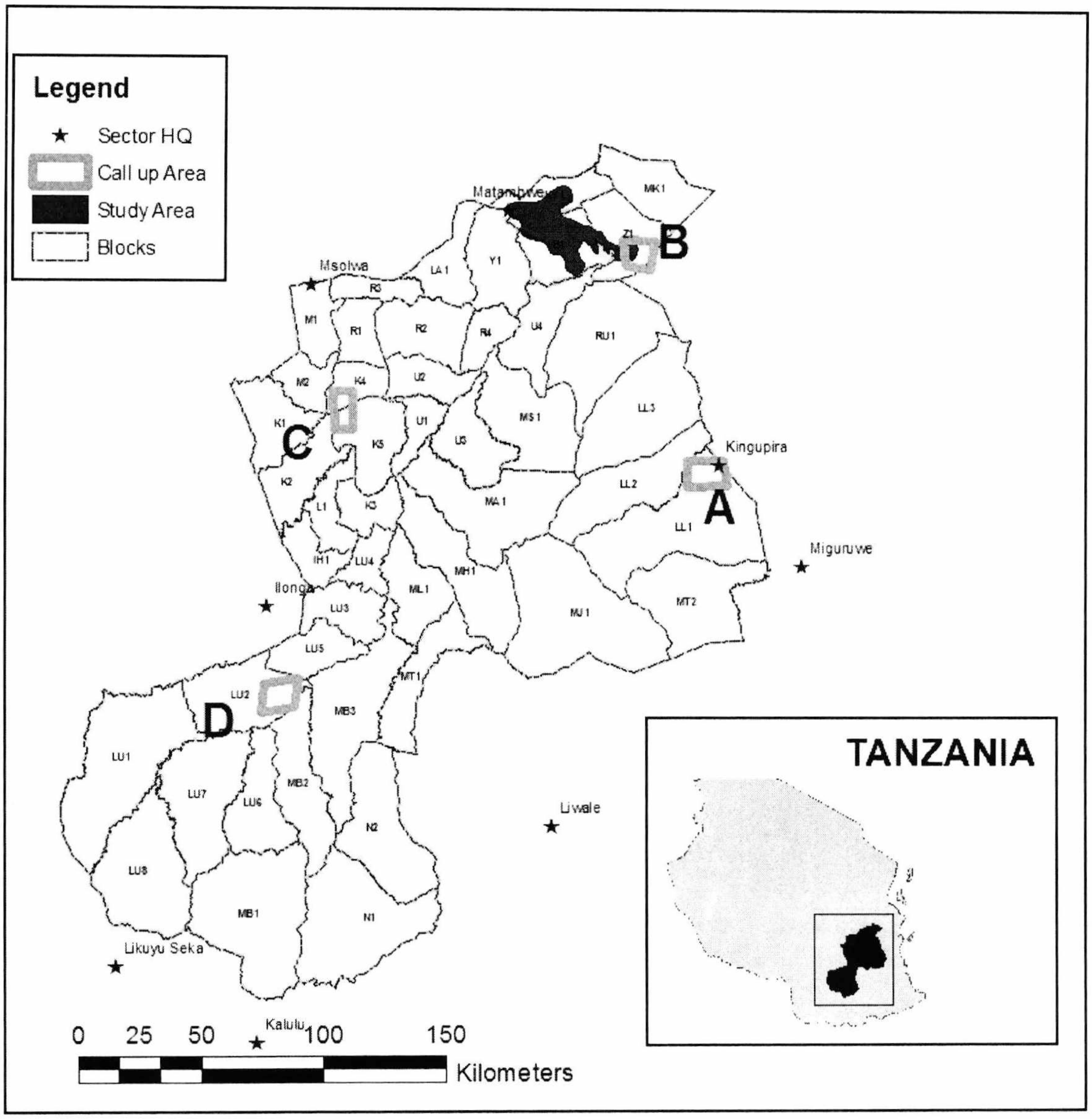


Figure 2.1: The Selous Game Reserve, showing the main study area and location of call-ups areas. Blocks were predominantly delineated in the 1960s and reflect topographic features, especially rivers. Accurate GIS layers of SGR blocks are only recently available (Cauldwell, 2004).

2.3.2 Monitoring lions:

An intensive search of lions was conducted on a daily basis (except during the rainy season of April to May) in the Matambwe study area. Individual photographic identification cards were produced for each lion using: whisker spot patterns; nose scars and colour; tongue rips; tooth breakage and wear; body size, and any other relevant identification features (Pennycuick & Rudnai, 1970; see Appendix 1). Lions are the most social species among large felids and cubs of either sex are totally dependent on their mothers for food and protection until 2-years of age (Schaller, 1972), so animals that were two years old or less were categorized as cubs and any older animal as an adult.

Two adult females were each fitted with a VHF radio collar from 25th October 2007 to 28th August 2009. One adult female was fitted with a GPS collar from 27th February 2008 to 31st August 2008. The GPS collar was set to take three fixes a day, at 1900, 0100 and 0800 hrs and allowed ranging data to be collected during the wet season for the first time in SGR. A wildlife veterinarian from Tanzania Wildlife Research Institute or Sokoine University of Agriculture was present at every darting to fit or remove collars. Anaesthesia was induced for around an hour by 300mg of Ketamine and 8mg of Medetomidine. Anaesthesia was reversed using 40mg of Atipamezole, and all lions were up and moving within one hour of the reversal of the immobilization drugs. A previous study in SGR suggested that 60 independent GPS fixes, with at least 24 hours between fixes, were necessary (Spong, 2002) to accurately predict territory size. However, recent work in Serengeti suggests that 15 data points collected over a two year period would give a fairly accurate representation by providing a 93% overlap with the pride's actual territory (Mosser & Packer, 2009); both types of data are presented in the results section (Table 2.4).

2.3.3 Call-up surveys

Buffalo (*Syncerus caffer*) distress calls are known to attract lions (Kiffner *et al.* 2007), so a recording of these calls lasting four minutes and 20 seconds was played from 0600 to 0800 hrs, and from 1700 to 2000 hrs at call-up sites during 2009. An MP3 Player was used to play recordings at full volume four times in every 40 minutes with a six minute period of silence between playbacks. The MP3 player was attached to a 12-volt FA2 (HiVi Inc) amplifier and two 8-ohm speakers (SRX-220, Ahuja) facing opposite directions from each other and mounted on the roof of the vehicle, about 2m above the ground. Call-up sites (within the four Call-up Areas; A-D; Figure 2.1) were spaced at least 3km from each other. At each call-up site the following information was recorded: the start and end time; GPS co-ordinates; habitat; and the presence of any incoming lions; spotted hyena (*Crocuta crocuta*) and wild dog (*Lycaon pictus*). As soon as the lions approached the car, the playback was stopped to prevent future habituation.

Call-ups have limitations as a sampling technique (Whitman, 2006), including: (i) male lions are more likely to respond than females, (ii) distance to the speaker is important, and (iii) response is sensitive to the location of the speaker within the pride's territory. Therefore, it is important to calibrate the technique prior to sampling. Consequently, 14 calibration experiments were carried out to 13 males, 24 females, and 25 cubs, where the distance from the lion to the speaker was varied randomly from 500 m to 1500 m. The distance was restricted to 1500 m because responses were not forthcoming from further than this in three trial runs at distances of 3000 m, 2500 m, and 2000 m. Only at 1500 m did the lion look in the direction of the speaker and begin moving towards it. Therefore the effective response radius was 1.5 km for lions in SGR, equivalent to sampling an area of 7.065 km^2 (πr^2) at each call-up site.

2.3.4 Data analysis:

ArcGIS 9.3 (ESRI) GIS software was used to map lion distributions and Hawth's tools ArcGIS extension to calculate territory area based on the adaptive kernel method (Beyer, 2004). The 50% contour was defined as the core of the territory and the 90% contour as the outer boundary of the territory (as used by Spong, 2002). SPSS for Windows (version 17.0, SPSS Inc.) statistical package was used to carry out tests to determine whether pride territory size based on >60 fixes had changed since a previous study from 1996-1999 (Spong, 2002) and investigate lion ranging behaviour. The actual density of lions was estimated from the call-up surveys by first calculating the total area sampled in each of the four call-up areas by multiplying the number of sites by the estimated sampling area of 7.065 km^2.

2.4 RESULTS

2.4.1 Lion density from individual recognition:

Over 40,000 km were driven in search of lions, and over 2079 sightings were made of 162 different individual lions, from 2006 to 2009. A total of 112 individually recognised lions were present in the 800 km^2 intensive study site in the Matambwe sector in August 2009, equivalent to a density of 0.14 lions km^{-2}, or one lion 7 km^{-2}. Although deaths, births and movements of lions into and out of the intensive study site occurred during the study, their total density remained relatively constant at 0.14 lions km^{-2}. Estimates of lion abundance in the same area from 1997 to 1999 (Table 2.1) recorded similar densities to those found from 2006-2009 (Figure 2.2). An even earlier study by Creel & Creel (1997) undertaken from 1991-1993 focused on a much smaller area of only 90 km^2 near Lake Manze (see Figure 2.3), and recorded very high lion densities. Some 25 lions, including 13 cubs were seen in 90 km^2, giving a density of 0.13 adults km^{-2} or a total density of 0.28 km^{-2}. This small area still supports similarly high lion densities, where the territories of three prides currently overlap, although this 90 km^2 only forms a part of each of their territories. Despite the overall lion population in the Matambwe Sector of Selous remaining relatively constant from 1997 to 2009, it is of concern that two of the three lions collared by the project were lost and their collars subsequently found in villages bordering the Sector (see Appendix 2 for detailed discussion).

Table 2.1: Number of individuals in different prides in Matambwe sector of SGR from1997-2009. Data from 1997-1999 derived from Creel & Spong (1997) and Spong *et al.* (2002). Where appropriate, pride names have been changed to facilitate comparison. For example, in 1997 to 1999, the Manze pride was called the Shortcut pride.

	1997		**1998**		**2006**		**2007**		**2008**		**2009**	
Pride	**Adult**	**Cub**	**Adult**	**Cub**	**Adult**	**Cub**	**Adult**	**Cub**	**Adult**	**Cub**	**Adult**	**Cub**
Beho Beho	6	7	8	9	4	10	3	9	3	7	10	-
Beho Beho II							4	2	3	7	3	6
Beho - Subs							3	-	3	-	-	-
Beho - (SPONG)	4	0	5	2								
Central	8	0	4	0	11	4	15	?	10	?	10	?
Central Ndgo			2	0	3	0	3	0	3	?	3	?
Fuga					3	0	3	0	3	?	3	?
Manze	10	3	9	4	6*	6	6*	5	10*	1	6*	4
Marsh					7	2	5	1	5	0	5	0
Matambwe					4	1	4	5	3	5	3	7
Mbuyuni	3	1	3	1	-	-	-	-	-	-	-	-
Mwana Mungu					2	?	2	5	2	2	4	-
Mzizimia	7	2	5	4	6	0	4	0	5	5	5	7
Siwandu			3	2	3	5	1	0	1	0	-	-
Nzerakera	9	12	9	11	5	0	5	3	5	8	4	8
Old Airstrip			4	0	3	3	6	0	4	5	4	5
Sand Rivers	6	7	7	5	4	?	4	1	5	?	5	?
Tagalala/Kiba			5	0	2	0	1	0	1	0	1	0
NOMADS	4		?		3	-	2	-	5	-	9	-
TOTAL	57	32	64	38	66	31	71	31	71	40	75	37
	Total	**89**	**Total**	**102**	**Total**	**97**	**Total**	**102**	**Total**	**111**	**Total**	**112**
AREA (km2)	650		650		800		800		800		800	

***In 2006-2009 data, males of Beho Beho and Mwana Mungu are included in Manze pride.**

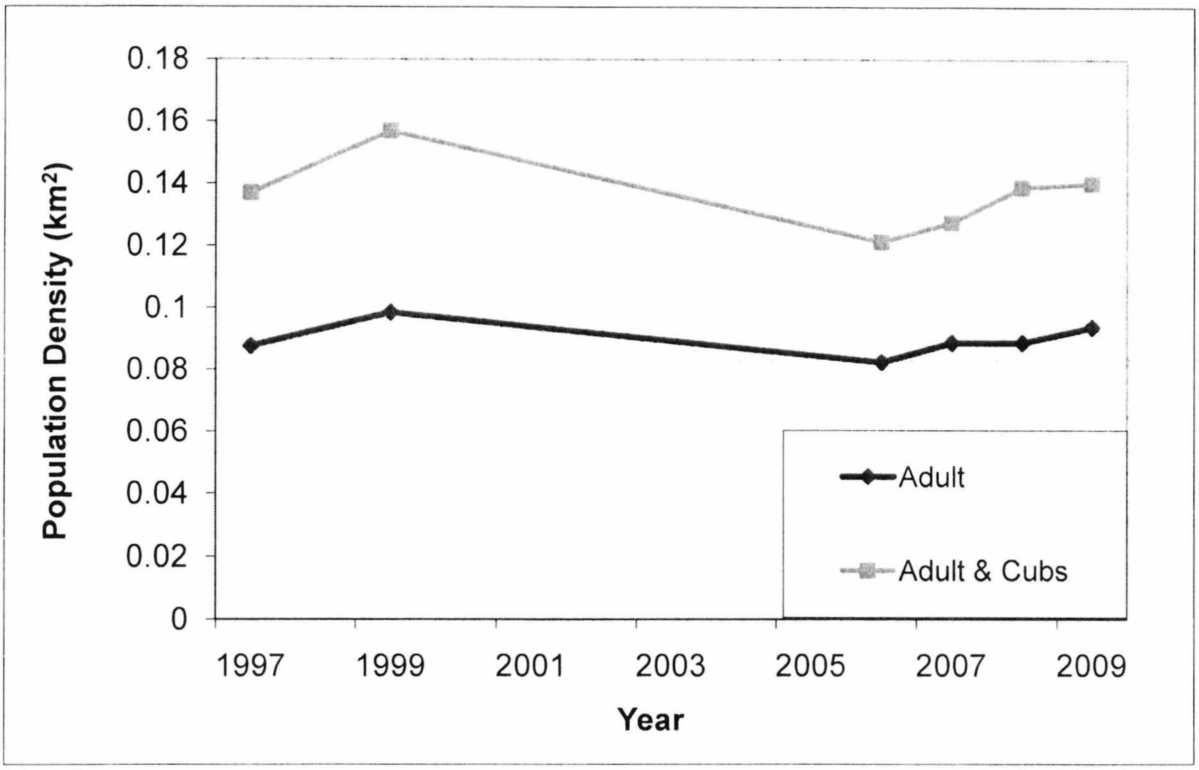


Figure 2.2: Lion population density in Matambwe sector of SGR over time.

The mean number of adults per pride was 4.9 ± 0.9 (mean ± standard deviation throughout the chapter), and the mean number of cubs was 3.4 ± 0.9. The breakdown of the population in terms of adult males, adult females, and cubs shows that males made up on average 31 percent of the adult population (Table 2.2). The largest male coalition recorded in the study area was five individuals, out of 40 coalitions of males the mean size was 1.7 ± 1.5. Female pride size was 3.3 ± 1.36 individuals (n = 39) with a range from 1-7 adult females. Table 2.2 also highlights the decrease in males to females in the adult sex ratio between 1997 and 2009. Of 61 cubs born between 2007 and 2009, 25 were male, 31 were female and five were unknown.

Table 2.2: Composition of the lion population in the Matambwe sector of SGR by age and sex class from 1997 to 2009. Adults are over two year old, cubs up to two years.

Year	% Adult female	% Adult Male	% Cub	Adult Sex Ratio M:F
1997	36.0	28.1	36.0	1 : 1.28
1999	45.3	18.9	35.8	1 : 2.40
2007	48.0	21.6	30.4	1 : 2.23
2009	50.4	16.8	32.7	1 : 3.00
Average	44.9 ± 6.3	21.3 ± 4.9	33.7 ± 2.7	-

2.4.2 Ranging patterns and pride territories:

The GPS collar showed that lion movement on a daily basis was highly variable, ranging from 6677 m in six hours to under 20 m in 24 hours. The majority of movement was at night and the least amount of movement was during the day, with a mean movement of 3600 m (± 2271) in 24 hours, and that there was significantly more movement on moonless nights than on full moon nights (see Table 2.3 and Appendix 3; ANOVA, $F(1,183)=21.26$, $P<.01$).

Table 2.3: Lion movement patterns (GPS collar; Old Airstrip pride).

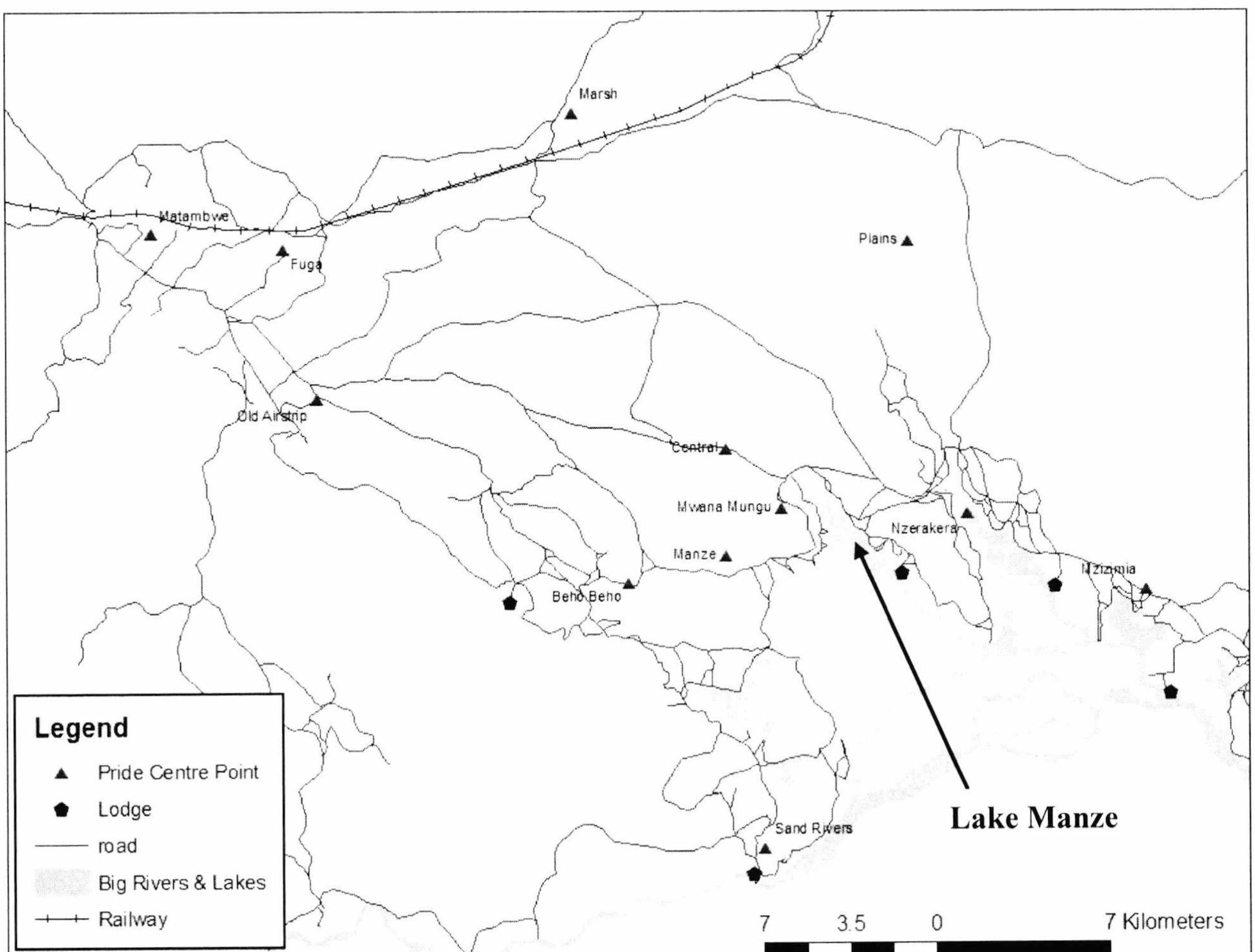
Period	Mean Distance Moved (m)	± SD
19:00 – 01:00	1675	1456
01:00 – 08:00	1085	1133
08:00 – 19:00	977	738
Moon Phase	**Mean Distance Moved (m)**	**± SD**
No Moon	4402	2444
Quarter Moon	4351	2603
Half Moon	3842	2239
Three Quarter	2944	1793
Full Moon	2231	1328

The GPS fixes of the lion sightings allowed their territories to be plotted, the centre point of the pride territories is shown in Figure 2.3, where it can be seen most of the territories are centred near the lakes and river. As seen from Table 2.4, the mean core area comprising the inner 50% of all fixes, or the area most intensively used by a pride, was relatively small at 12.7 ± 6.4 km^2. The entire territory of a pride, comprising the 90% boundary, covered a mean area of 48.5 ± 11.2 km^2. This core area covered an average of 25 ± 0.06% of the entire territory. Prides living near the lakes showed a higher degree of territory overlap than prides living away from the lakes. In one case, the high level of overlap between prides arose because prides had recently split from each other and were closely related. Comparison of pride territories between this study and the earlier study with >60 fixes (1997-1999; Spong, 2002) shows no significant difference (two sampled $t(8)=-.317$, $p=.76$). My study had a 50% core area of 12.7 km^2 for prides with >60 fixes, compared to 11.7 km^2 in the previous Spong study. The 90% core areas were also similar; 48.4 km^2 now and 52.4 km^2 then. However, the exclusiveness of core pride areas was higher in my study (81%), than in the previous study (52 %); however, the results were not significant (two sample $t(8)=1.749$, $p=.12$). All of the focal prides with >60 GPS fixes in the previous study were from the high-density area around the lakes.

Table 2.4: Descriptive statistics of lion territories in Matambwe sector of SGR from 2006-2009. Prides with more than 60 fixes in **bold** type. Mean values calculated from figures in **bold**.

Pride	Fixes	Area (km^2)		Proportion Exclusive		Core area accounts
		50%	90%	50%	90%	for % of total
Matambwe	**99**	**9.4**	**41.3**	**1.00**	**1.00**	**0.23**
Marsh	**70**	**17.6**	**62.4**	**1.00**	**1.00**	**0.28**
Nzerakera	**61**	**7.0**	**46.2**	**0.81**	**0.71**	**0.15**
Manze	**65**	**8.2**	**35.1**	**0.48**	**0.36**	**0.23**
Old Airstrip	**559**	**21.4**	**56.8**	**1.00**	**0.97**	**0.38**
Beho Beho	19	9.6	46.2	0.04	0.21	0.21
Mzizimia	18	7.7	37.9	1.00	0.88	0.20
Mwana Mungu	15	6.7	23.0	0.32	0.27	0.29
Mean		**12.7**	**48.5**			**0.25**

Figure 2.3: Centre point of pride territories of lions in Matambwe sector of SGR from 2006-2009.



2.4.3 Call-up surveys:

During the 14 trials to calibrate call-ups, 77% of males (n = 10), 63% of females (n = 15), and 8% of cubs (n = 2) responded within the 40-minute period. Consequently, call-ups only appear an effective tool to sample adults, which showed an average response probability of 0.73 ± 0.58. Lions either responded as a group, or not at all, leading to large standard deviations. The results of call-ups played in the four call-up areas in Selous show that more lions responded in the north and west and more wild dogs were seen in areas with less lions (Table 2.5).

Table 2.5: Results of the call-ups carried out in different parts of SGR

Sector*	Block	Dates	No. of Call-ups	Lion seen	Hyena seen	Wild Dog seen	Habitat+
Kingupira **(A)**	LL1	26/01-02/02/09	21	2	26	21	Cl wd*
Matambwe **(B)**	Z1	12/02-17/02/09	20	9	18	4	Cl wd*
Msolwa **(C)**	K4/5	21/06-25/06/09	12	6	17	0	Wd Gr R
Ilonga **(D)**	LU2	28/06-02/07/09	12	3	7	8	Op Wd R

Sector* on Figure 2.1: Kingupira is the eastern most call-up area; **Matambwe** is the northern most; **Ilonga** the southernmost; and **Msolwa** is the remaining site in a central/western location. **Habitat+ are following habitat categories: CL wd*** is closed woodland with grassland clearings, **Wd Gr R** is wooded grassland by river, and **Op Wd R** is open woodland by river.

Comparisons between different areas of SGR require the density of lions in each area. There was an effective response radius of 1.5 km for lions, equivalent to sampling an area of 7.065 km^2 (πr^2) at each call-up site. A total of 21 call-up sites were used at Kingupira, equivalent to a total sample area of 148 km^2 (21 x 7.065). If two lions were seen, this would be equivalent to a density of 0.01 lions per km^2 (2 /148). Given that not all lions responded to the call up, the density of the area was divided by the response probability (e.g. 0.01 / 0.73 for Kingupira) giving the estimated density of an area. On this basis, the Msolwa call-up site recorded the highest density of lions, while the Kingupira area recorded the lowest density (Table 2.6).

Table 2.6: Lion densities (km^{-2}) in different areas of SGR based on call-up data.

Sector	Number of Call-ups	Area Sampled	Number of Lions Seen	Adult Density in Sample Area (lion km^{-2})	Density with response probability
Kingupira	21	148.365	2	0.01	0.02
Msolwa	12	84.78	6	0.07	0.10
Ilonga	12	84.78	3	0.04	0.05
Matambwe	20	141.3	9	0.06	0.09

This call-up study sampled 459 km^2 or <1% of the total area of SGR (47500 km^2). The density of lions in the area sampled was 0.05 adult lions km^{-2}, or 0.06 adult lions km^{-2} if the response probability is taken into account. This would be equivalent to a total population of ~2850 adult lions in Selous. If the proportion of cubs (Table 2.2) is taken into account, this suggests a total population of ~4300 individual lions. Using the standard deviation of the estimated lion density (i.e. density with response probability) gave a total population that ranged between 1700 and 6900 individuals.

2.5 DISCUSSION

The importance of the Selous Game Reserve's lion population is recognised by conservationists and trophy hunters alike, and so there is an obvious need for up-to-date lion population data for this protected area. This study has successfully helped fill this gap by updating information of their demography and population status. This was achieved by using both individual recognition surveys in an intensive study area and call-up surveys over a more extensive area, providing updated data on densities of lions and allowing an estimate of lion numbers for SGR. This final population estimate will help guide decisions about trophy hunting within the reserve but also has wider implications when it comes to deliberations about the CITES listings of lions. Therefore, in this section these results will be discussed in more detail and the relevant context provided that should be considered when using this population data to make decisions.

The total number of lions in SGR is ~4300 individuals based on estimates of lion density derived from call up surveys, with a range of 1700 to 6900 individuals. Although these density figures are important, they should be viewed with caution because they can be influenced by a number of factors. For example, previous studies have shown that the response probability of lions clearly falls with distance and stress the importance of calibrating results (Whitman *et al.*, 2006). This is why extensive calibrating data was collected here, but it is worth noting that if the response radius was increased to 2.5 km (in

Ogutu & Dublin, 1998) or 3.5 km (in Kiffner *et al.*, 2009), then the SGR lion density values would drop from 0.06 adult lions km^{-2} to 0.02 or 0.01 adult lions km^{-2}. However, a comparison between density estimates from the individual recognition survey and the call-up survey of the Matambwe sector (Area B, Figure 2.1) show similar results, which provides support for the value of the SGR population estimate.

This means that call-up surveys offer the potential to compare relative abundances over a large area over a relatively short time, as is illustrated by this survey which consisted of one month of fieldwork. The results suggest that the Moslwa and Matambwe sectors have higher lion densities than the Kingupira and Ilonga sectors (Figure 2.1; Table 2.6). The lion densities recorded in the call-ups follow the pattern of prey distribution, as the north and northwest have higher densities of prey species (TWCM, 1998; Caro *et al.*, 2009), and explains why the northern and western hunting blocks are considerably smaller than the southern and eastern blocks (B. Nicholson in Matthiessen, 1981). It is also of interest that more wild dogs were sighted in the areas where few lions were seen, supporting suggestions of competition between the two species (Creel & Creel, 1996; Creel *et al.*, 2001).

It is useful from a management prospective to compare the Selous study population with other well studied lion populations across Africa (See Appendix 4 for comparison). The Selous lion densities are lower than the 0.2-0.3 lions km^{-2} recorded in the Kenya's Masai Mara (Ogutu & Dublin, 1998) or the 0.3 lions km^{-2} recorded in Tanzania's Ngorongoro Crater (Kissui *et al.*, 2010), but similar to the 0.1 adults km^{-2} recorded in South Africa's Kruger National Park (Funston *et al.*, 2003). However, it should be noted that lion densities vary temporally and spatially. For example, the 250 km^2 Ngorongoro Crater has varied from 0.04 to 0.40 lions km^{-2} from 1963 to 2003 (Kissui & Packer, 2004). Similarly, studies from an area of 2500 km^2 in the Serengeti have shown that lion density that has varied over time (Packer *et al.*, 2005a) and is also habitat dependent, with adult densities varying from 0.03–0.06 km^{-2} in the short grass plains to 0.2-0.3 km^{-2} in woodland edge habitats by rivers (Mosser *et al.*, 2009). Compared to the Serengeti study population, the Selous has smaller prides of 3.3 $\pm$ 1.36 adult females (4.64 $\pm$ 0.18 adult females in Serengeti; Mosser & Packer, 2009) in smaller territories of 48.5 $\pm$ 11.2 km^2 (56 km^2 with a range of 15-219 km^2 in Serengeti; Mosser & Packer, 2009). The largest territory in the Selous study area was 62 km^2. This study recorded wet season lion ranging data for the first time for Selous. Other studies have in general used 2500 – 3000 m as an average daily distance moved for lions (Creel *et al.*, 2001; Mosser & Packer, 2009), however, this study had an average daily movement of 3600 m ± 2271 m. As a nocturnal animal, it is not surprising the collared lion moved most between 19:00 – 01:00 and on nights with no moon.

The intensively studied area in Matambwe supported a total lion density of 0.14 km^{-2} in 2009, and these densities appear to have changed little since 1997, which initially suggests that lions are successfully conserved in the region. However, there is existing evidence that human-lion conflict is a problem in this area (see Packer *et al.*, 2005b) and anecdotal evidence that this continues. Moreover, during the radio-tracking study, two of the three collared lions were lost and their collars subsequently found in villages bordering the sector (See Appendix 2). It could not be established how the collars got to their final locations, but human-lion conflict was recorded in this area during the study period; a person was killed by a lion on 6th June 2008 and a sub-adult male lion was killed on 3rd September 2008. A further cause of concern comes from comparisons of the sex ratio of the Matambwe lion population, which has changed from roughly 1:1.3 in 1997 to 1 male to 3 females in 2009. Such changes in the sex ratio are often indicative of unsustainable male trophy hunting (Rodgers, 1974; Loveridge *et al.*, 2007), which tie in with recent studies of lion trophy hunting off-take from SGR showing that hunting decreased by 50% between 1998 and 2008 across Tanzania, with the steepest declines occurring where hunting is most intensive (Packer *et al.*, 2009; Packer *et al.*, 2010). Thus, managers should consider this bigger picture when assessing lion population density results.

The need for rapid assessments of lion populations is often driven by political pressure, such as a response to increased human wildlife conflict or drops in the number of trophy lions being shot. However, there is no quick way to collect such data, and long-term studies will always be needed when studying these cryptic carnivores. This requires high levels and consistent funding and support, which precludes their widespread application. These results do show the value of call-up surveys, which are relatively inexpensive, especially when trying to census shy animals such as those hunted individuals from SGR. However, the results also show that they should be used in conjunction with a detailed individual identification project. For example, it is only through these more intensive studies that it is known that the Matambwe population has remained relatively stable for more than a decade, but there has been a marked change in the adult sex-ratio. This is vital because the main driver for studying lion populations in Selous comes from concerns over unsustainable trophy hunting (Rodgers, 1974; Creel & Creel, 1997) and therefore continued support for lion monitoring in SGR is hoped for in the future.

3 Lion Distribution in northern Selous Game Reserve

3.1 ABSTRACT

Studies have used habitat or soil type (or amount of rainfall) as surrogate proxies for resource availability or measured prey availability directly in the field. Both methods are used here to determine what factors influence the distribution of lions (*Panthera leo*) in one of Africa's largest ecosystem, that of Selous Game Reserve (SGR). These methods can then be combined with anthropogenic variables to allow for an accurate measure of factors influencing lion distribution. The study focused on an 800km^2 study site in northern Selous. Lion distribution in northern Selous was best explained by lean or dry season prey biomass (r^2=0.33; y=0.0005x + 0.1336). The mean dry season prey biomass for the study site was 1436 kg km^{-1}, suggesting a lion carrying capacity for the study site of 164 lions (0.21 lions km^{-2}). However, by another method a carrying capacity of only 104 lions (0.13 lions km^{-2}) was suggested for the same area based on the average number of preferred prey species recorded on prey transects. In August 2009, at least 112 lions (0.14 lions km^{-2}) were observed in this 800km^2 area of northern SGR. Based on prey transects and field observations of lions on kills, lions in northern Selous showed a preference for buffalo, zebra, giraffe and wildebeest and an avoidance of warthog and impala. However, no relationship was noted between lion distribution and buffalo sightings. Environmental and anthropogenic factors that best explained lion distribution in northern SGR were distance to the reserve boundary and villages and soil type of an area.

3.2 INTRODUCTION

Twenty five percent of extant carnivore species are threatened with extinction due to reductions in their distribution and abundance (Ginsberg, 2001). Their conservation depends on the accurate assessment and understanding of their distribution and abundance to allow for informed management decisions (Fuller & Sievert, 2001). The African lion is one such species, and the Selous Game Reserve (SGR) in Tanzania is one of the lions' important strongholds (Baldus, 2004; see also previous chapter). While the majority of SGR is open to lion trophy hunting, a small area ($2995km^2$) in the northern part of the reserve has been set aside for photographic tourism. The factors driving lion distribution in this photographic area of northern SGR are investigated here.

Lion abundance is correlated with prey abundance, permanent water, and adequate denning sites (Hanby *et al.,* 1995); yet due to variations in prey abundance, suitable habitats and levels of human persecution, trying to extrapolate lion density estimates between different areas is potentially meaningless (Schaller, 1972). However, advances in Geographical Information Systems (GIS) allows for more accurate mapping of variables affecting lion densities and should therefore allow for a more accurate prediction of lion densities in areas not previously sampled for lions. This is especially important in large areas, where management budgets are restricted, as is the case in SGR. Mathematical models can be used to quantify the relationship between species' abundance and environmental characteristics, and this can then be used to predict species abundances at unsurveyed locations; such a technique was used to try and map lion abundances across Africa, with varying degrees of success (Loveridge & Canney, 2009).

Many have argued that carnivore densities can vary over several orders of magnitude within species, but, in natural ecosystems, generally reflect the abundance of their prey (Bertram, 1973; Van Orsdol *et al.,* 1985; Ogutu & Dublin, 2002; Hayward *et al.*, 2007a); and defined relationships between predator and prey density that apply across the order Carnivora, where 10,000kg of prey supports about 90kg of a given carnivore species (Carbone and Gittleman, 2002). Nonetheless, others have argued that while prey biomass may be important for lion survival, its effects appear secondary to environmental factors in determining lion demography (Celesia *et al.*, 2009); in particular noting that lion density was positively related to rainfall, soil nutrients and annual mean temperature. Loveridge &

Canney (2009) took it a step further, and combined anthropogenic and environmental factors to determine what may contribute to lion occurrence and population persistence.

Studies have used habitat, soil type or amount of rainfall as surrogate proxies for resource availability or measured prey availability directly in the field. This study uses both methods to determine what factors best explain the distribution of lions in one of Africa's largest ecosystem, that of SGR, for the first time. These methods were combined with anthropogenic variables to build a model to determine lion distribution in northern SGR.

3.3 METHODS

3.3.1 Study area:

The Selous Game Reserve (SGR) is divided into 47 blocks comprising 47,500 km^2. Four blocks (or six percent) of SGR are set aside for photographic tourism; the rest of SGR allow resource utilization in the form of trophy hunting (Caro *et al.*, 2009). An 800 km^2 area in the photographic blocks of northern SGR, southern Tanzania (latitude 7°35'S, longitude 38°10'E), was the focus of this study from 2006 to 2009. This is the same area intensively studied from 1995 to 1999 (Creel & Creel, 1997; Spong *et al.*, 2002). The study site comprises a mosaic of wooded savanna, miombo and *Combretum* thickets. The dry season runs from the end of June until October, and the main rainy season is normally from March to May; there are short rains towards the end of the year which are highly variable followed by a drier spell in January and February (Kibonde, 2009). For this study, data from June to October represent dry season data and data from November to March are considered wet season data. Heavy rains prevented access to the study site by car during April and May, and so no field data is available for this period.

3.3.2 Data collection:

Data were collected between June 2006 and August 2009. The location of all lion and buffalo sightings were recorded in Universal Transverse Mercator (UTM) coordinates (using Arc1960 datum) using a Garmin IV GPS (Garmin Corp, Ulathe, KA). Individual photographic identification cards were made for each lion in the study area using whisker spot patterns, nose scars and colour, tongue rips, tooth breakage and wear, body size and other identification features (as described in Pennycuick & Rudnai, 1970). At each lion sighting, the following were recorded: (i) spatial data, (ii) temporal data, (iii) individuals present, (iv) any prey species being eaten. Similarly, all buffalo (*Syncerus caffer*) sightings were recorded. No attempt was made to identify buffalo individuals, but the number of individuals was counted (below 50 buffalo) or estimated (if above 50 buffalo), the GPS location of the point of sighting and the distance and angle from the initial sighting were also recorded.

Three prey transects were driven each month from September 2008 to August 2009 (except April and May). The three transects were of different lengths (see Figure 3.1); Transect 1 was 25km, Transect 2 was 55km, and Transect 3 was 40km. A total of 120km of transect was driven each month, and 1200km in total over the ten month period. Transects were driven in the morning between 06:30 and midday. Fixed width transects were used to calculate prey densities, namely all possible prey sightings within 100m of transect were recorded. Body mass (kg) of prey species was derived from Hayward & Kerley (2005): 0.75 mean female body mass, to account for sub-adults and young, as recorded in Stuart & Stuart (2000) and Estes (1991). Prey transects were divided up into five kilometre segments to facilitate analysis and the kilometric abundance for each prey species was calculated (Maillard *et al.*, 2001), which represent an encounter rate per kilometre of road driven and was taken as a proxy for the rate at which lions encountered individuals of each prey species.

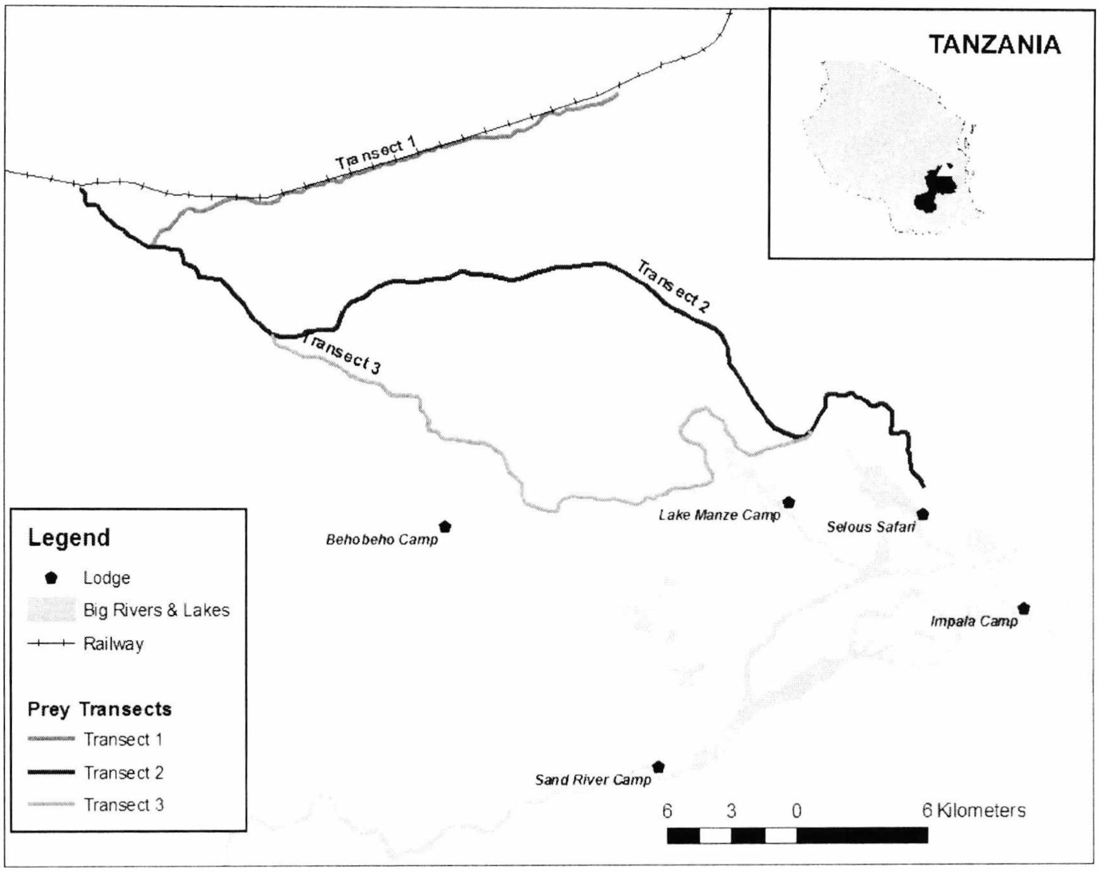
3.3.3 Prey preference:

Each of the many indices for selectivity includes some bias, for example a bias against animals of different size, and errors increase with small samples (Strauss, 1979). The analysis was restricted to totals of at least 100 animals sighted within 100m of prey transect. Jacob's index has been used in other studies of lion prey preference (Hayward & Kerley, 2005; Hayward *et al.*, 2007a) so was used here to facilitate comparisons between different sites across Africa. The index has the following form:

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

Where r is the proportion of the total kills at a site made by a species and p is the proportional availability of the prey species (Jacobs, 1974).

Figure 3.1: Location of prey transects in photographic area of SGR.



SGR marked in black on map of Tanzania; small white triangle in northern SGR marks study site.

3.3.4 GIS layers:

General lion population demographics for northern SGR are summarised in Chapter 2, which was used to create a lion density grid map at the 1km^2 level. Data of five variables that were thought to be important in determining the spatial distribution of lions were obtained from a variety of sources. Digital boundary and river vector files and habitat and soil polygons were obtained from the Selous Conservation Project (SCP) funded by the Organization for German Technical Cooperation (GTZ). The habitat and soil layers were based on FAO land cover maps (FAO, 1997). Data on village location was obtained for the government of Tanzania's Mapping and Survey Office. The accuracy of these layers was tested or ground truth in the field. All spatial data was imported in ArcGIS version 9.3 (ESRI Inc., Redlands, CA) for manipulation prior to analysis.

3.3.5 Data analysis:

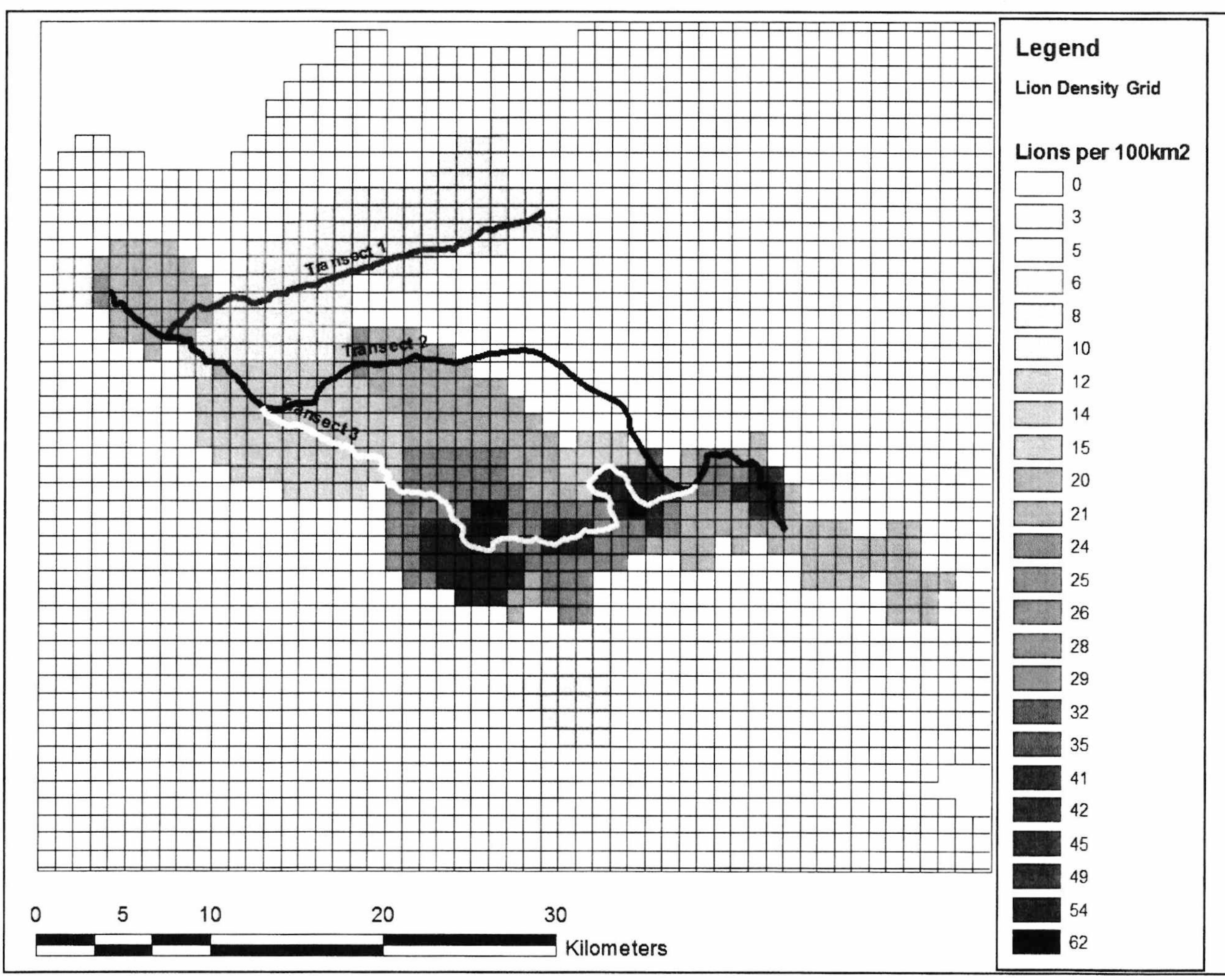
As the photographic area was intensively studied, it was felt the presence or absence of lions in a given grid square would be useful in explaining lion distribution in northern SGR. To facilitate data analysis, all variables were imported into ArcGIS and superimposed onto a 1 km^2 grid covering the 800 km^2 of the intensively studied photographic area of SGR. The predominant soil type and habitat type for each grid square was recorded. Habitat and soil type were reduced to three categories. The habitat types were grassland, open woodland and closed woodland/natural forest (see Appendix 5). The three soil types in northern SGR were fluvisols, cambisols and ferrasols, which are FAO soil units (see FAO, 1974). The boundary, village and river vector files were used to create raster distance maps at a 100m resolution in ArcGIS, and the mean distance from each of these features was calculated for each 1 km^2 grid square.

Analysis at the 1 km^2 grid cell level was carried out using SPSS version 17.0 (SPSS Inc., Chicago, IL). Principal component analysis (PCA) was carried out in ArcGIS on the distance data (i.e. to river, boundary and village); namely PCA 1, PCA 2, and PCA 3. When analysing spatial data there is a risk of non-independence caused by spatial autocorrelation (Koenig, 1999) because neighbouring cells share similar values in the dependent variable leading to correlation coefficients appearing more significant than they are. Spatial autocorrelation was tested using the Crimestats version 3.2a software package (N. Levine & Associates, Annandale, VA) where the dependent variables were tested using Moran's *I* statistic/Geary's *C* statistic. Grid cell data were randomly removed until the data were not likely to be significantly spatially autocorrelated. Spatial autocorrelation was a real concern as the data came from one part of the SGR. The remaining data were tested again using stepwise logistic regression to see if any relationships were still significant. Finally, Akaike Information Criterion (AIC) was used to corroborate the results of the stepwise logistic regression and suggest the best model to explain lion presence/absence in northern SGR. Model performance on the testing data was evaluated by calculating the area under the curve of receiver operating characteristics (ROC) plots (Pearce & Ferrier, 2000). ROC values range from 0.5 to 1.0. Values above 0.7 indicate a good model fit, while those above 0.9 indicate a highly accurate model (Swets, 1988).

3.4 RESULTS

In August 2009, there were 112 lions in the 800km^2 study site (see also Chapter 2). A lion density grid map was produced using lion demographic information from northern SGR, in particular using the pride territory size and pride composition, and shows highest lion densities on Transect 3 (see Figure 3.2). Lion densities are based only on areas within the study area that are part of a lion pride territories with the pride being seen on at least 15 independent data points in the three year period. So areas where few or no lions are seen are not included. Total density for this area, which comprises only 542km^2 of the total 800km^2, is high at 0.18 lions km^{-2}.

Figure 3.2: Lion density map for northern SGR; based on pride composition data and territory data.



*Grid map depicted as lions per 100km^2, to work out densities for each grid square divide number by a hundred (e.g. highest density is 0.62km^{-2} and lowest is 0.03km^{-2}). 0 = not sampled / prides in these areas seen less than 15 times over the three year period.

3.4.1 Prey transects

The following possible prey species were seen on the monthly transects: buffalo, bushbuck, eland (*Tragelaphus oryx*), elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), hippopotamus (*Hippopotamus amphibious*), impala (*Aepyceros melampus*), kongoni (*Alcelaphus lichtensteinii*), greater kudu (*Tragelaphus strepsiceros*), warthog (*Phacochoerus africanus*), waterbuck (*Kobus ellipsiprymnus*), blue wildebeest (*Connochaetes taurinus*), and zebra (*Equus burchellii*). Table 3.1 shows the distribution of the prey species and their biomass between the different transects. Table 3.1 highlights, for example, that giraffe make up 22.6 % of the available prey biomass of northern SGR, yet only accounted for less than five percent of the animals seen on the prey transect.

Table 3.1: Prey densities (km^{-2}) and prey biomass ($kg\ km^{-2}$).

Transect	Season	Kongoni	Buffalo	Elephant	Zebra	Giraffe	Wildebeest	Warthog	Impala	Eland	W'buc
T1	**Wet**	0.01	0.00	0.05	0.91	0.13	3.26	0.94	7.68	0.14	0.00
T2	**Wet**	0.00	0.50	0.06	0.64	0.98	2.68	0.20	4.46	0.00	0.00
T3	**Wet**	0.00	1.58	0.11	1.96	1.18	4.46	0.15	16.00	0.21	0.01
T1	**Dry**	0.00	0.00	0.11	0.84	0.33	1.89	0.41	3.93	0.00	0.00
T2	**Dry**	0.00	0.00	0.02	1.21	0.49	1.01	0.24	4.47	0.06	0.00
T3	**Dry**	0.04	0.13	0.11	2.28	0.65	9.24	0.42	13.65	0.00	0.04
Total seen		8	480	84	1577	826	4400	400	9835	75	10
Body weight (kg)		95	432	1600	175	550	135	45	30	345	188
Number per km		0.01	0.40	0.07	1.31	0.69	3.67	0.33	8.20	0.06	0.01
Kg per km		0.63	172.80	112.00	229.98	378.58	495.00	15.00	245.88	21.56	1.57
% Weight		0.04	**10.32**	6.69	**13.74**	**22.62**	**29.57**	0.90	**14.69**	1.29	0.09
% Numbers		0.05	2.71	0.47	8.91	4.67	**24.86**	2.26	**55.56**	0.42	0.06

*Numbers in bold, make up over ten percent of totals. Bushbuck, kudu and hippopotamus not included in the above table as less than four individuals of each seen in total on transects. W'buck⁺ is waterbuck.

3.4.2 Prey biomass

The mean total prey biomass for the study site in northern SGR was 1674 kg km^{-2}. As can be seen from Table 3.2, Transect 1 had the lowest prey biomass and Transect 3 the highest. It is also clear that prey biomass was higher in this area of northern SGR during the wet season months (i.e. the dry season is the lean period). However, it was also quite clear that there was enormous variation in prey biomass within each transect, which is highlighted in Table 3.3. Table 3.3 also shows that one 5km section of transect had nine times the prey biomass during the wet season than the dry season (i.e. section 25-30km on Transect 2), while other sections (e.g. section 5-10km on Transect 1) had more prey during the dry season.

Table 3.2: Mean biomass (kg km^{-2}) for each transect in dry season and wet season.

Transect	Wet Season	Dry Season	Overall Average
1	1148 ± 719	819 ± 719	984 ± 692
2	1465 ± 1433	825 ± 565	1145 ± 796
3	3023 ± 1981	2662 ± 1783	2842 ± 1263
Total	1918 ± 1682	1436 ± 1407	1674 ± 1248

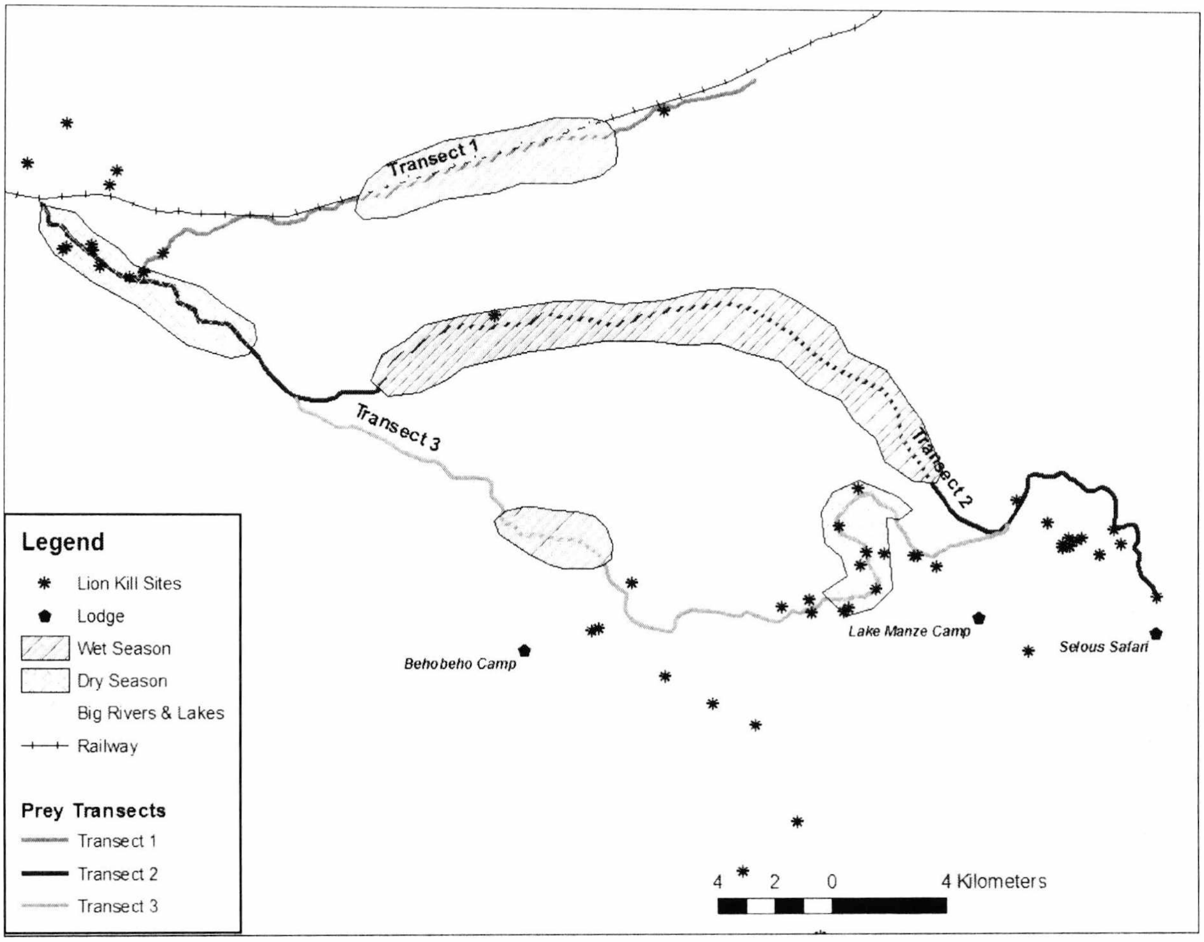
± Standard deviation

Table 3.3: Mean biomass (kg km^{-2}) per five kilometre section of transect.

Transect sections	Mean biomass (kg) wet	Mean biomass (kg) dry	Mean biomass(kg)	Ratio* Wet : Dry	Predominant habitat type
T1_5km	1277	1178	1228	1.1	Open woodland
T1_10km	597	772	685	1.3	Open woodland
T1_15km	534	151	343	**3.5**	Open woodland
T1_20km	1018	153	585	**6.7**	Open woodland
T1_25km	2313	1843	2078	1.3	Open woodland
T2_5km	78	490	284	***6.3***	Open woodland
T2_10km	187	1463	825	***7.8***	Open woodland
T2_15km	2381	1644	2013	1.4	Open woodland
T2_20km	472	122	297	**3.9**	Grassland
T2_25km	714	84	399	**8.5**	Open woodland
T2_30km	1840	197	1018	**9.3**	Open woodland
T2_35km	1652	733	1193	**2.3**	Wooded grassland
T2_40km	5154	708	2931	**7.3**	Grassland
T2_45km	876	954	915	1.1	Grassland
T2_50km	1858	1345	1602	1.4	Open woodland
T2_55km	900	1339	1120	1.5	Open woodland
T3_5km	1443	1295	1369	1.1	Open woodland
T3_10km	973	530	751	1.8	Open woodland
T3_15km	7409	1104	4257	**6.7**	Closed woodland
T3_20km	3543	2058	2801	1.7	Closed woodland
T3_25km	3331	3058	3194	1.1	Grassland
T3_30km	2944	5781	4363	***2.0***	Grassland
T3_35km	2138	4396	3267	***2.1***	Grassland
T3_40km	2401	3074	2737	1.3	Grassland

*Ratio divides the highest value of either dry season or wet season data to give a ratio of the difference. Bold in italics (grey) are sections with much higher prey biomasses in dry period; just bold is the same, but for the wet season.

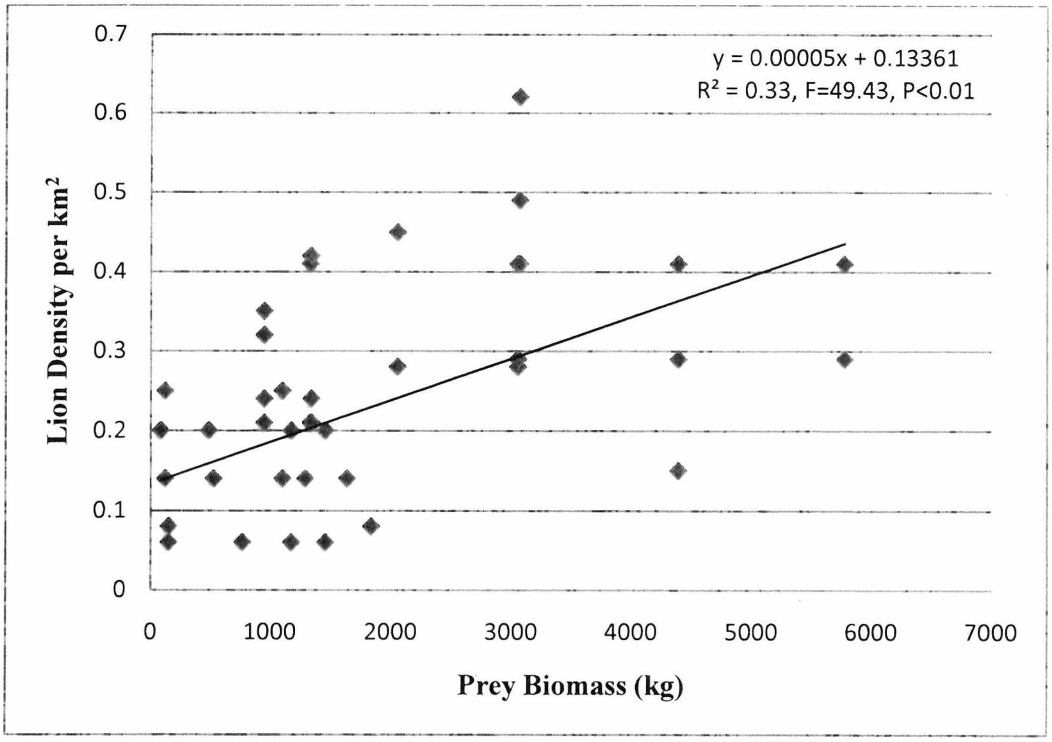
Figure 3.3: Wet season and dry season areas in northern SGR in terms of available prey biomass and sites where lions have made kills.



As seen in Table 3.3 certain areas had much higher prey biomass in the dry season, but most had higher biomasses in the wet season. Areas with at least twice as much prey biomass in either the wet season or dry season are highlighted in Figure 3.3. Both areas with higher prey biomass during the dry season are areas with permanent water. One of these areas is near the natural lake by Lake Manze Camp; the other is near the SGR headquarters, where several artificial water points have been introduced in the last decade. Most of the lion kills were recorded outside the areas with the highest difference between wet and dry seasons (71%). However, 21% of kills were recorded in areas with greater dry season prey biomass, and only one kill was recorded in the higher biomass wet sites.

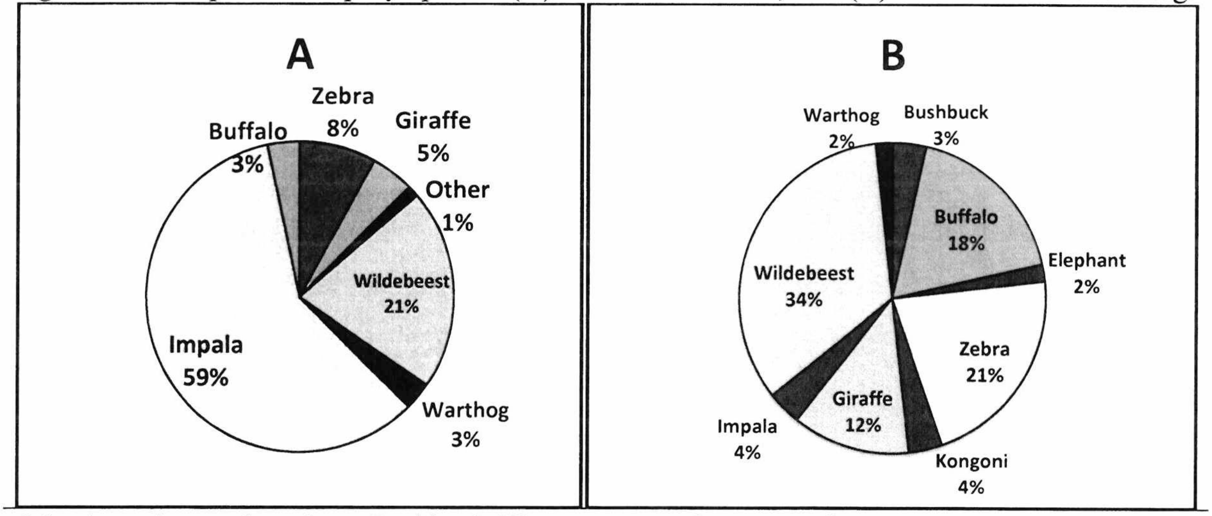
The best explanation of lion distribution based on prey biomass, was recorded between lion density and dry season prey biomass (or lean season prey biomass), which explained 33 % of the variance, and shows that lion density increased as prey biomass increased in the dry season (See Figure 3.4).

Figure 3.4: Dry season prey biomass versus lion densities.



3.4.3 Prey preference:

Figure 3.5: Proportion of prey species (**A**) seen on transects, and (**B**) on which lions feeding.



Other* species on chart **A** are Bushbuck, Hippopotamus, Greater Kudu, Kongoni, Waterbuck, Eland, Elephant.

Table 3.4 and Figure 3.5 are restricted to prey data from 100m of the prey transects. From this, impala and wildebeest were the most regularly sighted species on transects (Figure 3.5 **A**) while the most regular prey items were wildebeest and zebra (Figure 3.5 **B**). However, Jacob's index indicated the lions showed a preference for buffalo and an avoidance of impala (Table 3.4). While the small size of the impala and warthog carcasses may bias the results, as they may be eaten comparatively quickly and therefore be under-recorded, the results recorded here are comparable to other areas of Africa as linear regression showed that the model (Hayward & Kerley 2005; Hayward *et al.*, 2007a) accurately predicted the observed kills ($r^2 = 0.77$, $\beta = 1.02$, $P < 0.01$) and explained 77 % of the variation observed here (see Appendix 7). Furthermore, Hayward *et al.* (2007b) have used prey preference to work out carrying capacity based on the following equation: $y = 0.377x - 2.158$ (where x is the number of preferred prey species per km). Based on the average number of preferred prey species recorded on transects (from Table 3.1), the 800km^2 study site in northern SGR would have a carrying capacity of 104 lions.

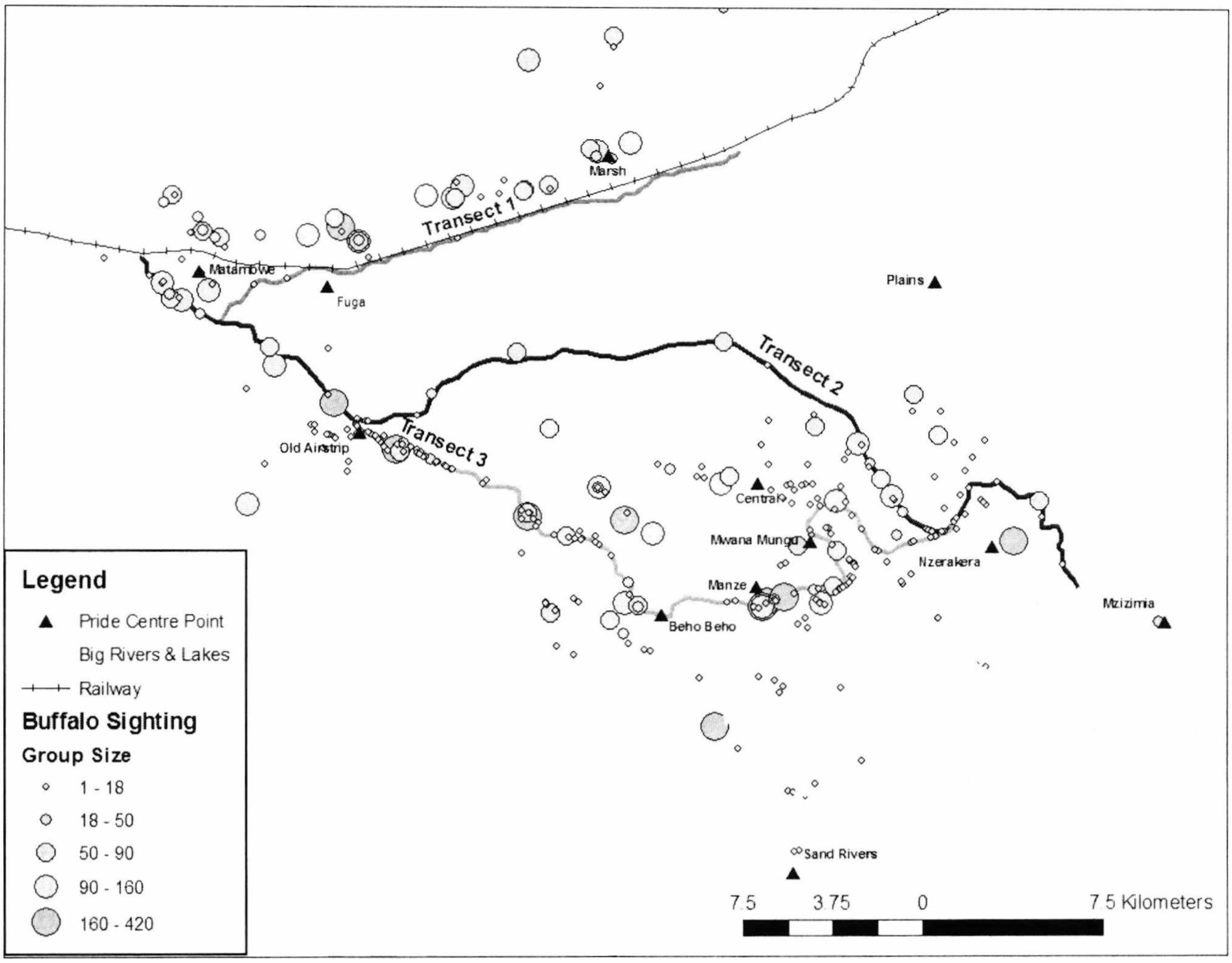
Table 3.4: Prey preference of lions in Matambwe sector of SGR from 2006-2009.

	Buffalo	Zebra	Giraffe	Wildebeest	Warthog	Impala
Total	446	1046	586	2716	374	7701
Sightings	17	129	254	193	146	883
Proportion	0.03	0.08	0.05	0.21	0.03	0.59
Kills Observed	10	12	7	19	1	2
Proportion	0.18	0.21	0.13	0.34	0.02	0.04
D (Preference)	0.72	0.51	0.50	0.32	-0.24	-0.95
D (H & K, 2005)$^+$	0.32	0.16	0.24	0.27	0.11	-0.73
Predicted*	4	6	4	24	2	3

*Restricted to species with plus 100 sightings on prey transects. Species to the left preferred. **D (H & K, 2005)**$^+$ is prey preference from Hayward & Kerley (2005) and numbers Predicted* based on their D value (see also Hayward *et al.*, 2007). Appendix 6 for full list.

Based on the preference index in Table 3.4, lions showed the strongest preference for buffalo. However, there was no strong correlation between buffalo numbers or times buffalo were sighted and lion densities (or lion numbers or times lion sighted). Figure 3.6 shows the sightings of buffalo in northern SGR, which were predominantly near the lakes and river and north of the railway tracks. The lion prides' territories centre points are also plotted on Figure 3.6 and most are near the lakes and rivers.

Figure 3.6: Buffalo sightings in northern SGR with pride centre points.



3.4.4. Explaining lion distribution using factors other than prey availability in northern SGR:

Initial correlation analysis between lion densities and distance to river, reserve boundary and villages showed lion densities were slightly negatively correlated to distance to river (r_s = -.35, P < 0.01), but positively correlated to distance to reserve boundary (r_s = .78, P < 0.01) and villages (r_s = .75, P < 0.01). Principal component analysis (PCA) of these distance variables (i.e. to river, boundary, and village; PCA 1-3 correspondingly) was carried out in ArcGIS and plotted. The PCA figures, habitat type and soil type for each grid square were recorded. To reduce the risk of spatial autocorrelation over two thirds of data grid squares (70.3%) were randomly deleted during the analysis. Stepwise logistic regression suggested PCA 2 + PCA 3 + Soil variables all had a significant impact on lion presence/absence, as shown in Table 3.5. The ROC value of 0.74 indicated a good model.

This was confirmed by AIC test and is shown in Table 3.6. No significant relationships were noted with habitat type.

Table 3.5: Logistic regression of variables determining lion presence/absence.

Variables	B	S.E.	Wald	df	P	Exp(B)
PCA_2	.000	.000	18.350	1	<.001	1.000
Soil_type			6.860	2	.032	
Soil_type(1)	.912	.555	2.703	1	.100	2.489
Soil_type(2)	-1.804	.870	4.306	1	.038	.165
PCA_3	.000	.000	17.880	1	<.001	1.000
Constant	-13.846	3.014	21.099	1	<.001	.000

Table 3.6: AIC best suggested model of significant variables.

Model	2loglikelihood	K	2K	AIC	ΔAIC	(-exp [ΔAIC/2])	Wi
PCA 1	216.840	2	4	220.84	19.31	0.00006	0.0001
PCA 3	216.782	2	4	220.78	19.25	0.00007	0.0001
PCA 2 + PCA 3	201.063	3	6	207.06	5.53	0.06285	0.0587
PCA 1 + PCA 2 + Soil	203.182	4	8	211.18	9.65	0.00801	0.0075
PCA 2 + PCA 3 + Soil	193.529	4	8	201.53	0.00	1.00000	0.9337

*PCA 1-3 represents principal component analysis of distance to river, reserve boundary and village respectively.

The values from Table 3.5 (column B) can be used in the following equation to model the presence or absence of lions in northern SGR:

A = (PCA 2 x coefficient) + (PCA 3 x coefficient) + Soil + Constant

A = (PCA 2 x 0.000133) + (PCA 3 x 0.000367) + (+0.912 or -1.804) + (-13.8346)

$$\text{Probability of lion presence} = \frac{Exp\ A}{1 + Exp\ A}$$

The results of the above equation described lion distribution in northern SGR at the 1km^2 grid level well, suggesting distance to the reserve boundary and villages and soil type of an area were most important in explaining lion distribution here.

3.5 DISCUSSION

Understanding lion distribution in northern SGR will allow for improved management of this species. Lion distribution in this area was best explained by lean season prey biomass. Lions in this area showed the strongest prey preference for buffalo. Other factors important in explaining lion distribution in northern SGR were distance to river, village and reserve boundary and soil type.

3.5.1 Prey biomass and lion density:

The mean total prey biomass for the study site in northern SGR was 1674 (± 1248) kg km^{-1}. Prey biomass was highly variable in this area of northern SGR and varied between location and time of year. Lion densities (km^{-1}), like prey biomass, was variable but both lion densities and prey biomass (kg km^{-1}) were highest on Transect 3 near the lakes. In terms of prey availability the best explanation of lion densities was provided by dry season prey biomass, but this only accounted for 33% of the variance. The dry season was the lean season in this area of SGR. This concurs with earlier studies by Van Orsdol *et al.* (1985) based on data from ten different habitats across Africa with lions, which showed a relationship between lion density and lean season prey biomass, but their study explained a greater proportion of the variance (r^2=0.48) and described the relationship as $y=0.0001x + 0.0870$; which represents a higher density of lions per kg km^{-1} prey biomass (see Figure 3.4). The mechanisms behind this increased lion density with lean season prey biomass is an inverse correlation between pride territory size and lean season prey biomass and increased lion cub survival to 12 months correlated with an increased lean season prey biomass (Van Orsdol *et al.*, 1985).

Prides near the lakes on Transect 3, where the prey biomass is highest in the dry season, have the smallest territories in northern SGR (see Spong, 2002; see also Appendix 8). Based on the relationship between mean dry or lean season prey biomass and lion densities, it is possible to work out the lion carrying capacity of this $800km^2$ area of northern SGR. The lean season prey biomass is 1436 kg km^{-1} (see Table 3.2), which would result in a lion carrying capacity for the $800km^2$ of 184 lions (0.23 km^{-2}) based on Van Orsdol's equation or 164 lions (0.21 km^{-2}) based on the observed dry season/lion density relationship (see Figure 3.4). The last census of this area had a total of 112 lions in this $800km^2$ area, well below the suggested carrying capacity. This either suggests that the census is not picking up all the lions in the area (i.e. under-representing the population) or that other factors are holding the population below carrying capacity. This 800km^2 photographic site in northern SGR, is ringed by hunting blocks with some of the highest lion trophy hunting pressures in Tanzania (see Chapter 4/5). Studies from other areas of Tanzania, Katavi National Park in particular, have suggested that lion population densities are well below the carrying capacity of the Park, based on prey biomass availability, as a result of excessive hunting in neighbouring hunting blocks (Kiffner *et al.*, 2009).

3.5.2 Prey biomass species composition and seasonal species movement:

The three most common prey species seen on transects were impala (8.20 km^{-1}), wildebeest (3.67 km^{-1}), and zebra (1.31 km^{-1}). More individuals of each species were seen on Transect 3, with the exception of warthogs. More warthogs were seen on Transect 1. However, as Table 3.3 highlights there are seasonal variation between transects. During the dry season there are more wildebeest and zebra on Transect 3 (25km – 35km section) by Lake Manze, but during the wet season the species are more dispersed and there is a movement of wildebeest and zebra towards Transect 1 and Transect 2. Although, impala accounted for over half of all individuals seen on the prey transects, in terms of biomass (kg km^{-1}) it ranked third after wildebeest (495kg km^{-1}) and giraffe (379kg km^{-1}) as highlighted in Table 3.1. Giraffe accounted for 23% of the available prey biomass in this area of northern SGR.

3.5.3 Prey preference:

In terms of prey preference, the lions of northern SGR closely follow those predicted by Hayward & Kerley (2005). In northern SGR, buffalo, zebra, giraffe and wildebeest were preferred, and warthog and impala avoided. In other areas where warthog are more abundant, they are frequent prey even if they are well below the lions preferred prey weight of 190-550 kg (Hayward & Kerley, 2005); this is true in Serengeti, where lions eat warthog and buffalo during periods of prey scarcity (i.e. when the zebra and wildebeest migration is in the Mara; Scheel & Packer, 1995) and in eastern SGR where warthogs are more abundant and made up 24 % of the total kills between 1967 and 1970 (Rodgers, 1974); wildebeest (34 %), buffalo (22 %) and zebra (six percent) were the other preferred species (there are no giraffe in this area). These results suggest that for lions, and probably other generalist predators, habitat definitions based on vegetation communities are less important than those based on prey availability (Hayward *et al.*, 2007a). Hayward *et al.* (2007b) have also used prey preference to work out carrying capacity; for this 800km^2 area of northern SGR their equation suggests a carrying capacity of 104 lions, which is slightly lower than the observed number of lions in this area. The prey preference carrying capacity has been used to good effect to assist in setting stocking levels in several small (70-185km^2) fenced reserves in South Africa (Hayward *et al.*, 2007b).

3.5.4 Other factors that explain lion distribution:

In this study, anthropogenic factors were captured by measuring distance to nearest village and the reserve boundary. While, soil type and distance to permanent water were seen as proxy measures of prey abundance. This study showed that distance to water, reserve boundary, village and the soil type were important in determining the probability of the presence of lions in a specific grid square in northern SGR.

A previous study in SGR recorded that the lions showed a significant preference for riverine and short-grass habitat, and a significant avoidance of acacia woodland (Spong, 2002), and noted that these preference ratios largely reflected prey availability in each habitat. A similar result was recorded in this study, with natural (or riverine) forests and grassland habitats having higher mean densities of lions than open woodland areas (see Appendix 5). Conversely, Hopcraft *et al.* (2005) showed that lion hunting success is associated with landscape features that enhance prey capture, rather than prey abundance itself (e.g. erosion embankments, access to water, and woody vegetation). Similarly, river confluence points have been identified as lion population sources, owing to their strong correlation with long-term average reproductive success in Serengeti (Mosser *et al.*, 2009). Various studies have used soil nutrients as a proxy for prey abundance (Loveridge & Canney, 2009; Celesia *et al.*, 2009); noting an increased lion density on richer volcanic soil associates than nutrient poor sands. In northern SGR, soil type was shown to be important in determining lion distribution, with higher lion densities on nutrient richer fluvisols and cambisols than on nutrient poorer ferrasols.

Anthropogenic impacts on lion population distribution have been noted here, with a strong positive correlation between distance to the reserve boundary and villages and lion densities. Other studies have noted this, with an increased human impact relating to a lower probability of the presence of lions (Loveridge & Canney, 2009). Furthermore, lions come into conflict with people, particularly where livestock is kept, invariably resulting in retaliatory killing and declining lion population (Kissui, 2008b). Over the three years of this study, there has been an increase in pastoralists settling in areas bordering northern SGR.

3.5.5 Conclusion:

The ultimate goal with looking at what factors influence lion distribution is to be able to predict lion distribution in areas not sampled, or where prey data is lacking. There is a dearth of prey or lion data for most of SGR. The model here accurately mapped lion distribution in northern SGR. Lion distribution in northern SGR was best explained by lean or dry season prey biomass. Lions showed a preference for buffalo, zebra, giraffe and wildebeest in this area. However, no relationship was noted between lion distribution and buffalo sightings. Environmental and anthropogenic factors that best explained lion distribution in northern SGR were distance to the reserve boundary and villages and soil type of an area.

4 Setting the Hunting Quota: Lion Trophy Hunting.

4.1 ABSTRACT

The sustainable management of hunting in Selous Game Reserve (SGR) is driven by a quota system, whereby the reserve is divided into 43 hunting blocks and each is allocated a quota of animals to hunt. The lion hunting quota in Tanzania is currently set through educated guesswork. A transparent means of setting quotas for lions in SGR is devised here. Recommendations are made at the block level as this is the level that management decisions are made. In particular, three different approaches were used to investigate the sustainability of the lion hunting quota: i) an approach based on hunting off-take and quota data; ii) an approach based on using Normalized Difference Vegetation Index (NDVI) and expert opinion to estimate lion populations per block; iii) an approach based on an individual-based stochastic model to examine three different lion population sizes, the impact of male breeding commencing at under three years of age or five years, and hunting at current quota levels. Based on lion off-take data from 1995 to 2008 a reduction to the quota is suggested to one lion 1000km^{-2}. Lion densities from a studied population in a 541km^{2} area were negatively correlated with NDVI values and this relationship was used to develop a quota for each block, based on a figure below ten percent of the adult male population. The results of the stochastic model showed that larger starting populations were better able to sustain high trophy hunting off-takes and populations where males reached a reproductive maturity at a younger age were also more robust. All three approaches showed the need for the lion quota to be reduced in SGR.

4.2 INTRODUCTION

Commercial forms of extractive use have developed as part of the choice in modern conservation paradigms, and trophy hunting is one such choice (Hutton & Leader-Williams, 2003). From a conservation standpoint, trophy hunting is useful only so long as it provides long-term protection of habitats and populations and, for these reasons must be conducted on a sustainable basis (Caro *et al.*, 1998). Tanzania has long been recognised for its high quality trophy hunting; which is sometimes also referred to as sport, tourist or recreational hunting (Leader-Williams *et al.*, 1996). This reputation comes from the varied game found in Tanzania, from the high quality of its trophies, and from the vast areas of wilderness (Baldus, 2009). Some 50 different mammal species can be hunted legally under licence in Tanzania by tourists, and Tanzanian residents can shoot a total of 22 species for meat with permits (Caro *et al.* 2009). The Selous Game Reserve is internationally designated as a World Heritage Site. Despite being an inaccessible area infested with tsetse flies and underlain by poor soils, Selous supports one of Africa's largest big game populations and has developed a considerable reputation as a tourist hunting destination (Leader-Williams & Hutton, 2005).

Hunting by tourists for sport is a complex activity, whose product is as much a quality of its experience as it is of meat or trophies (Loveridge *et al.*, 2006). Nonetheless, as in any branch of natural resource utilization, the science of trophy hunting revolves around sustainability (Milner-Gulland *et al.*, 2009); what is the effect of hunting on populations, and how can this be used to improve its management? A sustainable off-take is a yield that can be taken year after year without jeopardising future yields (Sinclair *et al.*, 2005). However, unlike other forms of hunting, such as commercial fisheries, there is often an assumption in trophy hunting that there is a management authority that can influences hunting rates and choose a sustainable level of hunting (Milner-Gulland *et al.*, 2009); which in the case of trophy hunting in Tanzania is focused on setting hunting quotas at sustainable levels.

The Selous Game Reserve is divided into 43 hunting blocks. These hunting blocks are leased, typically for a period of five years, by the Tanzanian government to licensed and registered hunting companies, who are responsible for organising and selling hunting safaris to tourists (Rohwer, 2009). Each hunting block has a quota for a range of species that can only be hunted from the start of July to the end of December each year (Caro *et al.*, 2009). Overall management of the reserve is in the hands of the Wildlife Division (WD) of the Ministry of Natural Resources and Tourism (MNRT) and all fees are paid to the WD.

Buffalo, lions and leopard are the main attractions for tourist hunting in Tanzania, with these three key species responsible for generating 25% of the management authority's total income (Baldus & Cauldwell, 2004). Annually, approximately 250 lions are taken by tourist hunting in Tanzania, of which 75-90 are taken in Selous Game Reserve (Baldus, 2004). The trophy fees for lion are high, and therefore increasing the number of lion on quota greatly increases the quota value and is one of the easier means for the management authorities to increase revenue, as hunting operators have to achieve 40% of their total quotas (Ndolanga, 1996). However, research using models parameterized with 40 years of Serengeti demographic data strongly suggest that tourist hunting of lions would be sustainable if only males over five years are hunted, as this would allow males the opportunity to remain resident in a pride long enough to rear a cohort of young (Whitman *et al.*, 2004). A relatively high off-take would be possible provided no young lions are removed and the quality of trophies would be much improved. These results imply that strict adherence to off-take of only old animals would make quotas for lion obsolete, and highlights the importance of being able to age lions in hunting situations. Nose colour has been suggested as a means to age lions accurately (Whitman *et al.*, 2004). The Tanzania Hunters and Outfitters Association (TAHOA) accepts the notion of only hunting older male lions, and set a minimum age requirement of six years on lion trophies in 2004, yet pictures of under-aged males (as young as two years old) that have been shot in Tanzania could still be found on hunting company web-sites in 2008 (see Packer *et al.*, 2009). Furthermore, individuals working at various hunting companies have questioned the validity of using Serengeti data across Tanzania and stressed the difficulty of aging lions in hunting situations.

Lion populations have been modelled over time using an age- and stage-structured model (Caro *et al.*, 2009) and an individual-based stochastic model (Whitman *et al.*, 2004) to examine various aspects of lion life history/biology and the impact of trophy hunting. Caro *et al.* (2009) analysed the impact of trophy hunting levels on a range of species and breeding systems, in particular focusing on male help in rearing off-spring, male infanticidal behaviour, and differing harem sizes. In addition, Whitman *et al.* (2004) focused on lions and modelled the impact of hunting males of different ages on the population size. As mentioned previously, hunting of males over five years is recommended as they would have had a greater chance of rearing a cohort of offspring. However, data from Kruger National Park, South Africa, recorded a prolonged period of association of sub-adult males with their natal prides and a delay at which males begin breeding to five years (Funston *et al.*, 2003). This would have serious implication on the minimum age at which a lion can be shot.

The management of hunting in Selous Game Reserve is driven by a quota system, whereby each hunting block is allocated a quota of animals to hunt. Studies of lion trophy hunting have suggested an off-take of ten percent of the adult male population or two percent of the total population appears to be sustainable (Chardonnet, 2002; Baldus, 2004; Packer *et al.*, 2010), while Caro *et al.* (2009) used models to suggest an off-take of 4.6 % of the total population before negative growth starts to impact on the population. Currently the lion hunting quota in Tanzania is set through educated guesswork by the WD (Severre, 1996). The setting of quotas remains an area of contention within the trophy hunting industry (Leader-Williams, 2009); with some stating that hunting quotas need to be based on detailed prior knowledge of the population biology of the hunted population (Milner-Gulland & Ackakaya, 2001), while others argue that quotas can be set through an adaptive management approach (Rosser *et al.*, 2005). The aim of this study is to devise a transparent means of setting quotas for lions in Selous Game Reserve, an iconic hunting destination. Recommendations are made at the block level as this is the level that management decisions are made. In particular, three different approaches are used to investigate the sustainability of the lion hunting quota: i) an adaptive management approach using hunting off-take and quota data; ii) a Normalized Difference Vegetation Index (NDVI) and expert opinion approach to work out lion populations per block; iii) an individual-based stochastic model to look at three different lion population sizes, the impact of male breeding commencing at two and half years of age (as in Serengeti National Park) or five years (as in Kruger National Park), and hunting at current quota levels.

4.3 METHODS

4.3.1 Study area:

Field work was carried out between June 2006 and August 2009. The Selous Game Reserve (7˚17' - 10˚15' S, 36˚04' - 38˚46' E) is divided into 47 blocks comprising 47,500 km^2 (see Figure 4.1). Four blocks (or six percent) of Selous Game Reserve (SGR) are set aside for photographic tourism (see Figure 4.1); the rest of SGR allows resource utilization in the form of trophy hunting (Caro *et al.*, 2009). The mean block size is 1002 ± 586 km^2 (± standard deviation throughout); with the mean hunting block being 1011 ± 598 km^2 and photographic blocks being 749 ± 150 km^2. The Rufiji River, and its tributaries the Kilombero, Luwegu and Great Ruaha, is the main feature of SGR (see Figure 4.2). The SGR comprises a mosaic of wooded savanna, miombo and *Combretum* thickets; with the northern sixth of the SGR being open wooded grassland, and the rest of the Reserve being deciduous miombo woodland (see Creel & Creel, 2002 for details). Altitude ranges from 100 m above sea level (asl) in the north-east to 1200 m asl in the south west. Rainfall follows a similar east-west pattern, ranging from 750 mm in the east to 1250 mm in the west, falling predominantly between December and May (IUCN, 1998).

Figure 4.1: Photographic and hunting blocks in SGR.

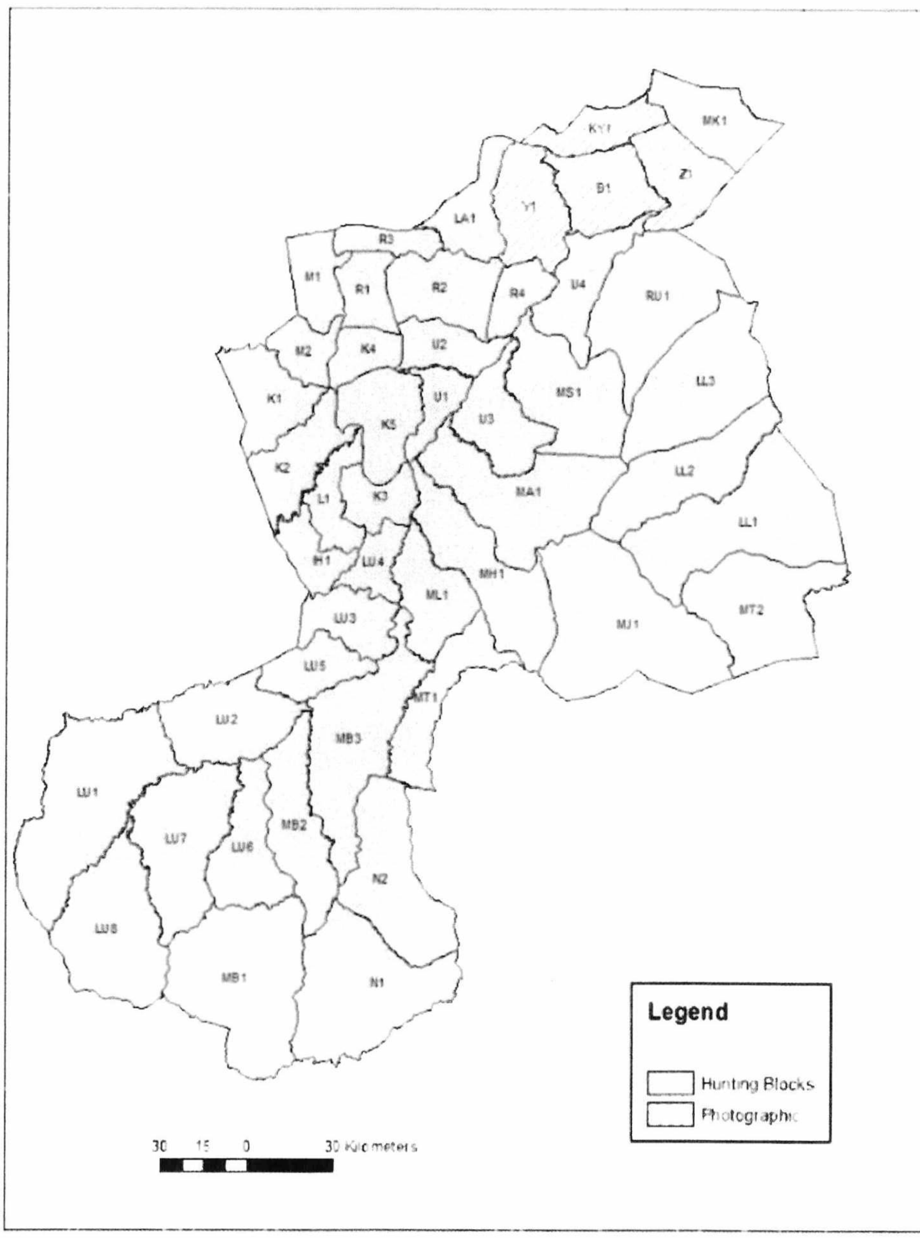
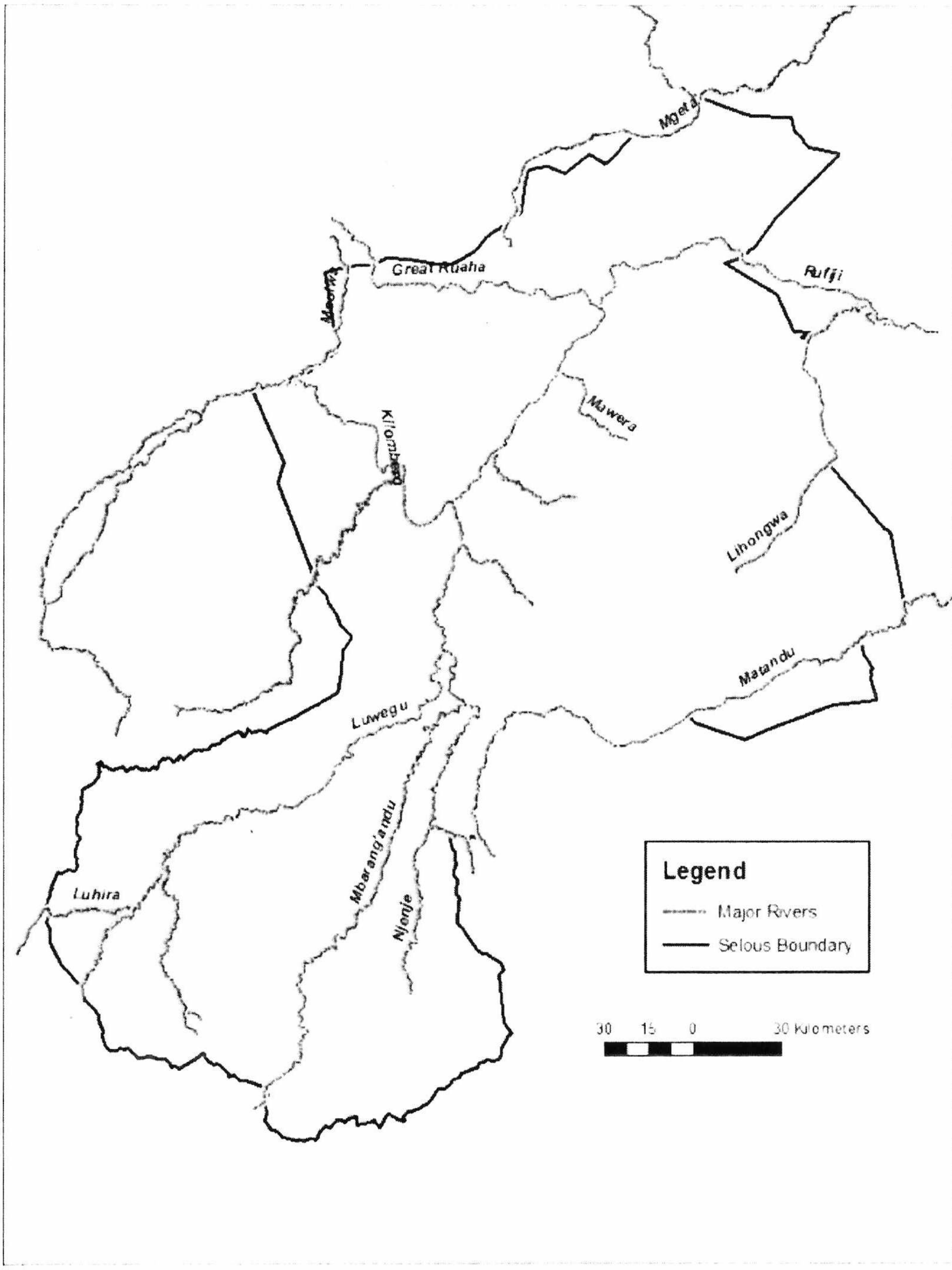


Figure 4.2: Major rivers of SGR.



4.3.2 Block and hunting off-take data:

Digital boundary polygons files of the SGR blocks were obtained from the Selous Conservation Project (SCP) funded by the Organization for German Technical Cooperation (GTZ) and Tanzania Wildlife Research Institute (TAWIRI). The SCP data are from 2003, while the TAWIRI data are more up-to-date and reflect 2009 boundary data. Field visits to different sectors of SGR were carried out to ground truth these layers. All spatial data was imported to ArcGIS version 9.3 (ESRI Inc., Redlands, CA) for analysis.

Data on trophy off-takes of lions in each hunting block of SGR were provided by the CITES office at the WD headquarters in Dar es Salaam. The off-take data are much more complete in SGR, as compared to the rest of Tanzania, due to the activities of the SCP and the Planning and Assessment for Wildlife Management (PAWM) project funded by USAid (Leader-Williams *et al.*, 1996; Baldus & Cauldwell 2004; Caro et al 2009). For each block, the hunting pressure is defined as the average annual off-take per block per 1000km^2 from 1996-2008. Furthermore, the "initial intensity of hunting" is defined as the average annual off-take per 1000 km^2 in 1996-1999 per block. The regression coefficient for each block off-takes was then estimated starting in 1996 and ending in 2008. The "annual change" in trophy off-take is the regression coefficient multiplied by the initial intensity, and the "annual rate of change" in trophy off-take is this annual change divided by the initial intensity multiplied by one hundred. This represents a similar methodology used to look at the sustainability of trophy hunting of lion and leopard across Tanzania (see Appendix 14.b: Packer *et al.*, 2010).

4.3.3 Working out lion populations using NDVI:

Satellite imagery and expert opinion from fieldwork were used to identify three broad habitat categories based on Normalized Difference Vegetation Index (NDVI) values. Lion density figures and NDVI values were tested to see if there were any correlations. NDVI layers of SGR were acquired from the Land Processes Distributed Active Archive Center (LP DAAC), located at the U.S. Geological Survey (USGS) Earth Resources Observation and Science (EROS) Center (lpdaac.usgs.gov). NDVI determines the density of green on a patch of land by measuring the wavelengths of visible light absorbed by the plant pigment chlorophyll (see also earthobservatory.nasa.gov), and can be described by the following equation, where NIR is near infrared radiation and VIS is visible radiation.

$$NDVI = (NIR - VIS) / (NIR + VIS)$$

NDVI has been used to measure a wide variety of vegetation conditions (Pelkey *et al.*, 2003); and has been used as a measure of net primary productivity (Coops *et al.*, 1998). The NDVI data for the peak dry season months of October to December from 2006 to 2009 was used in this study. The average NDVI score for each one km^2 grid cell for this period was calculated, and it is this figure that is used in the study. Dry season data were used here because it has been shown that this represents the lean season in SGR (see Chapter 3), and other studies have shown that lean season prey biomass provides the best explanation of lion distribution (Van Orsdol *et al*,. 1985). NDVI scores should offer a good proxy of prey biomass and therefore lion density. While NDVI is a useful tool in assessing prey biomass, it is not a perfect measure, as recent work showed that larger sample areas tended to under-represent African ungulates and satellite indexes have limitations in very sparsely or densely vegetated areas (Pettorelli *et al.*, 2009).

NDVI values for SGR ranged from -673 to 8798. NDVI values were divided into three groups based on expert opinion for the analysis, namely: i) 5559 to 8798, ii) 4168 to 5558, iii) -673 to 4167. When analysing spatial data there is a risk of non-independence caused by spatial autocorrelation (Koenig, 1999) because neighbouring cells share similar values of the dependent variable leading to correlation coefficients appearing more significant than they are. Spatial autocorrelation was tested using the Crimestats version 3.2a software package (N. Levine & Associates, Annandale, VA) where the dependent variables were tested using Moran's I statistic/Geary's C statistic. Grid cell data were removed randomly until the data were not likely to be significantly spatially autocorrelated (i.e. where Moran's I was close to 0, and Geary's C close to 1). Spatial autocorrelation was a particular concern as the lion density data came from one part of the SGR (see Chapter 3). Data on lion population densities were collected between June 2006 and August 2009 and methods employed are described elsewhere (Chapter 2 & 3). A one km^2 grid was used to recorded lion density data for a 541km^2 area of northern SGR (as described in Chapter 3). NDVI layers were overlain onto a lion density grid of northern SGR in ArcGIS to identify any relationship between lion density and NDVI score.

4.3.4 Modelling hunting:

The SimSimba model is Windows-driven C++ model (described in detail in Whitman *et al.*, 2004, Whitman *et al.*, 2007), and is used here to model the impact of trophy hunting under several population scenarios. In the model, female lions and their dependent offspring are organized into 'prides' that defend spatially arranged and interconnected territories. The model ignores environmental stochasticity, so the maximum number of territories and maximum pride size is held constant for a given set of simulations. In this case, an 11-territory convex landscape, with a carrying capacity of 171 lions was created, which was thought to be a good approximate of hunting blocks in SGR. The model distinguishes between sex and age class and tracks individuals by social and reproductive status. Only 3–13-year-old females produce cubs; females are not able to breed again until they lose their entire litter or their surviving offspring reach 2 yr of age. Males are classified as either sub-adult, nomadic or resident; lone males may join up with other lone males or groups of two. Nomadic and sub-adult males move freely between and within pride territories a specified number of times per time step, but do not breed with females. Residents may be affiliated with up to three prides at once. Competition for pride residence is determined by using a competition matrix that weights overall competitive strength according to male age and coalition size. Cubs are killed with an age specific probability when new males first enter a pride.

At each time step, the model simulates cub production using a random number for each eligible female that draws her litter size from a distribution, determines individual survival, updates ages for survivors, organizes 2-yr-old males in each pride into sub-adult male groups, promotes 3-yr-old males into nomadic groups, and determines the fate of sub-adult females. Recruitment of females into their natal pride depends on the number of adult females already in the pride and the specified upper limit for that pride (which can be temporarily exceeded by no more than two females). If the sub-adult females cannot be accommodated in their natal pride, they are allowed to search for empty territories, but they die if they cannot find any vacancies. At 'equilibrium' or carrying capacity, the simulated populations had a male : female : cub ratio of 20 : 30 : 50. To test the effects of trophy hunting, each simulation was run for 50 years with 15 replicates of each population scenario.

The initial seed population was run for 100 time steps (or 50 years) for each of the 15 replicates so that the population reached carrying capacity (or 171 lions). For ten of the 15 replicates, lions were selected at random to delete, such that five of the replicates contained a population of 43 individuals and five replicates contained a population of 107. Each starting population was run ten times for 100 time steps (so 50 for each of the population size of 43, 107 or 171 individuals). Five separate starting populations for each simulation were used to rule out the possibility of starting conditions affecting the results. Each simulation was run under two different male reproductive parameters, namely: i) male reproduce from age two and half years and adult age is four years (as in Serengeti); ii) male reproduce from age five years and adult male age is five years (as in Kruger). For all scenarios, hunting was of males age three years and older – three males were hunted every year if available.

4.4 RESULTS

4.4.1 Lion hunting off-take and quota:

Lion trophy hunting peaked in SGR in 1998 and has fallen by 50% since then, yet the quota has remained relatively constant since then (see Figure 4.3). Between 1995 and 2008, an average of 39.2% of the quota was utilized annually in SGR; in 1998 63.7% of the quota was utilized. The average annual quota between 1995 and 2008 per block was 3.49 ± 0.25 and the average off-take per block was 1.38 ± 0.42. Figure 4.4 shows the spatial spread of the lion trophy hunting in SGR, with the highest average annual off-take to be in the blocks to the east of the reserve. However, these eastern blocks tend to be much larger (~1700km^2) than the blocks in the north and west of the reserve (~580km^2). To account for this difference in block size, the hunting pressure of each block was estimated (average number of lions shot annually per block per 1000km^2; Figure 4.4;**B**). It can be seen that the hunting pressure is much higher in the hunting blocks of the north and east of SGR. Figure 4.5 shows the hunting pressure and the annual rate of change of hunting off-take for each block – and shows that the higher the hunting pressure, the greater the decrease in the annual rate of hunting off-take between 1996 and 2008 (r^2=0.30, n=43, p<0.01). That is the blocks with the most lions shot per 1000km^2 experienced the greatest annual decrease in the number of lions harvested.

Figure 4.3: Average number of lions shot per block in SGR and the average quota for lions per block per year.

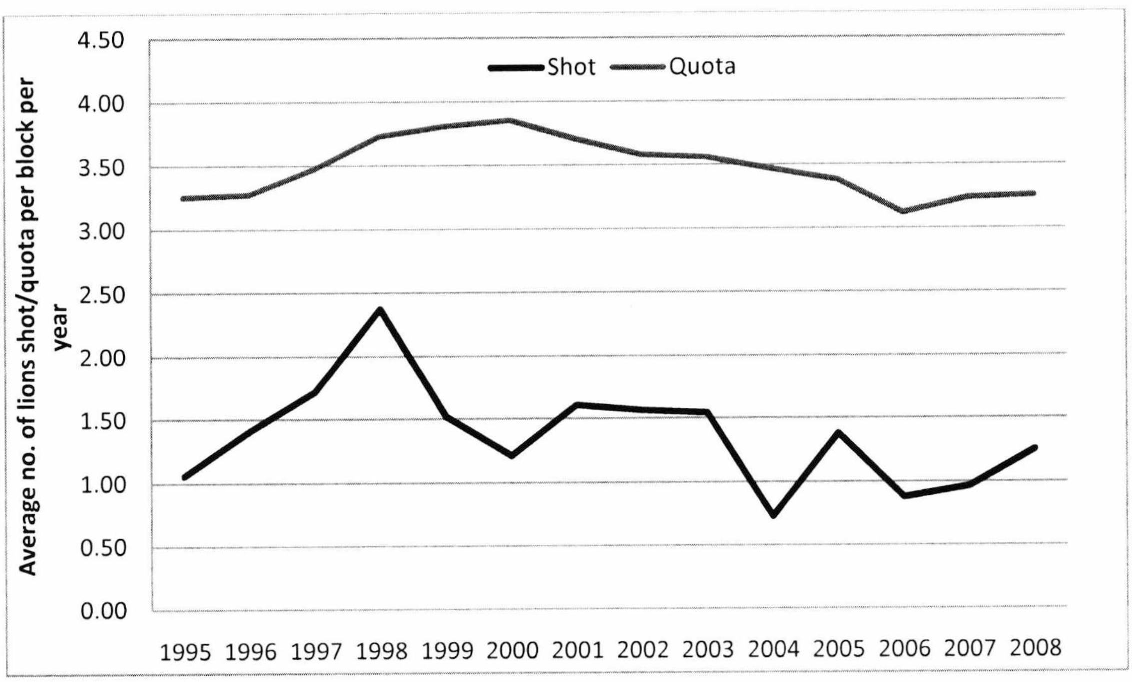


Figure 4.4: A) Average number of lions shot each year from 1996-2008 (with actual location of lions shot in 2003 marked as dots); **B)** Hunting Pressure on lions (average shot per block per $1000km^2$ between 1996 and 2008).

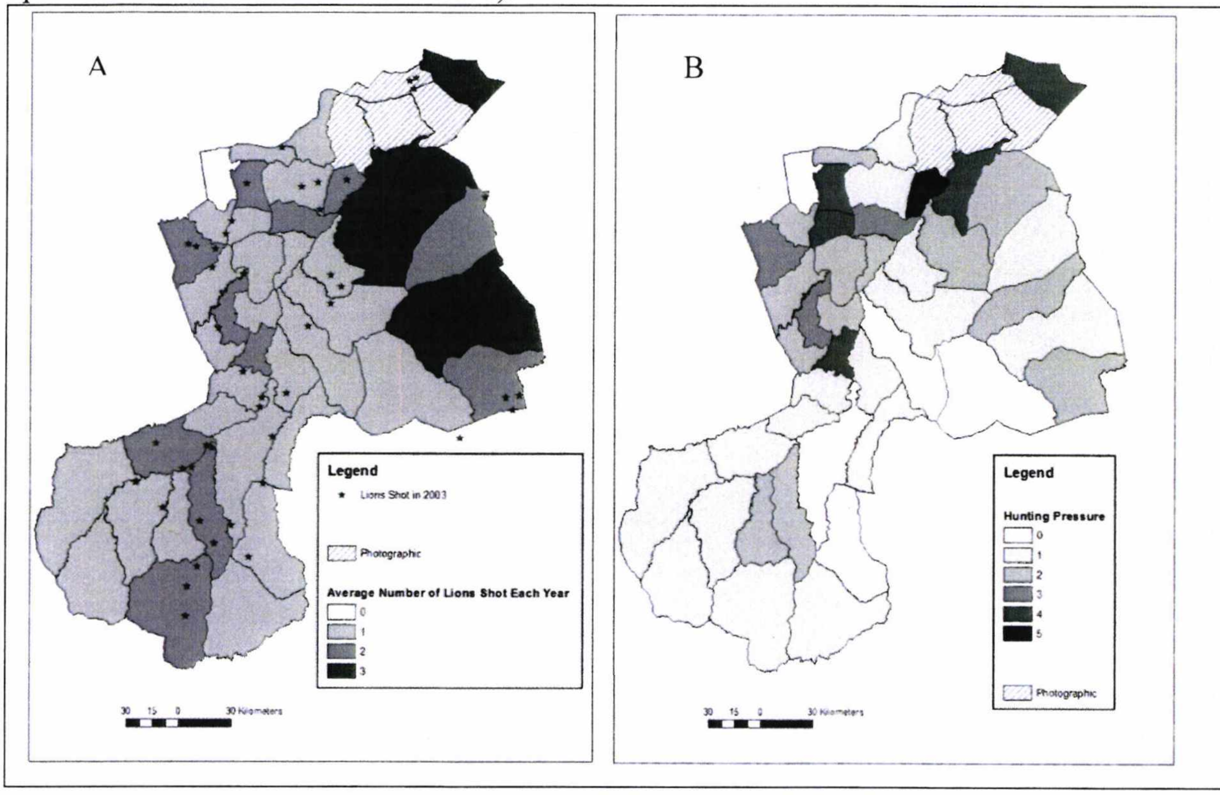
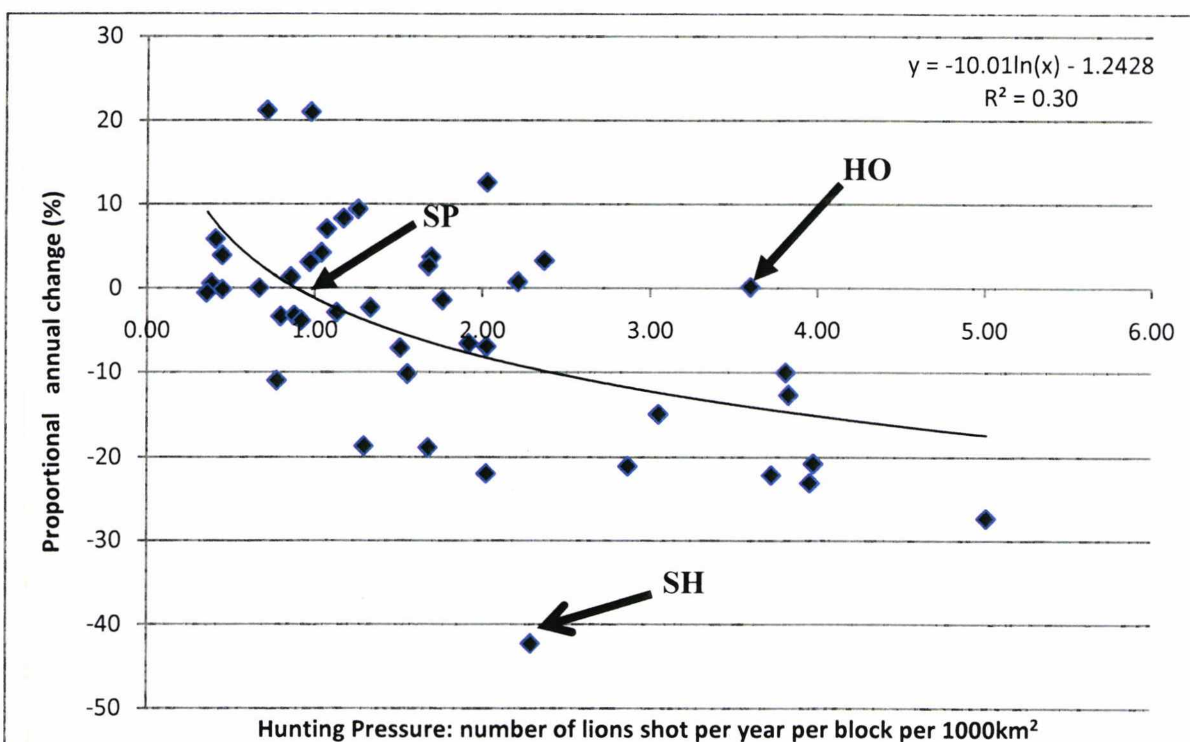


Figure 4.5: Lion hunting pressure versus rate of annual change.



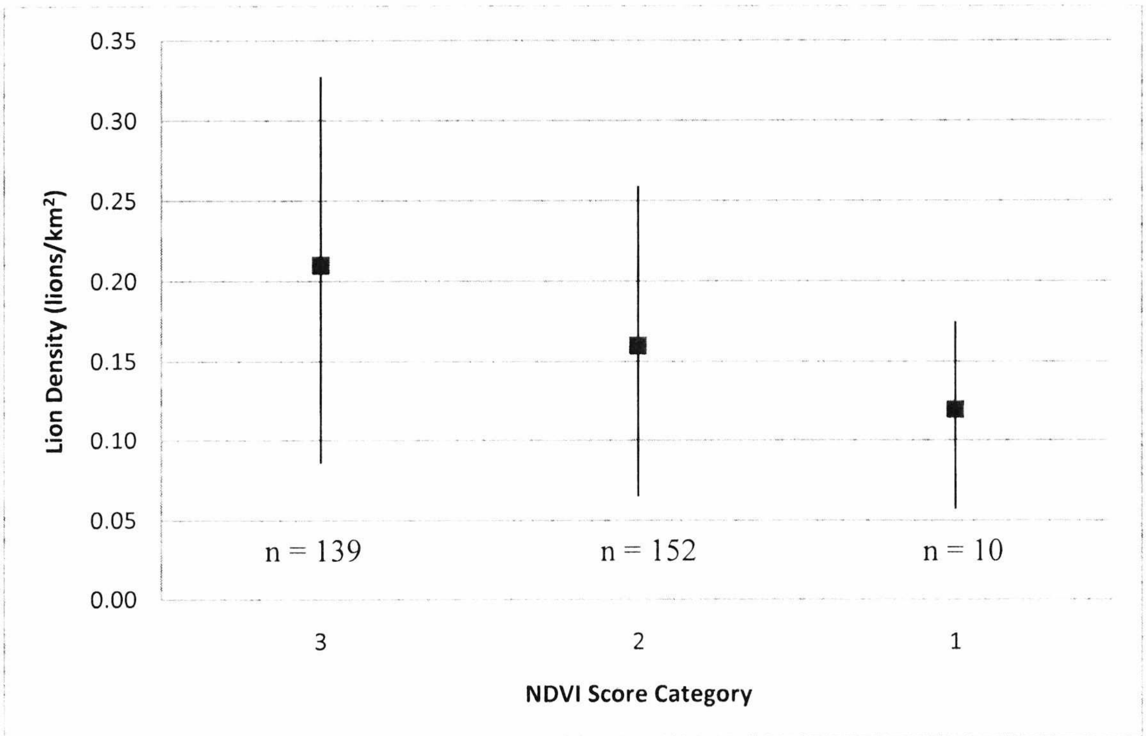
SP: sustainable point. **HO:** High off-take no decrease. **SH:** Stopped hunting.

These results strongly suggest that in SGR, setting the quota at a level of one lion 1000 km^{-2} would be sustainable (see also Appendix 14.b; Packer *et al.*, 2010) and marked SP or sustainable point on Figure 4.5. That is a hunting pressure of one lion 1000 km^{-2} should not result in a decrease in off-take over time. However, there are blocks on the graph where a high hunting pressure has not resulted in a decrease in off-take (marked HO or high off-take on graph). The largest decrease is noted at point SH (stopped hunting), whereby the hunting company operating in the block were so concerned at off-take levels of neighbouring blocks that they stopped hunting lion in their block in the early 2000s.

4.4.2 NDVI and lion numbers:

To eliminate the risk of spatial autocorrelation, almost half of the lion density and NDVI data grid squares (44% of 541 grid squares) from northern SGR were randomly deleted during the analysis. Spearman rank-order correlation showed that lion densities in northern SGR were negatively correlated with NDVI score (r_s = - .23, P<0.01). The NDVI scores were grouped into 3 categories (1: 5559 to 8798; 2: 4168 to 5558; 3: -673 to 4168) and the mean lion density plotted in Figure 4.6 (mean ± standard deviation throughout). The results of Kruskal-Wallis test of the mean rank of lion densities per grid square are significantly different between each NDVI score category (H = 15.29, 2 d.f., P<0.01).

Figure 4.6: NDVI score categories and lion density



The three NDVI categories from Figure 4.6 were used to produce a map of suitable lion areas (Figure 4.7); areas with NDVI scores between -673 and 4168 are scored a three and support the highest densities of lions (Category 2: 4168 to 5559; Category 1: 5559 to 8798). So the darker areas of the map support higher densities than the lighter areas of the map, but only inside the reserve (the darker area outside SGR to the west represents the Kilombero Valley, which is very fertile area with high human densities and therefore few lions). Although the previous chapter highlights the importance of edge effects on lion densities in northern SGR, no clear pattern could be seen on lion trophy hunting off-take in Tanzania as a result of edge effects (see Appendix 14.b; Packer *et al.*, 2010) and the lack of lion density data from other parts of SGR, meant that it has not been considered here.

Figure 4.7 has been used to work out lion numbers per block, by adding up the number of NDVI grid squares of each category per block and then multiplying the number in the different categories by the lion density highlighted in Figure 4.6. As the lion density figures used in the analysis are from northern SGR, which supports higher lion densities than other parts of the reserve (see Chapter 2; Creel & Creel, 1997; Caro *et al.*, 2009), a cautious approach has been adopted here and the lowest point in the standard deviation of the mean has been used in working out populations. So within a block all NDVI category 3 were added together and multiplied by 0.09; category 2 by 0.07; and, category 1 by 0.06. These results are presented in Table 4.1 and also include two other recent estimates of lion numbers for SGR blocks (*Caro & #IGF). The other estimates were higher than the NDVI based estimates (Table 4.1). The average annual lion hunting quota for each block during the periods 1988 to 1997 and 1997 to 2008 are comparable (average $\pm$ standard deviation; 3.6 $\pm$ 1.2 for 1988-1997, and 3.5 $\pm$ 1.1 for 1997-2008), but off-takes are very much higher in the 1997-2008 time frame (0.9 $\pm$ 0.7 for 1988 – 1997, and 1.5 $\pm$ 0.8 for 1997 – 2008; Table 4.1). There was no significant difference in the mean rank of the quota between the periods (Kruskal-Wallis; $H = 0.053$, 1 d.f., $P=.82$), but there was a significant difference in the off-take mean ranks between the periods (Kruskal-Wallis; $H = 8.295$, 1 d.f., $P<.01$).

Figure 4.7: NDVI map used to predict lion densities.

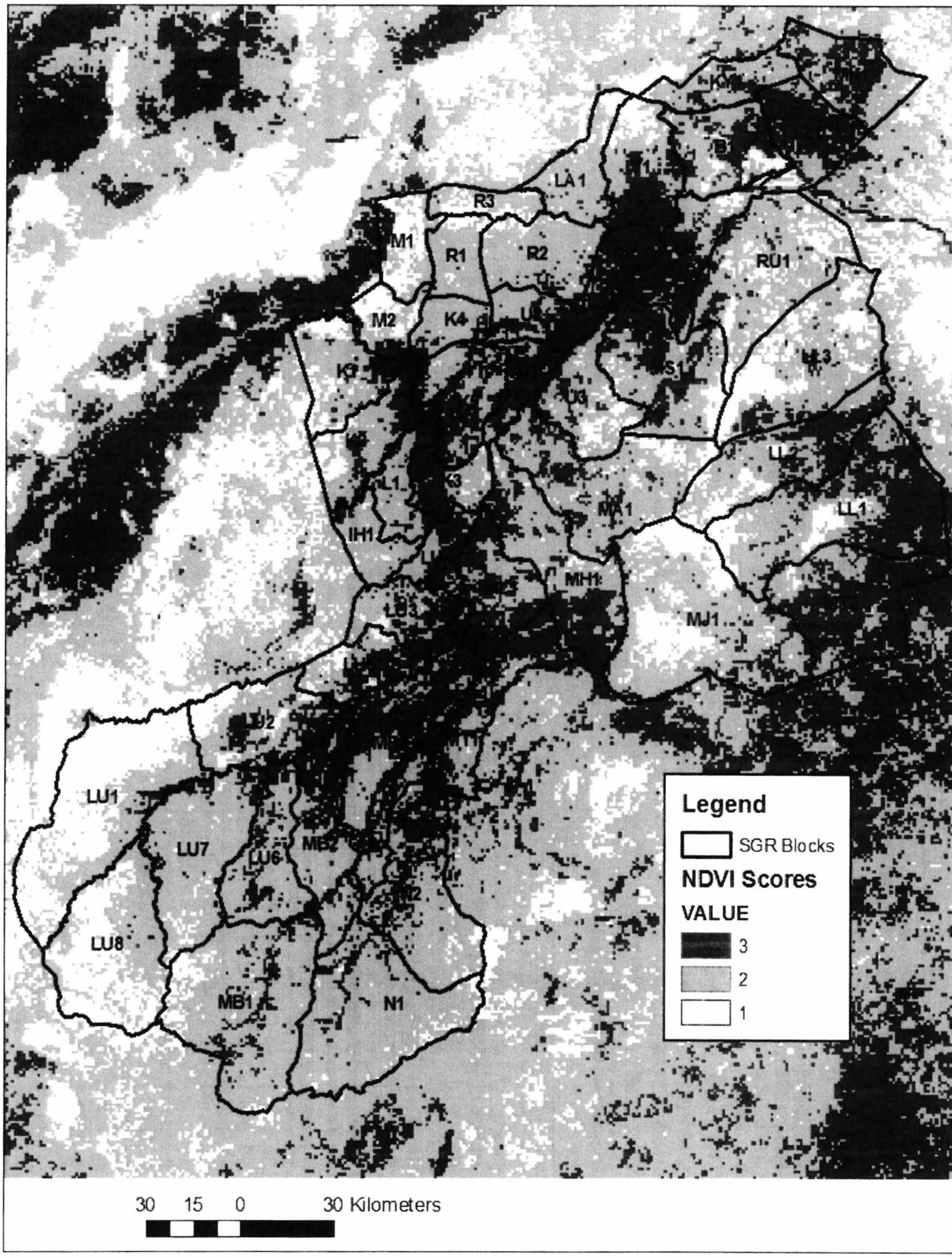


Table 4.1: Lion numbers for each block and current and past quotas and hunting off-take.

Block	Area (km^2) & difference to 2003	Lion Nos. *Caro	Lion Nos. #IGF	Lion Nos. NDVI	1988-1997* Quota Off-take	1997-2008 Quota Off-take
B1	841	-	119	57	Photographic	Photographic
IH1	425	47	-	29	1.0 0.5	2.2 0.6
K1	399 **-381**	86	39	30	4.0 0.0	4.7 2.3
K2	683 **-68**	83	76	54	4.0 0.0	3.9 1.5
K3	455	50	27	38	5.0 0.0	3.4 1.1
K4	379	41	22	28	3.9 0.5	4.9 1.3
K5	592 **-215**	89	35	43	6.1 0.8	4.4 1.3
KY1	533	59	76	43	-	Photographic
L1	464	51	27	38	5.0 0.2	4.5 2.1
LA1	548 **-67**	68	65	44	4.0 0.7	2.3 0.8
LL1	2171 **+11**	238	201	172	4.0 1.7	4.6 2.5
LL2	1272 **+12**	139	205	97	4.0 1.9	4.6 3.1
LL3	1702	186	201	119	5.0 1.5	4.0 2.6
LU1	2443 **+243**	-	139	149	-	3.8 1.4
LU2	1156 **+59**	121	102	90	2.1 1.3	3.0 1.3
LU3	613	67	54	50	2.0 0.1	3.2 0.8
LU4	373	-	44	28	-	3.1 1.7
LU5	510 **-53**	62	30	37	4.0 0.3	2.6 0.7
LU6	883	97	78	58	3.0 2.5	3.8 1.6
LU7	1460	160	129	108	1.9 1.9	3.3 1.3
LU8	1628	179	143	103	2.0 1.1	3.3 1.2
M1	432 **-94**	58	31	32	4.0 0.2	3.0 0.1
M2	409	45	47	31	4.0 0.1	4.1 0.2
MA1	1684	184	199	122	4.0 0.6	4.2 1.2
MB1	2157	237	190	152	3.1 2.4	4.3 2.3
MB2	1054 **+10**	115	124	80	3.0 2.0	4.3 2.3
MB3	1686	185	198	148	2.0 1.5	1.8 0.5
MH1	1366	150	161	96	2.0 1.1	1.3 0.6
MJ1	1935 **-537**	272	228	135	1.9 1.1	1.3 0.5
MK1	812	89	48	69	6.1 1.4	4.9 2.8

Block	Area (km^2) & difference to 2003	Lion Nos. *Caro	Lion Nos. #IGF	Lion Nos. NDVI	1988-1997* Quota Off-take	1997-2008 Quota Off-take
ML1	792	87	70	73	2.0 1.0	2.0 0.7
MS1	1342	147	79	101	5.0 1.6	4.9 3.4
MT1	872 **+27**	93	77	70	2.0 1.0	1.3 0.8
MT2	2018 **+565**	160	237	172	4.0 2.1	4.6 2.4
N1	1800 **-112**	210	159	136	2.9 1.7	4.2 1.6
N2	1032 **-405**	158	91	76	2.1 1.3	2.0 0.6
R1	454	50	40	30	4.0 0.4	4.0 1.8
R2	687 **-192**	97	40	51	4.0 0.3	4.0 1.4
R3	378 **+49**	36	39	28	3.0 0.1	2.2 0.6
R4	581 **+197**	42	68	48	4.0 0.7	3.8 1.9
RU1	1786 **+95**	186	201	129	5.0 1.5	4.9 3.3
U1	589 **+221**	40	35	53	4.0 0.1	3.2 0.9
U2	519	57	31	36	4.0 0.3	2.9 1.6
U3	776	85	91	58	4.0 0.2	4.7 0.7
U4	783	86	92	69	5.0 1.7	4.0 2.9
Y1	863	95	51	68	5.0 0.7	Photographic
Z1	664 **-95**	-	108	65	Photographic	Photographic

- **Lion Nos. *Caro** from Caro *et al.*(2009) and is derived by multiplying the block area (2003 area data used) by a lion density of 0.11. Is also source of 1988-97* quota and off-take data.
- **Lion Nos. #IGF** from IGF report (Mesochina *et al.*, 2010) on the conservation status of lions in Tanzania and the numbers are derived from 'expert' interviews.
- **Lion Nos. Using NDVI** worked out by calculating the number of Category 1, 2, and 3 NDVI km grid squares per block, and multiplying Category 1 by 0.06, Category 2 by 0.07 and Category 3 by 0.09, all figures added up.

4.4.3 Modelling lion trophy hunting:

The results of the SimSimba simulations showed that larger starting populations were better able to sustain high trophy hunting off-takes and populations where males reached a reproductive maturity at a younger age (i.e. 2.5 years) were also more robust (see Table 4.2 and Appendix 9). In the model, three male lions over three years of age are hunted each year if available, which is equivalent to the current average lion hunting quota per block in SGR (see Figure 4.3).

Table 4.2: Results of the SimSimba model on trophy hunting under different scenarios

Starting Population Size	Male Reproductive Age	Populations Survival Percentage*	Description
43	2.5	10%	For 10% of replicates, trophy male numbers start low but recover to sustainable numbers.
43	5	0%	No more trophy males in 10 years and populations die out in 20 years.
107	2.5	99%	Trophy males average about 21 individuals in sustainable populations.
107	5	80%	In populations that do not go extinct, average number of trophy males is 34.
171	2.5	100%	Trophy males decrease from an average of 31 individuals to 21 individuals, but populations survive.
171	5	100%	Hunting in this scenario appears to be the most sustainable; average of 33 trophy males.

- Populations survival percentage* represents the number of populations that survived the 50 simulation runs.

4.4.4 Suggested Quota:

The suggested population figures from Table 4.1 have been used to suggest a quota for each block (Table 4.3); whereby the population figures are multiplied by 0.21 (the average proportion of adult males in SGR; see Chapter 2, Table 2.2) and then multiplied by 0.1 to suggest a quota that is ten percent of the adult male population; as hunting less than ten percent of the adult male population appears sustainable (Chardonnet, 2002; Packer *et al.*, 2010). Table 4.3 also shows the suggested quota of only hunting 1 male 1000 km^{-2}, which were lower than the population based quotas. Based on only hunting 1 lion 1000 km^{-2}, 18 blocks would have a quota of a lion every other year, while 13 blocks would have a quota of one lion a year, and 12 blocks would get two lions per year.

Table 4.3: Suggested quota for each block of SGR.

Block	Suggested Quota				Average	2008
	1 : 1000	*Caro	#IGF	NDVI	Quota*	Quota
IH1	0.5	1.0		0.6	1	2
K1	0.5	1.8	0.8	0.6	1	2
K2	1	1.7	1.6	1.1	1	1
K3	0.5	1.1	0.6	0.8	1	4
K4	0.5	0.9	0.5	0.6	1	5
K5	0.5	1.9	0.7	0.9	1	2
L1	0.5	1.1	0.6	0.8	1	5
LA1	0.5	1.4	1.4	0.9	1	3
LL1	2	5.0	4.2	3.6	4	4
LL2	1	2.9	4.3	2.0	3	4
LL3	2	3.9	4.2	2.5	3	4
LU1	2		2.9	3.1	3	4
LU2	1	2.5	2.1	1.9	2	3
LU3	0.5	1.4	1.1	1.1	1	3
LU4	0.5		0.9	0.6	1	3
LU5	0.5	1.3	0.6	0.8	1	2
LU6	1	2.0	1.6	1.2	2	4
LU7	2	3.4	2.7	2.3	3	4
LU8	2	3.8	3.0	2.2	3	4
M1	0.5	1.2	0.7	0.7	1	3
M2	0.5	0.9	1.0	0.7	1	4
MA1	2	3.9	4.2	2.6	3	4
MB1	2	5.0	4.0	3.2	4	5
MB2	1	2.4	2.6	1.7	2	5
MB3	2	3.9	4.2	3.1	4	2
MH1	1	3.2	3.4	2.0	3	1
MJ1	2	5.7	4.8	2.8	4	1
MK1	1	1.9	1.0	1.4	2	4
ML1	1	1.8	1.5	1.5	2	2
MS1	1	3.1	1.7	2.1	2	5
MT1	1	2.0	1.6	1.5	2	1
MT2	2	3.4	5.0	3.6	4	4
N1	2	4.4	3.3	2.9	3	4
N2	1	3.3	1.9	1.6	2	2
R1	0.5	1.1	0.8	0.6	1	4
R2	0.5	2.0	0.8	1.1	1	3
R3	0.5	0.8	0.8	0.6	1	3
R4	0.5	0.9	1.4	1.0	1	3
RU1	2	3.9	4.2	2.7	3	5
U1	0.5	0.8	0.7	1.1	1	2
U2	0.5	1.2	0.7	0.8	1	2
U3	1	1.8	1.9	1.2	2	4
U4	1	1.8	1.9	1.4	2	4
Average ± SD	1.0±0.6	2.4±1.3	2.1±1.4	1.6±0.9	2.0±1.2	3.3±1.2

The **1 : 1000 column** shows the quota based on one lion per 1000km^2, numbers below one have been rounded to 0.5 or 1 (e.g. a block of 378km^2 would have a quota of 0.38 lions, which has been rounded up to 0.5 lions). **Average Quota*** is the average of three columns (*Caro, #IGF, NDVI) rounded to a whole number.

The average annual quota per block ranges from one to four lions, with 19 blocks having a quota of one lion, ten blocks with two lions, nine blocks with three lions, and five blocks with four lions. The actual quota from 2008 is presented in the last column of Table 4.3 for comparison with the suggested quotas, and it can be seen based on comparison with the one lion 1000km^{-2}, the quota would have to be reduced for every block. However, if comparing to the averaged quota; five blocks would stay the same, 34 would have to be decreased, but four blocks could be increased. If the average off-takes in 1997-2008 (Table 4.1) are compared to the suggested average quota, 32 blocks would have an off-take that is within quota, but 11 are above the quota. However, based on the one lion $1000km^{-2}$ suggested quota, 14 blocks would currently be within quota, but the rest would have to reduce their off-take.

4.5 DISCUSSION

Areas with lower NDVI scores were shown to have increased lion density. NDVI scores were divided into three categories. The three NDVI categories were used to map suitable lion areas in SGR (Figure 4.7) and it can be seen that areas with the lower NDVI scores tended to follow the major water courses in the reserve (see Figure 4.2 for map of rivers). The NDVI scores, along with data on lion trophy hunting off-take have been used to set a lion quota for SGR, and are discussed in detail in the following sections. Several authors have suggested that the lion quota in SGR is too high (Creel & Creel, 1997; Caro *et al.*, 2009), but do not suggest what it should be reduced to. A quota for lions for each block of SGR has been suggested, and overall this would result in a decreased lion quota for the reserve. The method used to suggest the quota is transparent and straightforward, which should allow for its widespread application.

4.5.1 Lion hunting off-take:

The trophy hunting of lions peaked in 1998 and has fallen by some 50% since then (Figure 4.3). Economic liberalisation at the end of the 1980s led to a flood of investment in the wildlife-based tourism sector in the 1990s; tourism revenue grew at over ten percent annually for a decade (Nelson *et al.*, 2007). This is reflected in lion trophy hunting in SGR; in 1988, 23 lions were shot in SGR, and by 1998 115 lions were shot in SGR (Baldus, 2004). Yet over the last decade lion trophy hunting has decreased by some 50% in SGR to 53 lions hunted in 2008. This would suggest that either there is less demand for lion trophies, fewer visitors coming to Tanzania to hunt lions, hunting companies are showing restraint and hunting less lions, or the lions cannot easily be found. Over the last two decades the lion quota has remained relatively constant (Figure 4.3) and the numbers of tourists visiting SGR for hunting safaris have increased from 99 in 1988 to 479 in 2003 (Baldus & Cauldwell, 2004). Furthermore the number of tourists visiting Tanzania to go on 21 day hunting safaris increased by some 40% in 2004 and has remained at these high levels since (Packer *et al.*, 2010). The demand for lion trophies and number of tourists visiting Tanzania to hunt, it would seem, has increased over the last two decades.

Hunting companies invest enormous effort locating lions. Typically four to five baits are put up in different locations in a hunting block prior to the arrival of the tourist hunter. If any of the baits are taken by lion, the area is re-baited and a hide constructed for the tourist hunter to shoot a lion. Male lions are especially susceptible to baiting since they are frequent scavengers (Schaller 1972). Therefore, hunting off-take levels should be a good guide as to the health of the lion population in SGR. Excessive hunting in the late 1990s has led to a decrease in the lion population of SGR, and the lion quota should be reduced to one lion per 1000km^2 (see Figure 4.5). This would mean that a block of 2000km^2 would get a quota of two lions per year and a block of 500km^2 would get a quota of one lion every other year.

The reaction from the various hunting companies to suggestions of a reduced quota has by and large been negative; their objections have focused on three points, which are discussed in detail in the following paragraphs: i) the quota should not be reduced, it is rarely met; ii) certain areas have higher densities of lions, and therefore these areas should be allowed to continue to harvest at higher levels; iii) the reduction in off-take has been a result of self-regulation.

Creel & Creel (1997) examined lion trophy hunting in the early 1990s and noted that the "current off-take is sustainable, but current quotas are probably too high." However, the off-takes of the early 1990s were very much lower than in the 2000s (as shown in last two columns of Table 4.1). Baldus (2004) questions the figures used to arrive at population estimates by the Creels, and concludes "in any case the quota is not utilized, therefore it is rather hypothetical whether it is too high or not." This is true, on average only ~40 % of the annual quota is met. The hunting companies argue that they need the high quotas to sell the *opportunity* to hunt to tourists, and that they do not expect to fill the quota. This is true of many companies, but there are companies that have a quota of four lions, a block of 800km^2, and shoot all four lions on their quota. The challenge has always been how to regulate the companies that over harvest their blocks. A reduction of the lion quota to one 1000km^{-2} would reduce the quota from 499 for the whole of Tanzania (as it was in 2008) to 230, but this would still be higher than the 162 lions hunted in 2008 in Tanzania. What it would mean is that the spread of hunting would be more even (i.e. you would not have areas of over harvesting).

Certain areas have higher densities of lions, and therefore these areas should be allowed to continue to harvest at higher levels; there are blocks harvesting at two or three lions per 1000km^2 that have not shown a reduction in off-take over time (the point marked HO in Figure 4.5). While this may certainly be true, there have been almost no studies from hunting areas. This issue has been addressed here by trying to divide the SGR into areas with differing lion densities based on NDVI scores (Figure 4.7), but this should be validated with independent research confirming that they do indeed have higher densities, as all the lion population data used here is from a 550km^2 area in northern SGR. Conversely, it could be argued that these high levels of off-take have been maintained by increased hunting effort or illegal practices (e.g. hunting at night with spotlight) masking a reduction in the overall population and a sudden decrease in off-take is imminent.

These reductions in off-take have been a result of self-regulation; that is, hunters are showing restraint and only hunting older animals or good trophy animals. In fact, "many professional hunters in the SGR say that they voluntarily do not shoot their full quota, as it is too high for their particular area" (Baldus, 2004). While this may be true of several companies, it does not explain why the greatest decrease in lion hunting is seen in areas with the highest hunting pressures. Nor does it explain the general perception among government officials and professional hunters in SGR that there are fewer lions now (see Chapter 6) nor the fact that under-aged lions are still being shot in Tanzania in 2008 (see Packer *et al.*, 2009).

4.5.2 Lion model:

Tanzania's management authority, the WD, recognises that it must apply a more scientific approach to the setting of hunting quotas (Severre, 1996) and monitoring wildlife populations in SGR is both costly and difficult (Baldus & Cauldwell, 2004). Models offer the opportunity to simulate harvests on populations and explore the impacts of different harvest strategies on populations or account for the impact different breeding systems have on harvests (Caro *et al.*, 2009). The modelling can be done relatively cheaply and is particularly important because much of Tanzania's current game hunting policy was developed in the early 1970s, where scientists and wildlife managers believed that females were solely responsible for rearing offspring (Caro *et al.*, 2009). Behavioural ecologists now know that male care is important in many species (Clutton-Brock, 1991). This is clearly demonstrated in lions, where infanticide by males was first demonstrated by Bertram (1975), and adult male lions have an important role in parental care in keeping other unrelated males out of their territories, therefore preventing infanticide of their offspring (Packer, 2000).

In the model used here the off-take rates are set at the average block quota level of three lions per block per year (this is almost double the current off-take average of 1.38) and illustrate that larger populations are, not surprisingly, better able to cope with these high off-takes (Table 4.2). Based on the model, populations of 43 individuals subjected to an attempted annual off-take of three adult males over three years of age would soon go extinct. Some 14 blocks have lion populations comparable to 43 individuals (Table 4.1) most with a quota above three lions annually, some above four lions. Clearly, real life populations would not go extinct; trophy hunting would become uneconomical long before that point in these blocks. Of greater interest was the attempt to model differing ages at which males begin breeding of two and half years as in Serengeti or five years as in Kruger. The Serengeti is a 'plains-like' ecosystem, while Kruger is a woodland ecosystem (Funston *et al.*, 2003); SGR is comparable to Kruger system (Creel & Creel, 2002). Populations where males begin breeding at five years were more susceptible to overharvesting than those that began at two and half years (Table 4.2). Funston *et al.* (2003) note that the minimum age of first breeding in males in Kruger was five years and the average male residence in a pride is 17 months; this would suggest that if an aged based approach (as in Whitman *et al.*, 2004) to harvesting in systems similar to Kruger was adopted, only lions above six/seven years should be hunted.

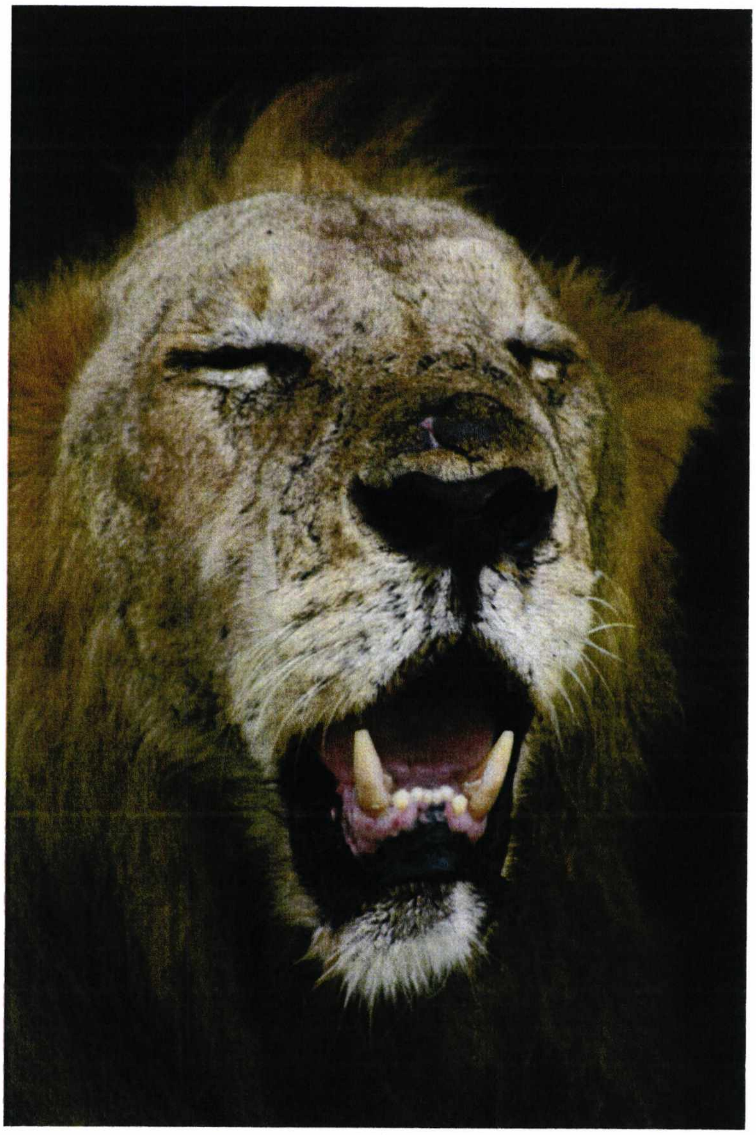
4.5.3 Suggested Quota:

The establishment of quotas are often based on guesswork because of the logistical difficulties and the lack of resources to conduct accurate game counts (Baker, 1997). As stated earlier, for lions the removal of young males may have significant population effects even where quotas appear conservative (Whitman *et al*,. 2004). Table 4.3 suggests a quota for lions for each hunting block of SGR using different population estimates, which is based on harvesting less than ten percent of the adult male population, where adult males make up 21 % of the total population. What is abundantly clear is that the current quota would have to come down for SGR. The debate would be how much to reduce the individual quotas of each block. A transparent and straightforward means to setting the lion quota for SGR has been attempted here. Nonetheless, there may be questions surrounding the validity of the different population estimates presented in Table 4.1 that were used to work out the quotas, and there may be debate surrounding the lion density figures used for the different NDVI scores. Conservative figures for lion densities have been used to work out the lion numbers across SGR based on NDVI scores (Table 4.1) because lion density data for SGR was only available from northern SGR and this area tends to support higher densities of game than other areas of SGR (Creel & Creel, 1997). This meant that the lowest possible density value was used for each of the NDVI scores in Figure 4.6, that is areas with a NDVI score of 3 were assigned a density value of 0.09, NDVI score 2 a density of 0.07 and 0.06 for NDVI 1 (and not the density figures recorded in northern SGR of 0.12, 0.16, and 0.21 for NDVI scores 1, 2, and 3 respectively). Nonetheless, several different quota figures are presented in Table 4.3 for each hunting block of SGR as well as the current quota for the blocks for comparison.

The current (2008) lion quota for a block in SGR ranges from one to five, with an average of a quota 3.3 lions per block. The average annual suggested quota per block ranges from one to four lions, with 19 blocks having a quota of one lion, ten blocks with two lions, nine blocks with three lions, and five blocks with four lions (average quota of 2.0 lions per block). It can be seen based on comparison between the actual and suggested quotas that with the one lion 1000km^{-2} suggested quota, the quota would have to be reduced for every block. However, the other suggested quotas also show that a reduction is necessary, but to a lesser degree. The current off-take in some of the blocks, but not all, would have to be decreased to be within the suggested quotas.

Tanzania supports a successful and expanding trophy hunting industry (Lindsey *et al.*, 2007a), yet there is increasing evidence of over hunting of lions (Packer *et al.*, 2009; Packer *et al.*, 2010), a key species to the trophy hunting industry. Suggestions of making the lion quota more sustainable have been made here, but it is expected that such suggestions will be resisted by the hunting industry in Tanzania. The hunting industry in Tanzania is well established, influential, and paranoid that any suggestions of a reduction to the hunting quota is a small but irreversible step to banning trophy hunting in Tanzania (as happened in Kenya in the 1970s and Botswana recently). So it should be made absolutely clear that there is no suggestion of a ban of lion trophy hunting, merely a plea to reduce quotas to more sustainable levels.

5 Lion Trophy Hunting: A Question of Tenure



5.1 ABSTRACT

Tanzania is vital for lion conservation, supporting between half and a quarter of the remaining free-ranging lions in the world and is the most important destination for sport hunting of wild lion trophies. The organised hunting of wild animals for sport or trophies by tourists can have notable conservation benefits. The Selous Game Reserve (SGR) has developed a considerable reputation as a trophy hunting destination. In Tanzania, hunting companies lease one or several hunting blocks from the government, and the company is allocated a species-specific quota for each block for the hunting season. This chapter investigates what the impact of length of block tenure has on trophy hunting of lions in SGR. The blocks in SGR with the highest lion hunting pressure (i.e. the most lions shot per 1000 km^2 per year) were also the blocks that experienced the steepest declines in trophy off-take from 1996 to 2008 and tended to be under short-term tenure. These high pressure hunting blocks, however, brought in the greatest amount of revenue for the government per km^2 of area. This paper supports the move towards a competitive market-based approach for block allocation with a long-term tenure, and away from the current over reliance on the pay-as-you-use trophy fee per animal shot approach.

5.2 INTRODUCTION

Biodiversity conservation outcomes are closely related to the rules and institutions that govern the use of natural resources (Smith *et al.*, 2003; Smith & Walpole, 2005). Since the 20th century the use of statutory protected areas has been a cornerstone of biodiversity conservation strategies in most countries of the world (Gallo *et al.*, 2008; Adams, 2004). However, in developing countries mean operating budgets of these protected areas cover only 30% of their budgetary needs (James *et al.*, 1999) and there seems to be a reluctance for society to cover the costs of conserving biodiversity in reserves (James *et al.*, 2001; Pearce, 2007). There is increasing acknowledgement of the importance of the private sector in funding and managing conservation strategies in the 21st century (Langholzi & Lassoie, 2001; Mitchell, 2005).

Creating local incentives for conservation through more secure resource tenure is central to conservation outcomes in sub-Saharan Africa, and are therefore centrally concerned with governance dynamics and institutional reform processes, such as decentralization of property rights, and how best to achieve such reform (Nelson, 2008). Within the sub-Saharan context, Tanzania is hugely important for wildlife conservation, for example Tanzania supports between half and a quarter of the remaining free-ranging lions in the world (Bauer & Merve, 2004; Chardonnet, 2002). Nonetheless, a review of protected area tenure arrangements in Tanzania noted that all land is ultimately owned by the state, and may only be leased by companies/individuals for set periods of time, no longer than 99 years, and an almost bewildering range of possible collaborations between the state, private and communal bodies is possible (Carter *et al.*, 2008).

In southern and eastern Africa, the organised hunting of wild animals for sport or trophies by tourists can have considerable conservation benefits (Lewis & Jackson, 2005; Lindsey *et al.*, 2007a; Booth & Cumming, 2009). For example, areas set aside for the hunting of big game animals protect habitats that might otherwise be turned over to agriculture (Loveridge *et al.*, 2006), protect populations of large mammals (Caro *et al.*, 1998; Rohwer, 2009), and can benefit local people (Jones, 2009). However, exploitation of a species always has the potential to reduce populations to levels where the hunting is no longer profitable or in extreme cases cause population extinctions (Adams, 2004; Leader-Williams, 2009).

Tourist hunting in Tanzania has developed over a long period and is now a well established industry and a principle source of income for vast areas of the country (Baldus &

Cauldwell, 2004). Tanzania has long been recognised for its high quality trophy hunting opportunities (Leader-Williams *et al.*, 1996). The industry has demonstrated an impressive growth in recent years and is an important source of foreign exchange to Tanzania (Baldus, 2006). In addition, Tanzania is the most important destination for sport hunting of lions (http://www.unep-wcmc.org/citestrade/), exporting an average of 243 wild lion trophies per year between 1996 and 2006, compared to 96/yr from Zimbabwe, and 55/yr from Zambia, while no other country exported more than 20/yr (Packer *et al.*, 2009).

Due to Tanzania's importance to wildlife conservation, 24% of the total land surface is under wildlife protected status (MNRT, 2007). This protected area network is made up of National Parks (NP), Game Reserves (GR), Game Control Areas (GCA), and Wildlife Management Areas (WMA). No human settlement is allowed in NPs and GRs (17% of the total land area), while humans coexist with wildlife in all other protected areas (i.e. GCA, WMA). Tanzania has set aside some 300,000 km^2 for trophy hunting (also referred to as sport or tourist hunting), and is permitted in any PA other than the NPs and the Ngorongoro Conservation Area. The Selous Game Reserve, unlike other GRs, has an area set aside for photographic tourism where trophy hunting is not permitted. Nonetheless, the Selous has developed a considerable reputation as a tourist hunting destination (Leader-Williams & Hutton, 2005) and is internationally designated as a World Heritage Site.

In Tanzania, hunting companies lease one or several hunting blocks which are segments of GRs, GCAs or Open Areas (see Figure 5.1 & 5.3), and the company is allocated a species-specific quota for each block for the hunting season (Caro *et al.*, 2009). A portion of this quota is then offered to clients by the hunting company, who stay at hunting camps for 1, 2 or 3 week periods (lions are only available on a 21day safari, and only males are hunted). Clients may fly between different hunting blocks leased by the same company in order to shoot different species only found in certain areas. However very little information is available on the industry and many aspects are shrouded in secrecy (Lindsey *et al.*, 2007a). In particular, many of the concessions are leased to local companies that do not have the capacity to market their hunting opportunities, thus leading to a system of subleasing mostly to foreign professional hunters without any residence status in Tanzania, and this has implications for revenue collection and long-term utilisation of the blocks (Baldus & Cauldwell, 2004). Because this hunting is subleased at low rates and much of the income generated never enters Tanzania, the Tanzania Revenue Authorities are unable to access much of the funds that should be due for taxation. Furthermore, as the blocks are sub-leased for short periods it has been suggested that this would encourage over-utilization of the blocks. This chapter seeks to investigate, for the first time, what the impact of length of block tenure has on lion trophy hunting in Selous Game Reserve.

5.3 METHODS

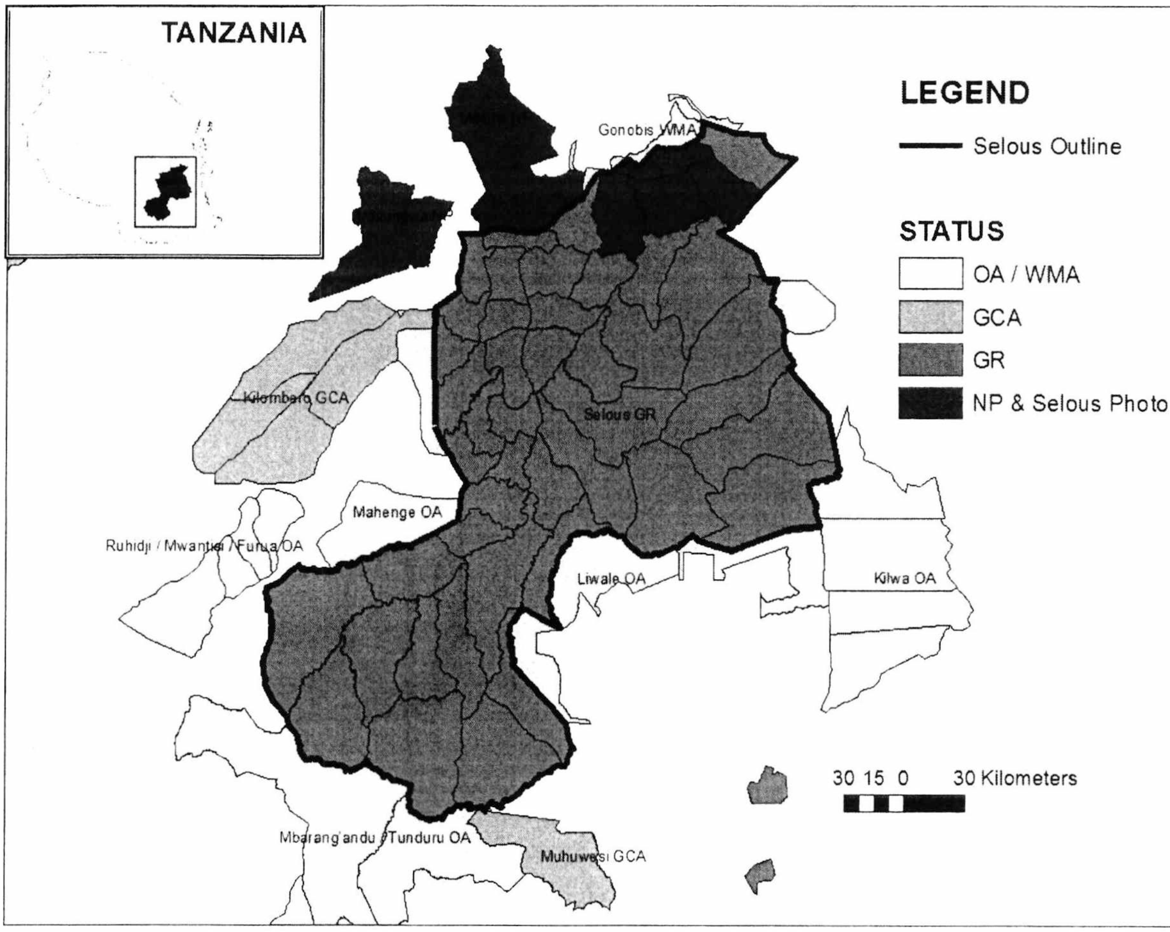
5.3.1 Study area:

Field work was carried out between June 2006 and August 2009. The Selous Game Reserve (7°17' - 10°15' S, 36°04' - 38°46' E) is divided into 47 blocks comprising 47,500 km^2 (see Figure 5.1 & 5.2). Four blocks (or six percent) of Selous Game Reserve (SGR) are set aside for photographic tourism (marked in dark grey as Selous Photo in Figure 5.1); the rest of SGR allows resource utilization in the form of trophy hunting (Caro *et al.*, 2009). The SGR comprises a mosaic of wooded savanna, miombo and *Combretum* thickets (see Creel & Creel, 2002 for details). Altitude ranges from 100 m asl in the north-east to 1200 m asl in the south west. Rainfall follows a similar east-west pattern, which ranges from 750 mm in the east to 1250 mm in the west, falling predominantly between December and May (IUCN, 1998). From Figure 5.1 it can be seen that that the SGR is surrounded by a network of different protected areas, namely: National Parks (NP), Game Control Areas (GCA), and Open Areas (OA) or Wildlife Management Areas (WMA).

5.3.2 Protected Areas around SGR:

The distinction between hunting blocks on GCAs, WMAs and OAs is not clear cut, (i.e. all allow for human settlement and wildlife to coexist, and hunting is only permitted under licence) but reflect when the blocks were established. GCAs are the oldest, and most were set-up prior to the early 1990s. The WMAs reflect Tanzania's attempt to introduce community-based management of wildlife in the late 1990s, with the idea that control of and benefits from wildlife would be decentralised to the communities living in the area. The re-designation of some WMAs as OAs and the designation of new hunting blocks in 2004/5 as OAs reflect both the central governments apparent reluctance to surrender power to the local communities and the preference of hunting companies to deal with one central authority (for a detailed discussion see Nelson *et al.*, 2007). In the Selous ecosystem there are 64 hunting blocks; 43 of which are within SGR, 7 are in areas surrounding SGR and have been hunted since the 1990s, while another 14 have more recently been designated and have only been hunted since 2002. For management purposes SGR is divided in eight sectors (see Figure 5.2).

Figure 5.1: SGR and bordering hunting blocks and national parks.



5.3.3 Block tenure and hunting fees:

Twenty hunting companies are listed as leasing blocks in SGR (see Figure 5.3), however, three of the main companies (Gerard Pasanisi, Barlette and TAWISA; covering half of SGR, or 22,126 km^2) are all controlled by one individual (Baldus & Cauldwell, 2004). Twenty six of the blocks are viewed as being under long-term tenure. That is these blocks have been under the same individuals since the early 1990s. Short-term blocks are those that have changed hands several times in the 1990s and 2000s, or have been sub-leased by Tanzanian nationals to various foreign professional hunters during this period (process described in detail in Baldus & Cauldwell, 2004). There are 17 short-term blocks.

Average government income per block is only available for blocks in SGR from 1996-2003 (listed in Baldus & Cauldwell, 2004); and during this period government income from hunting activities was heavily reliant on trophy fees (accounted for 59% of the income). The lion trophy fees account for almost ten percent of the overall trophy fees. Block leases in 2003 were only $7500 per block, and therefore only accounted for 11% of the government income. Block fees have subsequently increased to $12,000, and then $27,000 in 2008.

Figure 5.2: Sectors and blocks of SGR.

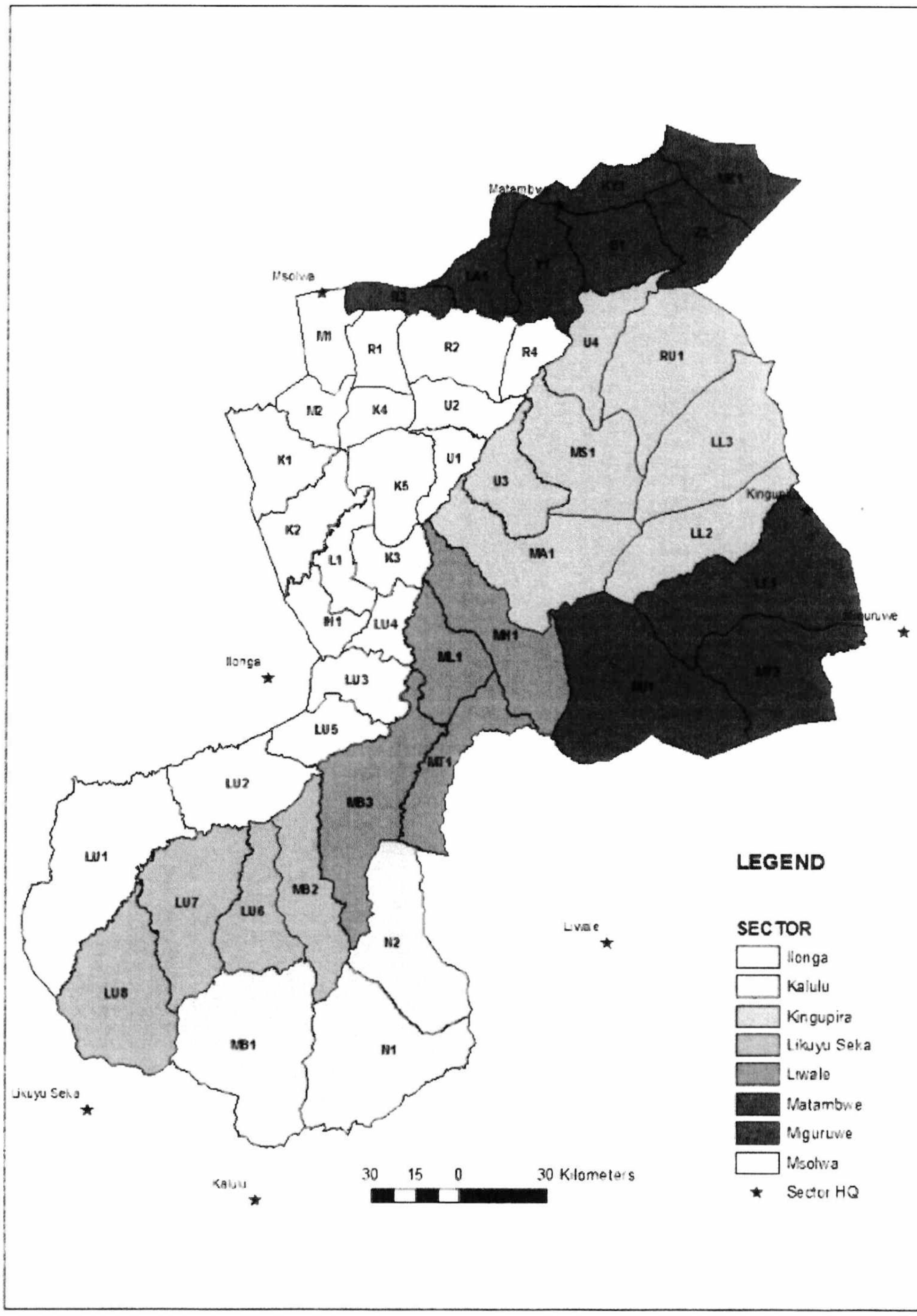
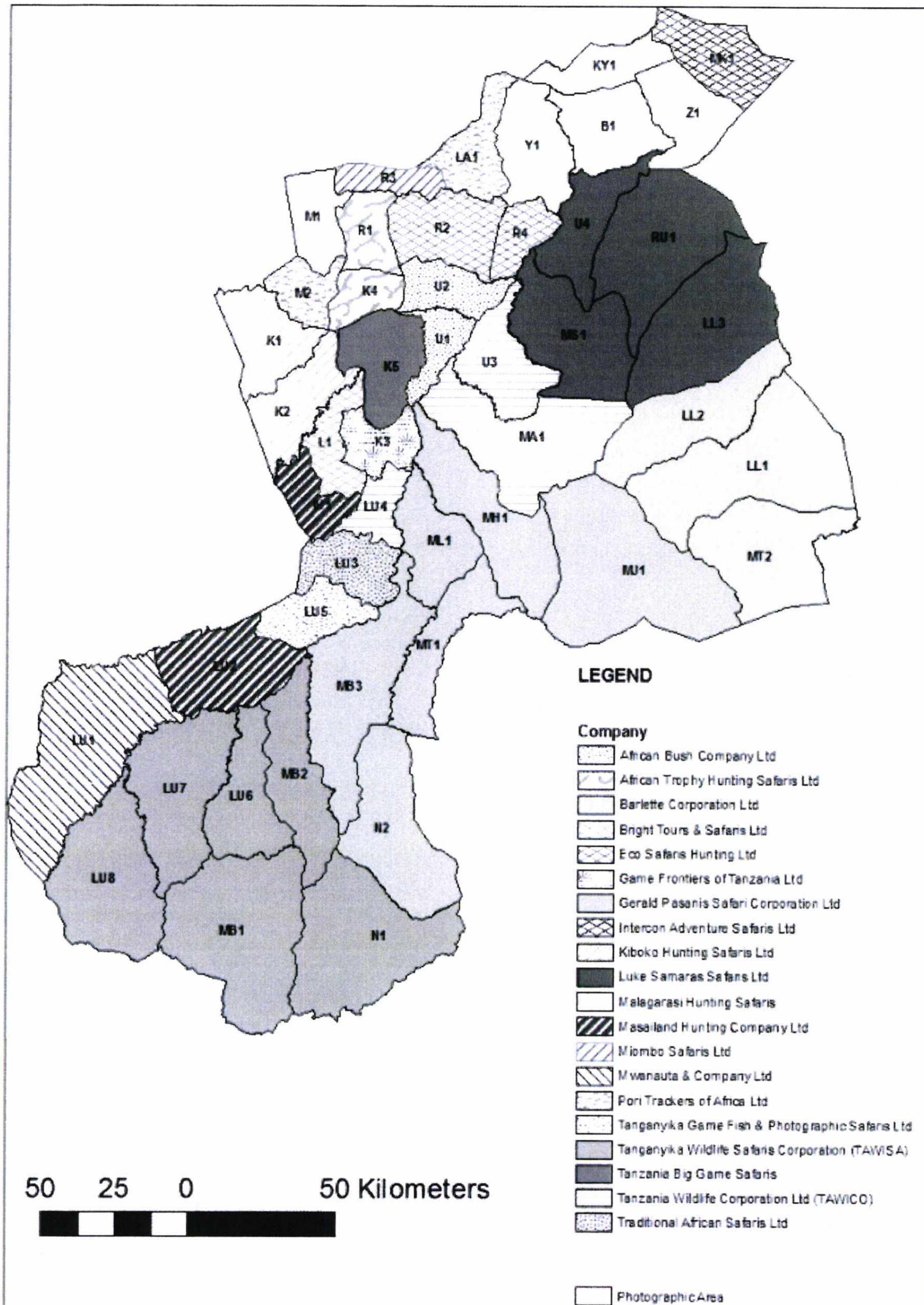


Figure 5.3: Hunting companies operating in SGR



5.3.4 Block data:

Digital boundary polygons files of the SGR blocks were obtained from the Selous Conservation Project (SCP) funded by the Organization for German Technical Cooperation (GTZ) and Tanzania Wildlife Research Institute (TAWIRI). The SCP data was from 2003, while the TAWIRI data was more up-to-date and reflected 2009 boundary data. Field visits to different sectors of SGR were carried out to investigate the accuracy of these layers. All spatial data was imported in ArcGIS version 9.3 (ESRI Inc., Redlands, CA) for analysis.

5.3.5 Lion hunting off-take data:

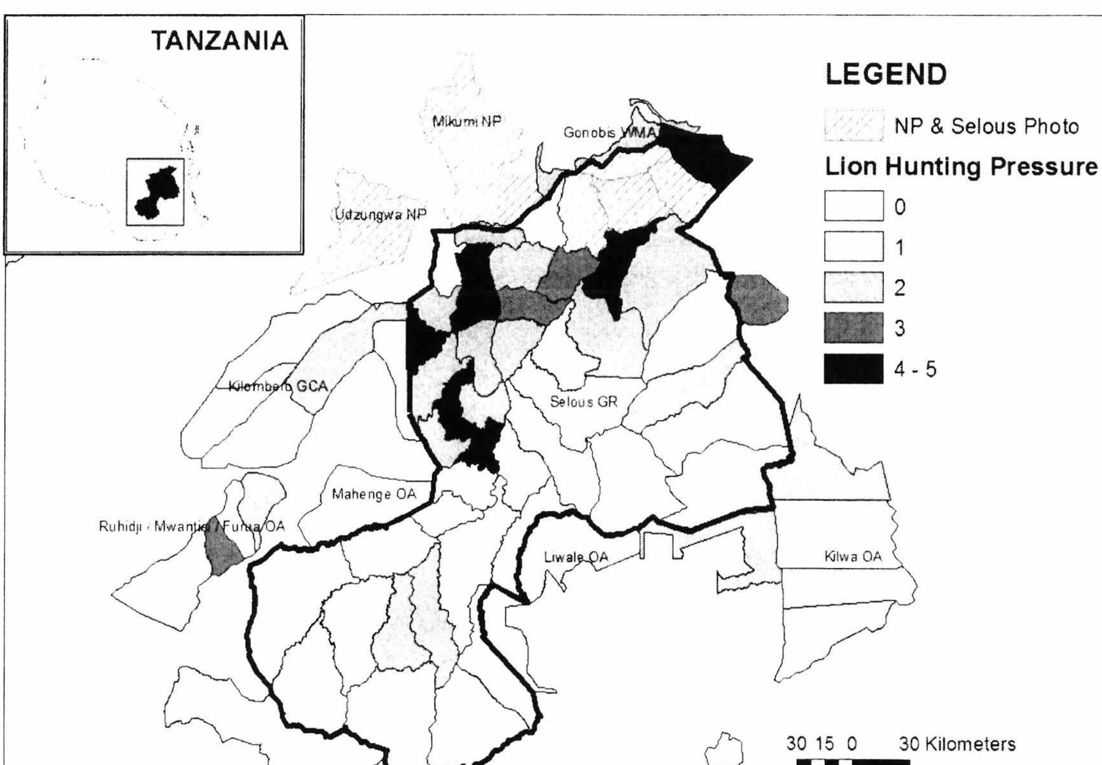
Data on trophy off-takes of lions in each hunting block of SGR were provided by the CITES office at the Wildlife Division Headquarters in Dar es Salaam. The off-take data were much more complete in SGR, as compared to the rest of Tanzania, due to the activities of the SCP and the Planning and Assessment for Wildlife Management (PAWM) project funded by USAid (Leader-Williams *et al.*, 1996; Baldus & Cauldwell 2004; Caro et al 2009). For each respective block, the hunting pressure is the average annual lion off-take per block per 1000 km^2 from 1996-2008. Furthermore, the "initial intensity of hunting" is the average annual off-take per 1000 km^2 in 1996-1999 per block. The regression coefficient for all block off-takes was then calculated starting in 1996 and ending in 2008. The "annual change" in trophy off-take is the regression coefficient times the initial intensity, and the "proportional annual change" in trophy off-take is this annual change divided by the initial intensity times a hundred.

5.4 RESULTS

5.4.1 Lion hunting pressure and hunting trends:

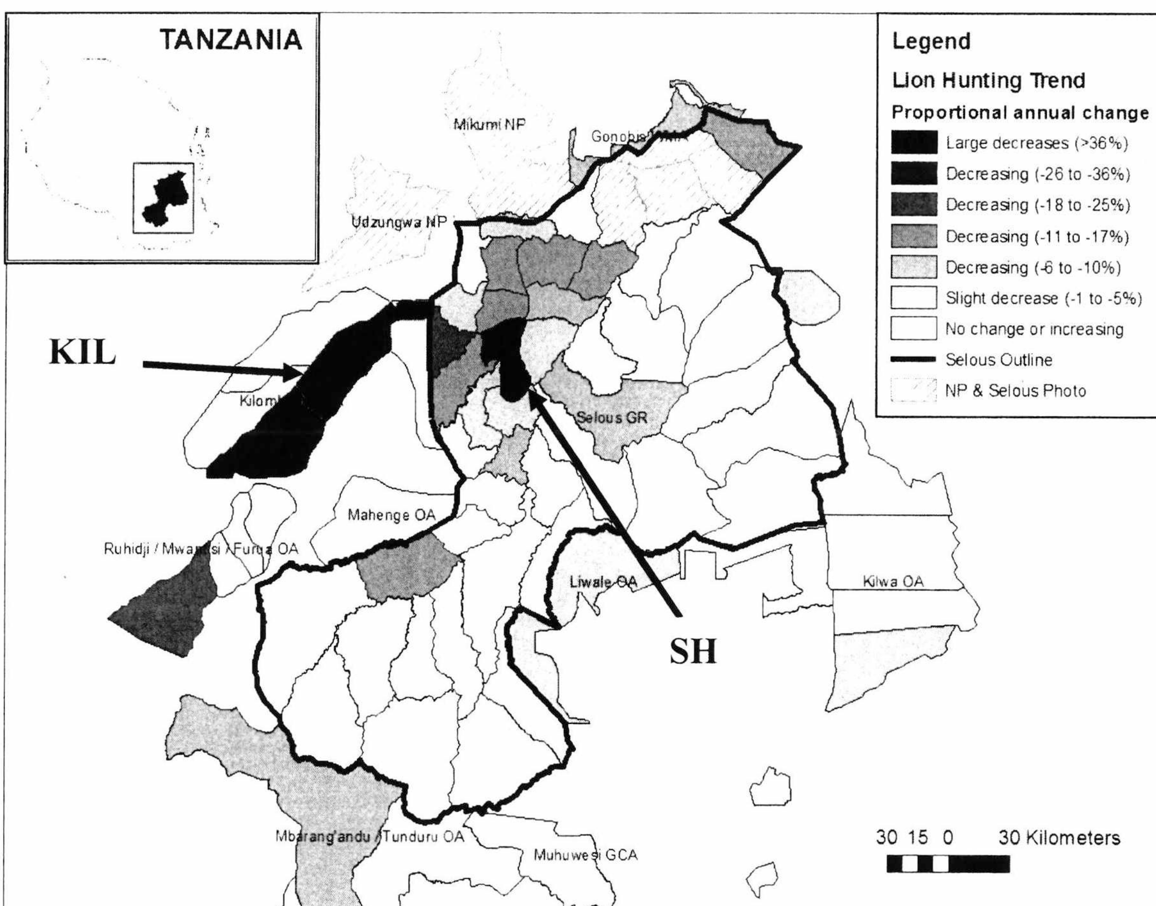
The lion hunting pressure (number of lions shot per 1000 km^2 per annum) was higher inside SGR, especially in the north western part of the reserve (see Figure 5.4); that is the Msolwa, Ilonga and Matambwe sectors (see Figure 5.2 and Table 5.1). The Sectors with the highest hunting pressures are also the same sectors that have seen the greatest reduction in lion trophy hunting between 1996-2008 (see Figure 5.5 and Table 5.1). Furthermore the blocks that had the highest hunting pressure are also the same blocks that experienced the greatest fall in lion off-take over the period 1996-2008 as seen in Figure 5.7. There was a significant negative correlation between number of lions shot per 1000 km^2 per block and annual change in lion hunting off-take (r_s = -.54, P < 0.01). Figure 5.5 also highlights the fact that some blocks outside the SGR, despite having relatively low lion hunting pressures, experience marked declines in off-take between 1996 and 2008. These blocks outside SGR are all on the western side of the reserve where the human population is the highest (see Appendix 10).

Figure 5.4: Lion hunting pressure in SGR and surrounding hunting blocks.



The two areas that experienced the greatest decline in lion trophy hunting (i.e. >36% decline) between 1996 and 2008 are discussed here in detail (marked KIL and SH on Figure 5.5). In the area marked SH (also on Figure 5.7) inside SGR, the company operating in the block stopped lion trophy hunting in the block in the early 2002 because they were concerned at the high levels of lion hunting in neighbouring blocks (Raul Ramoni, pers. comm.). It should be noted that since 2008, many of the blocks in this sector (Msolwa) have changed owners. The block labelled KIL are the Kilombero South blocks, where in the early 2000s the second largest lion trophy recorded was taken in this block (and an average of three lions shot annually), since then there has been increased conflict with pastoralists, with 22 lions poisoned in this area in 2005-2006 (Ryan Shallom, pers. comm.). Since 2006 no lions have been taken from the Kilombero South blocks.

Figure 5.5: Change in annual lion hunting (1996-2008) in SGR and surrounding blocks.



KIL = Kilombero South Blocks; SH = Owners stopped lion hunting in block from early 2000s.

5.4.2 Sectors within SGR and government income from trophy hunting:

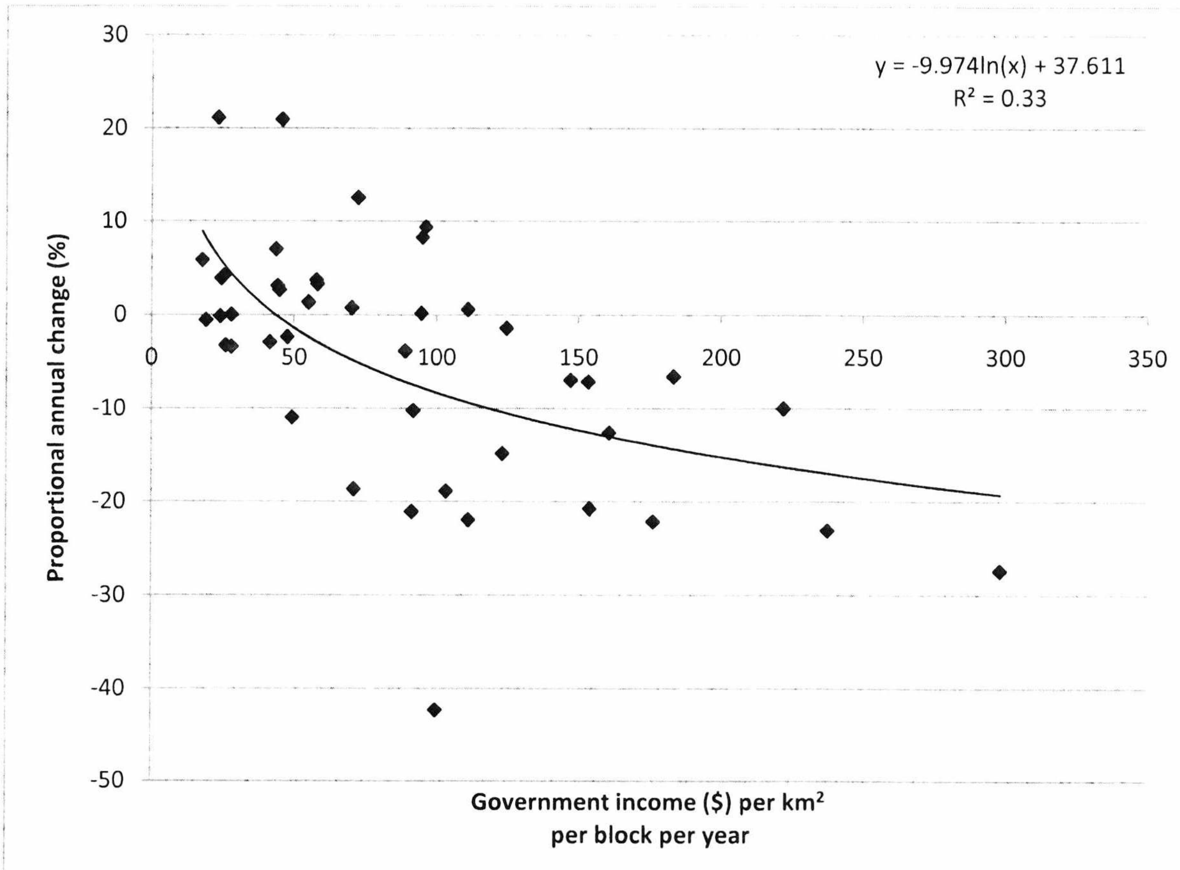
Table 5.1 highlights data by sector, namely, the number of blocks, the total area, the average hunting pressure, the rate of change in hunting off-take, and the average government income (\$ per km^2). There was a significant difference in the mean rank of the income per sector (Kruskal-Wallis; $H = 27.40$, 7 d.f., $P < 0.01$), proportional annual change in lion off-take per sector (Kruskal-Wallis; $H = 14.80$, 7 d.f., $P < 0.04$), and hunting pressure per sector (Kruskal-Wallis; $H = 14.97$, 7 d.f., $P < 0.04$). The sectors that had the highest lion hunting pressure, experienced the steepest declines in hunting off-take from 1996-2008, but provided the government with the greatest income per km^2 from 1996 to 2003. Spearman rank correlation showed that government income per km^2 per block of SGR was negatively correlated with the proportion of change in lion hunting off-take ($r_s = -.62$, $P < 0.01$) and is shown in Figure 5.6. That is blocks that experience the greatest reduction in lion off-take from 1996-2008 were the same blocks that generated the highest amount of income per km^2 per annum from 1996-2003 for the government.

Table 5.1: Data from within SGR by sector.

Sector	No. of Hunting Blocks	Total Area of Sector (km^2)	Average Lion Hunting Pressure*	Proportional Annual Change in Hunting$^+$	Average to Government Income (\$)*#
Ilonga	10	7521	2.25 ± 1.48	-6%	130.16 ± 82.50
Kalulu	3	4989	0.86 ± 0.19	0%	26.57 ± 1.36
Kingupira	7	9345	1.82 ± 0.97	0%	65.08 ± 20.42
Likuyu Seka	4	5025	1.36 ± 0.72	6%	44.85 ± 22.76
Liwale	4	4716	0.67 ± 0.28	3%	35.30 ± 17.32
Matambwe	3	1738	2.22 ± 1.53	-7%	134.09 ± 33.95
Miguruwe	3	6124	0.86 ± 0.43	1%	34.73 ± 13.56
Msolwa	9	4642	2.38 ± 1.14	-18%	135.27 ± 51.59
Total	43	44100	1.55 ± 0.70	-	75.75 ± 48.86

*** Mean ± Standard Deviation throughout.+Data based on 1996-2008. #Per km^2 from 1996-2003**

Figure 5.6: Proportional annual change in lion off-take (1996-2008) and average income per km^2 per hunting block (1996-2003).

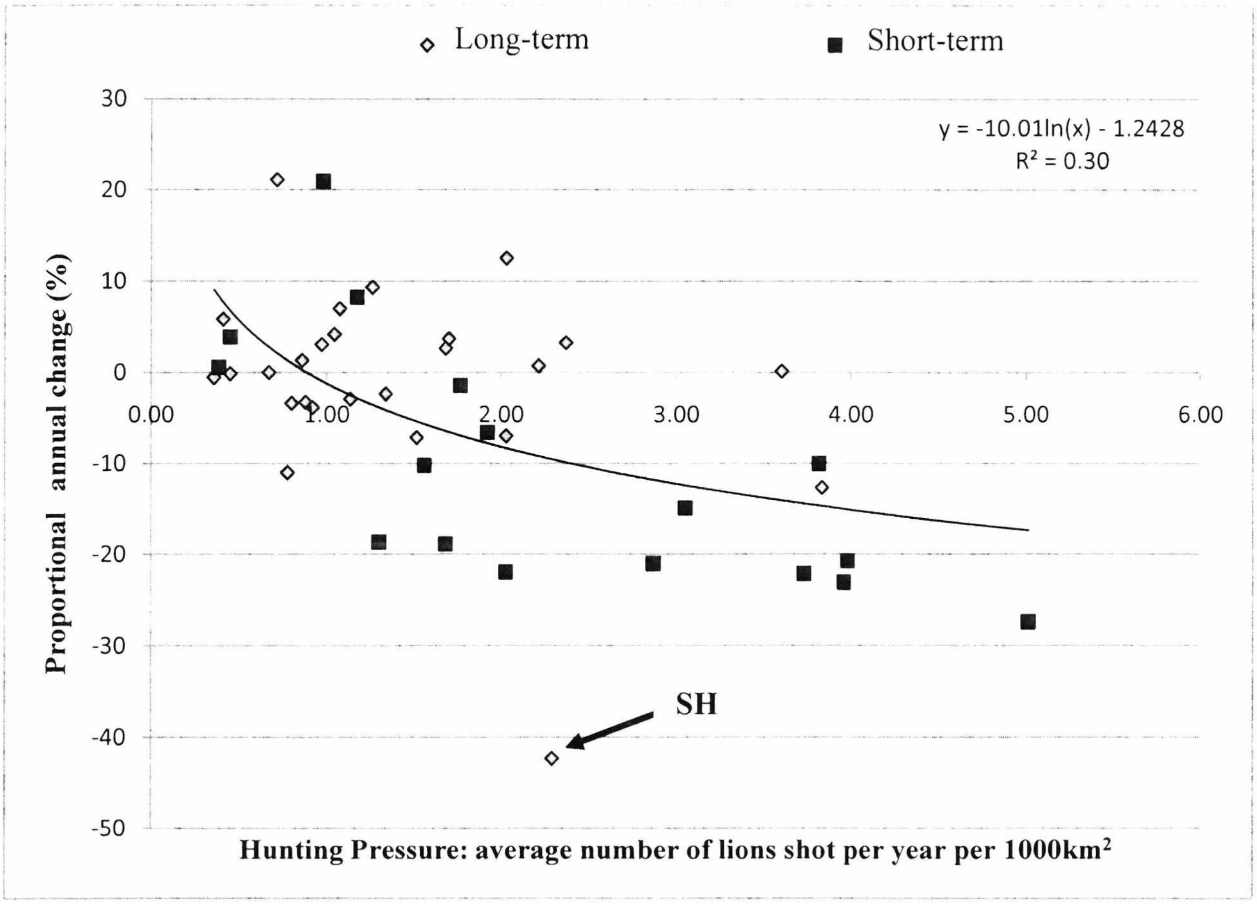


5.4.3 Block tenure, long-term versus short-term:

Blocks that have been leased by a company over the long-term have a lower hunting pressure (average 1.41 ± 0.90) and annual change in lion off-take between 1996-2008 (average -0.80 ± 10.99 %) than blocks that have only been leased over the short-term (average hunting pressure 2.33 ± 1.38; average annual change in off-take -10.76 ± 13.36%), and is highlighted in Figure 5.7 and the box plots in Figure 5.8 (which show the median values). The block that has been leased long-term and stopped lion hunting in the early 2000s is marked SH on Figure 5.7 and is included in all analysis. There is a highly significant negative correlation between hunting pressure and rate of annual change in lion hunting from

1996-2008 in the short-term blocks (r_s = -.79, P < 0.01), but no clear pattern in the long-term blocks (r_s = -.13, P = 0.53). Mann-Whitney test between short-term and long-term blocks shows a significant difference in the rate of annual change in lion hunting off-take from 1996-2008 (Z = 2.686, P < 0.01) and lion hunting pressure (Z = 2.261, P < 0.03). Long-term blocks also provided the government with less money (average per km^2 was \$62.20 ± 41.66) than short-term blocks (average per km^2 was \$133.17 ± 71.20). This difference in government income was significantly different between long-term and short-term blocks (Mann-Whitney; Z = 3.577, P < 0.01).

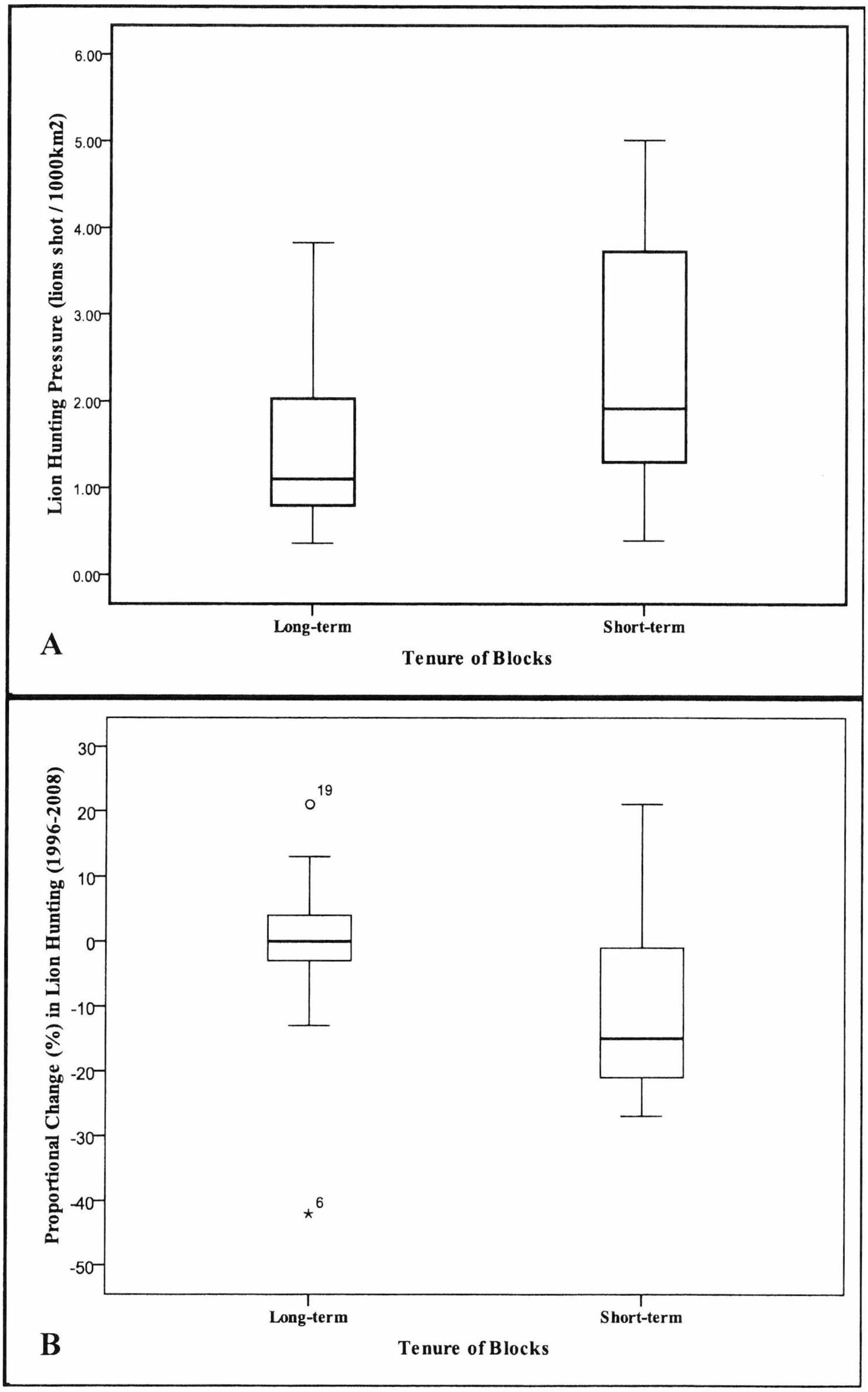
Figure 5.7: Long-term versus short-term tenure in SGR; proportional annual change (%) and hunting pressure.



SH = Stop Hunting

Figure 5.8: A) Lion hunting pressure, long-term versus short-term block tenure;

B) Proportional annual change in lion hunting off-take, long-term versus short-term tenure.



5.5 DISCUSSION

In SGR the greatest decrease in lion hunting off-take has been recorded in blocks with the highest hunting pressure. These blocks with the highest hunting pressure tended to be under short-term tenure that brought the government the most income. This short-termism is driving the over-hunting of lions, leading to declines in the lion population in these hunting blocks. There has been an increase in the number of tourist hunters visiting Tanzania over the last decade, but lion trophy hunting off-take in Tanzania has declined by up to 50% since 1998 (Packer *et al.*, 2010). The following sections will discuss in more detail this apparent contradiction, ending with recommendations on reforming the system.

5.5.1 Hunting pressure and hunting trends:

Retaliatory killing and habitat loss have been considered to be the primary threats to large felids across Africa (IUCN 2006, 2008), with overhunting a possible cause of concern especially in felid species, like the lion, where infanticide is common (Whitman *et al.*, 2004; Caro *et al.*, 2009). Within Selous ecosystem, in areas outside SGR, it is clear that decreases in lion populations as a result of conflict with people have occurred in the Kilombero South blocks (marked KIL on Figure 5.5). However, it is only recently that enough evidence has been gathered to suggest that trophy hunting of lions is having a negative impact on populations (Loveridge *et al.*, 2007; Kiffner *et al.*, 2009; Packer *et al.*, 2009; Packer *et al.*, 2010). Sport hunters are extremely efficient in locating their quarry, trophy hunting specifically targets adult males and male replacement has profound impacts on the reproduction of multiple females (Packer *et al.*, 2010).

Knowledge of the history of trophy hunting in Tanzania is important to understanding current trends in hunting off-takes. Trophy hunting was established as a viable industry during the colonial period in the 1930s. After independence, hunting was banned from 1973 to 1978, and then nationalised and re-started under control of the newly formed Tanzania Wildlife Corporation (TAWICO), a government parastatal. The 1980s were a difficult time in Tanzania because of the country's economic conditions brought on by its socialist policies and 1978-79 war with Uganda (Nelson *et al.*, 2007), resulting in rampant poaching as highlighted in large declines in elephant numbers in SGR (from over 100,000 elephants in 1976 to under 30,000 elephants in 1989; Seige & Baldus, 2000). Economic liberalisation in the 1990s led to a flood of investment into the wildlife-based tourism sector; tourism revenue grew at over ten percent annually for a decade (Nelson *et al.*, 2007). This is also highlighted in the number of lions shot in SGR during this period, which increased from 23 in 1988 to 115 in 1998 (Baldus, 2004), which reflects the re-emergence of tourist trophy hunting as an economically viable option in many wilderness areas of Tanzania. However, in terms of lion trophy hunting in Tanzania and SGR in particular, it peaked in the late 1990s, and has declined by up to 50% by the late 2000s (Packer *et al.*, 2009; Packer *et al.*, 2010). The blocks of SGR with the highest lion harvests per 1000 km^2 showed the steepest declines in hunting (see Figure 5.4, 5.5, & 5.7). Trophy hunting since the late 1990s was having a negative impact on lion populations in SGR, and the lion trophy hunting quota for SGR should be reduced to one lion per 1000 km^2 to make it sustainable (Packer *et al.*, 2010). This decline in hunting quota would only represent a slight decrease in the 2008 overall lion hunting off-take of SGR from ~50 lions a year to ~45 lions a year, but would result in a much more even spread in lion hunting across SGR. It is important to try to understand why lion trophy hunting in some areas of SGR is unsustainable, in particular, what is driving this process.

5.5.2 Government income per block:

In Tanzania, the government has been over reliant on trophy fees to raise income from trophy hunting (Baldus, 2004); whereby the value of wildlife as dead trophies creates pressure for issuance of large and increasing quotas (Lindsey *et al.*, 2007a; Baldus & Cauldwell, 2004), and as shown here in lions leads to high hunting pressures and then declines in off-take. The blocks with the greatest declines in lion trophy hunting from 1996-2008 were the same blocks that provided the government with the most income per km^2 from 1996-2003 (see Figure 5.6). The trophy fees for lion are high ($4900/lion in 2008), and therefore increasing the number of lion on quota greatly increases the quota value. This is one of the easier means for the government to apply pressure on hunting companies to increase revenue, as currently companies have to achieve 40% of their overall quota. Hunting companies are content to continue this system of over reliance on trophy fees for income as it is easier to pass such costs to clients than it is to transfer costs like block fees to clients.

It has been surmised that companies that sublease are not paying the government all the fees or taxes due, as much of the revenue generated never enters the country (Baldus & Cauldwell, 2004). Nonetheless, because of Tanzania's over reliance on trophy fees to raise government income from trophy hunting these short-term blocks (and in most cases sub-leased blocks) provided almost twice the revenue per km^2 than the blocks that have been under long-term stewardship ($133 per km^2 short-term to $62 per km^2 long-term). The

Msolwa, Ilonga and Matambwe sectors of SGR are the sectors where the most subleasing occurs, and they are also the sectors with the highest lion hunting pressure, the greatest declines in annual lion hunting off-take from 1996-2008, and provided the government with the most revenue per km^2 from 1996-2003 (see Table 5.1). From 2004 to 2008, hunting fees increased; with lion trophy fees doubling ($2500 to $4900) and annual block leasing fees trebling (from $7500 to $27000). The increase in block fees has resulted in several hunting companies in the Msolwa and Ilonga sectors changing hands in 2008/9 (four companies with a total of seven blocks).

5.5.3 Block tenure:

Hunting companies that retain the same hunting blocks over 20 years probably take a long-term view over husbanding hunting opportunities in their blocks (Leader-Williams *et al.*, 2009). This relationship is clearly highlighted by the lion trophy hunting data here. That is, long-term hunting company blocks have a lower lion hunting pressure and annual change in lion off-take between 1996-2008, than blocks that have only been leased over the short-term (see Figure 5.7 & 5.8), and this difference between blocks is statistically significant. Figure 5.8 shows the median value of hunting pressure in long-term blocks is around one lion per 1000 km^2, while the short-term blocks is around two lions per 1000 km^2. A recent study across Tanzania of lion trophy hunting suggests setting the lion quota at one lion per 1000 km^2 in SGR for a sustainable off-take (Packer *et al.*, 2010). These suggestions are supported here, with the long-term blocks keeping annual off-take relatively constant from 1996-2008, and the short-term blocks declining during this period (see Figure 5.8).

Blocks under short-term tenure were predominantly on the western side of SGR (Msolwa and Ilonga sectors). These blocks experienced very high hunting pressures in the late 1990s and then subsequent declines in hunting off-take in the early 2000s. However, by 2009 parts of the Msolwa sector had some of the highest lion densities in SGR (see Chapter 2). It is thought that the overharvesting of the late 1990s, led to a scarcity of lions to hunt, which made it difficult to attract clients to the blocks, allowing lion populations there to recover by 2009. The fact that a block in the heart of the Msolwa sector stopped hunting lion in 2002 (SH on Figure 5.5) probably helped this recovery. Over the last few years, several blocks that have been over utilised in the past, have recently change hands, to what is hoped will be, more responsible hunting company owners.

5.5.4 Conclusion and recommendations:

The blocks in SGR with the highest lion hunting pressure were also the blocks that experienced the steepest declines in trophy off-take from 1996 to 2008 and tended to be under short-term tenure. These high pressure hunting blocks, however, brought in the greatest amount of revenue for the government per km^2 of area. The blocks that have been leased to the same company for over twenty years had the most sustainable lion hunting off-takes. It is therefore strongly recommended that ten year leases be encouraged. With such a long lease, it will be important to verify on an annual basis that companies are indeed managing their blocks sustainably, and this may be a role for the Tanzanian Wildlife Research Institute (TAWIRI). The adoption of the 1995 Policy and Management Plan for Tourist Hunting (MNRT, 1995), which was accepted by the then Director of Wildlife, but has yet to be implemented (Leader-Williams *et al.*, 2009), would go some way to achieving these goals as it would allocate hunting blocks through market-based competition with a long-term lease, thereby reducing the importance of trophy fees. The 1995 Management Plan focuses on a more equitable distribution of revenue and had six main recommendations:

- "The allocation of hunting blocks through a tender system that allows equitable distribution of blocks, without compromising the existing high standards of many outfitters or prejudicing the long-term economic returns from tourist hunting to Tanzania (<u>open allocation</u>);
- The adoption of a fee structure that combines a right to use concession fee paid by the outfitter in return for a long-term lease of that block, and a trophy fee per animal shot (<u>improved fee structure</u>);
- The setting of sustainable hunting quota that promote trophy quality on a scientific basis (<u>sustainable quotas</u>);
- The adoption of codes of conduct by outfitters and the overseeing of examinations for professional hunters that ensure their competence in the practice of hunting and in providing the necessary services to their hunting clients (<u>codes of conduct and professional examinations</u>);
- The sharing of revenues and benefits with rural communities from hunting carried out on their land (<u>community benefit</u>); and
- The reinvestment of part of the funds derived from tourist hunting in the management of game reserves (<u>Game Reserve retention</u>)".

6 Trophy Hunting as a Tool in Conservation: Perceptions, Questionnaires & Interviews

6.1 ABSTRACT

An important factor in the long-term survival of the lion in the wild will be human attitudes and actions. Tanzania supports most of the world's remaining free-ranging lions, and the Selous Game Reserve (SGR) has the largest lion population. Lion trophy hunting occurs in Tanzania and SGR. By looking at articles in four daily newspapers throughout 2008, the perceptions of the Tanzanian press have been highlighted, for the first time, to big cat conservation and trophy hunting. The articles can broadly be divided into positive stories on lion conservation and the importance of lions to Tanzanian tourism, and negative stories on human-lion conflict. Most of the stories were related to human-big cat conflict (82 articles), closely followed by stories related to big cats and tourism (71 articles). Trophy hunting, on the other hand, had the least number of stories (36 articles) and the articles were largely negative (58% of the time) and tended to be linked to corruption. The perceptions of wildlife managers and key players in the lion trophy hunting industry in SGR were sought through questionnaires (n= 47) and detailed interviews (n=10). The highest number of respondents (49%) thought the lion population was decreasing in SGR, and 78% of respondents thought the lion hunting quota should be reduced. The detailed interviews with key informants, highlighted many different possible ways to reform lion trophy hunting; all accepted that if they only hunted older lions it would be sustainable. There was, however, disagreement or confusion on how to age lions, but the fact that the majority of lions are shot at baits would allow for more time to observe and age lions. Most suggested reforms or changes to the trophy hunting industry in Tanzania were perceived in a negative light by the hunting respondents.

6.2 INTRODUCTION

Trophy hunting is permitted in 23 sub-Saharan African countries generating some US$201 million per annum from some 18,500 clients; South Africa has the largest hunting industry in terms of numbers of visitors and revenue, Tanzania has the largest geographical area set aside for trophy hunting (Lindsey *et al.*, 2007a). Trophy hunting (also known as 'sport,' 'safari,' or 'tourist' hunting) of wildlife is often considered a necessary part of wildlife conservation and management and has been a driving force in conservation since the early 20^{th} century (Adams, 2004). Well managed trophy hunting involves low off-take and high prices creating incentives for the conservation of threatened and endangered species (Leader-Williams *et al.*, 2005), and significantly may generate revenue for conservation in areas which may not be suitable for other forms of tourism (Lindsey *et al.*, 2006). However, poorly defined objectives, institutional failure, lack of management capacity and corruption may limit the benefits to conservation (Smith, 2003; Leader-Williams *et al.*, 2009) and hunting may reduce population sizes to levels where hunting is no longer profitable or in extreme cases cause population extinctions (Adams, 2004). The importance of trophy hunting to conservation, combined with its potential for negative outcomes, makes the perceptions and attitudes of practitioners and managers important, as it is these people that will largely determine its success or failure.

The focus here is the hunting industry in Tanzania, where over 160 hunting blocks covering an area in excess of 300,000 km^2 (or a third of the country; see Figure 6.1) are leased to hunting companies or outfitters by the state. More than 60 species can be hunted on a tourist hunting licence (Caro *et al.*, 2009). Lions are one of three critical species for the hunting industry (Creel & Creel, 1997; Baldus, 2004) and Tanzania exported an average of 243 *wild* lion trophies per year between 1996 and 2006 (Packer *et al.*, 2010), no other country comes close to these numbers (Zimbabwe exports 96/year and Zambia 55/year, the rest export less than 20/year; Packer *et al.*, 2009). Four of the continent's six largest remaining populations of lions occur in Tanzania, and the Selous Game Reserve supports the largest population (Bauer & Merwe, 2004).

Throughout Africa, lions are subject to widespread loss of habitat, prey depletion, and human–animal conflicts that are associated with rapid human population growth (e.g. Baldus, 2004; Woodroffe & Frank, 2005). The lion range in Tanzania is still extensive (~750,000 km^2 or 90% of the country), with the majority (~80%) living in 335,000 km^2 of protected areas (Mesochina *et al*., 2010). Most of the protected areas owe their funding to trophy hunting (~90%), yet recent research suggests that trophy hunting has had a negative impact on lion populations in Tanzania and across Africa (Packer *et al*., 2009; Packer *et al*., 2010). Recommendations to only hunt older lions (Whitman *et al*., 20004) or reduce the lion hunting quota (Creel & Creel, 1997; Baldus, 2004; Packer *et al*., 2010) have been suggested, which would make lion trophy hunting sustainable. Yet there seems to be reluctance in the Tanzanian hunting industry to deal with the problem, preferring to stick to the formula of stating that Tanzania has many lions and most are killed illegally, as the recent hunting industry funded report on the conservation status of the lion in Tanzania highlights in its abstract (Mesochina *et al*., 2010): "around 200 free-ranging lions legally harvested per year [through trophy hunting]. This figure remains far smaller than the number of lions illegally killed for various reasons, such as ritual killing, snaring for bushmeat, retaliation in reaction to human casualties and livestock losses." The hunting industry has control over the lions killed legally for trophies, yet prefers to focus on the illegal killings, which it has no clear notion of the scale of activity or control over. It is important to study attitudes and perceptions within the hunting industry to understand what could lead to its reform.

Few factors affecting the persistence of large carnivores fail to have a human component, the lion is no exception. Wildlife management depends on recognition of the interplay between science, values and politics (Kellert & Clark, 1991). Research in Tarangire ecosystem, Tanzania has investigated attitudes of the trophy hunting industry, photographic tourism industry, and Maasai community to lions to highlight conditions necessary for lions and humans to coexist (Lichtenfeld, 2005). There has also been research on the conservation attitudes of local people around Selous Game Reserve to wildlife related benefits (Gillingham & Lee, 1999). Of more relevance to lion trophy hunting is a study of the preferences of hunting clients and operators at two US hunting conventions (Lindsey *et al*., 2006), which concluded that "hunting clients are more adverse to hunting under conditions whereby conservation objectives are compromised than operators realize, suggesting that client preferences could potentially drive positive change in the hunting industry." The vital factor in the long-term survival of the lion will be human attitudes and actions. Tanzania and the Selous Game Reserve in particular, are important to the long-term viability of the African lion in the wild. This chapter seeks to look at perceptions of wildlife managers and key players in the hunting industry in Selous to lion trophy hunting, and national perceptions on lions and trophy hunting from newspaper stories in four Tanzanian dailies.

6.3 METHODS

The Selous Game Reserve (SGR), at 47500 km^2, is Tanzania's largest protected area, and serves as a good example of conservation issues and practices in Tanzania. Data on perceptions of lions and trophy hunting in Tanzania are collected through studying four Tanzanian daily newspapers from January to December 2008, questionnaires of people working in SGR, and ten key informant interviews also of people working in SGR.

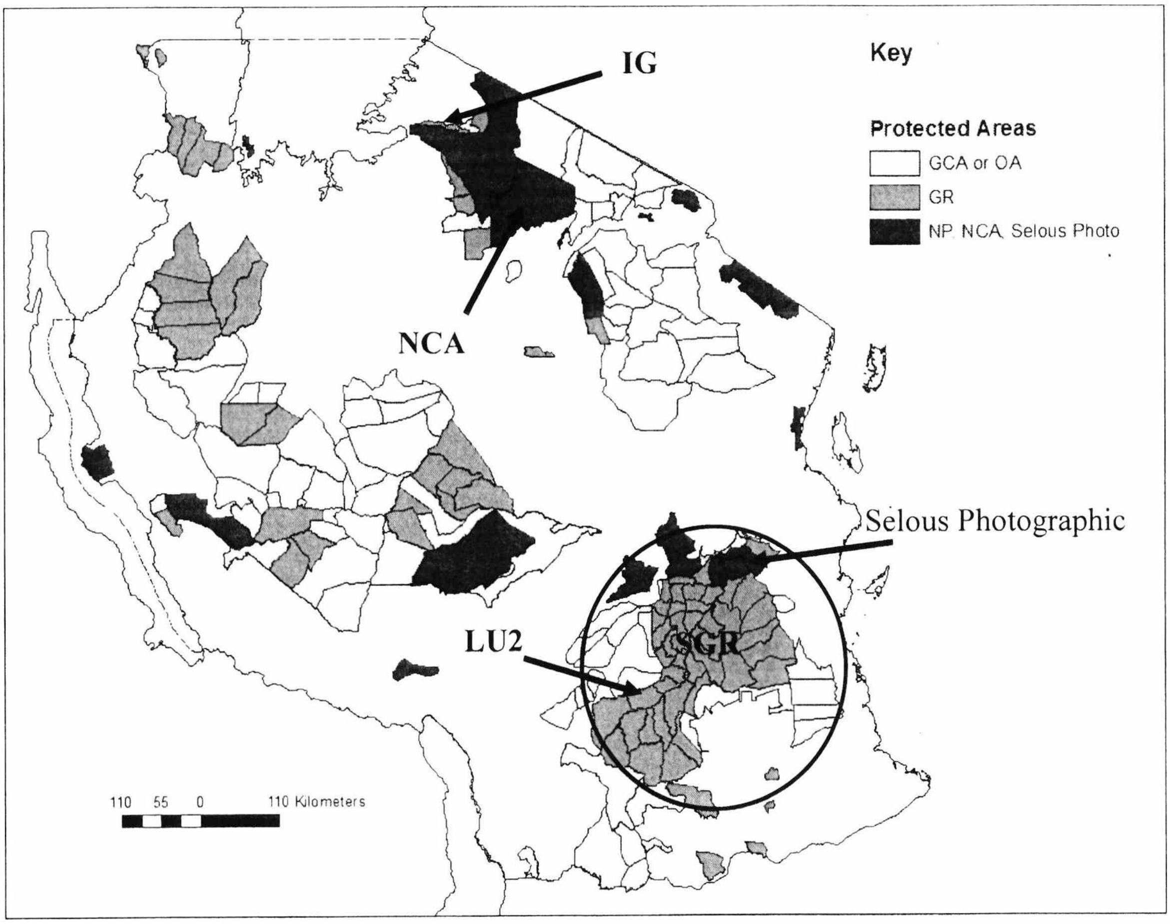
6.3.1 Study area:

Tanzania supports an extensive network of protected areas for wildlife conservation (see Figure 6.1), which are made up of National Parks (NP; 38,365 km^2), Game Reserves (GR; 102,049 km^2), and Game-Controlled Areas or Open Areas (GCA or OA; 202,959 km^2). The three types of areas are governed by different regulations. In NPs, with the exceptions of management headquarters and tourism lodges, no settlements, and no wildlife hunting are allowed. All regulations in NPs are managed by Tanzania National Parks (TANAPA). The Ngorongoro Conservation Area (NCA) is included in the NP category (marked NCA in Figure 6.3a), but is managed by the Ngorongoro Conservation Area Authority (NCAA) and Masai settlements are allowed within its boundaries, but no wildlife hunting is permitted. GRs, like NPs, prevent settlements and use of natural resources without permission from the management authorities, the Wildlife Division (WD) of the Ministry of Natural Resources and Tourism (MNRT). However, unlike NPs, trophy hunting is allowed for six months of the year (July-December) in GRs. GRs are divided up into blocks that are leased from the WD by hunting companies, who are responsible for marketing and organising hunts with tourists. The SGR (Figure 6.1) is the exception to the rule in that it is a GR with four former hunting blocks (or six percent of SGR) set aside for photographic tourism where trophy hunting is not permitted. GCAs and OAs are multi-use areas controlled by the WD with human settlements. Most OAs/GCAs are within tourist hunting blocks where hunting is limited to the block owner and their clients. Many OAs were formerly known as Wildlife Management Areas (WMAs).

The distinction between hunting blocks on GCAs, WMAs and OAs is not clear cut; all allow for human settlement and wildlife to coexist, and hunting is only permitted under licence, but reflects when the blocks were set up. GCAs are the oldest, and most were set-up prior to the early 1990s. The WMAs reflect Tanzania's attempt to introduce community-based management of wildlife in the late 1990s, with the idea that control of and benefits from wildlife would be decentralised to the communities living in the area. The re-designation of some WMAs as OAs and the designation of new hunting blocks in 2004/5 as OAs reflect both the central governments extreme reluctance to surrender power to the local communities and the preference of hunting companies to deal with one central authority (for a detailed discussion see Nelson *et al.*, 2007).

Each hunting block is allocated an annual quota, and the hunting company must undertake to utilize 40% of its quota or pay the WD a top-up payment to meet this 40% minimum. In 2003, the Grumeti Community and Wildlife Conservation Fund (a NGO funded by a tour and hunting operator) operating in the Ikorongo and Grumeti GRs (marked IG on Figure 6.1) purchased all legal hunting rights yet disallow the use of these rights, effectively eliminating legal hunting in these GRs. The Fund has sufficient funding, personnel and equipment to patrol their management area efficiently (Knapp *et al.*, 2010). Similarly, in 2009 the Selous Project purchased hunting rights and did not utilise them in the Lukula area of SGR (marked LU2 on Figure 6.1). Adventure tourism is being attempted in these areas.

Figure 6.1: Tanzania's protected area network.



6.3.2 Newspapers:

Four Tanzania daily newspapers were studied for the period January to December 2008 for articles relating to lion conservation, lion-human conflict, lions and tourism, and anything about trophy hunting (see Appendix 11 for information extracted). After an initial pilot study, it was felt that the study would benefit from expanding the study to include any articles relating to big cats (e.g. leopards, cheetahs), as the issues facing their long-term conservation are similar. The newspapers were the Guardian and Daily News in English, and, Mtanzania and Nipashe in Swahili. The newspapers were held at the University of Dar es Salaam library (missing issues were located at the respective newspaper offices). The articles location in the paper, its length and whether it had any pictures were also recorded. Although subjective, whether the article was positive or negative about its subject was also recorded.

6.3.3 Questionnaires:

The SGR is divided into eight sectors, each sector has a Sector Warden in charge, and overall there is a Project Manager in charge of the reserve, who reports to the Director of the WD. The SGR employs 380 support staff to manage it (UNESCO, 2008). Questionnaires from 29 WD staff employed in Selous have been completed (this includes three Sector Wardens, one former Project Manager, and just over 50% of respondents had over 15 years experience of working in Selous). There are 20 hunting companies, owned by 15 individuals that operate in Selous. Eight individuals in senior management /ownership roles from different companies completed the questionnaires. Within the boundaries of SGR there are eleven photographic lodges/camps, ten questionnaires from lodge managers from eight of the lodges were filled in. A total of 47 questionnaires have been completed, 21 in Swahili and 26 in English (see Appendix 12 for questions asked). The questionnaires looked for information on: i) wildlife population trends; ii) lion sightings; iii) illegal resource use; iv) perceptions of the management of SGR; v) trophy hunting.

6.3.4 Interviews:

There is very little information about the hunting industry and many aspects are shrouded in secrecy. This fosters a climate of distrust, making engaging in open discussion difficult. People involved in the trophy hunting industry were engaged in discussion, to find out whether they thought practices were sustainable and to learn what they thought was important to the long-term future of lion conservation and trophy hunting in Tanzania.

However, this has proved difficult and many individuals were reluctant to talk to 'outsiders.' Nonetheless ten semi-structured interviews with key players in the trophy hunting industry in SGR were carried out (see Appendix 13 for structure of the interview). The interviewees had over 100 years experience of working in or managing the trophy hunting industry in Tanzania.

6.4 RESULTS

This section highlights the results of a study of four daily newspapers in 2008, 47 questionnaires, and 10 two hour interviews to highlight perceptions on lions and trophy hunting in Tanzania, with a focus on SGR.

6.4.1 Newspapers:

In 2008, the Daily News had the most articles related to big cats and trophy hunting (Table 6.1), with 61 of the articles related to conflict between people and big cats. This was largely the result of the Daily News serializing in 45 articles the 1938 adventures of Jim Corbett in India, which predominantly involved hunting tigers or leopards, in its "Man against Man-Eaters" series. Although it could be argued that the Corbett articles were about hunting, they approached the subject from a problem animal control (PAC) stand-point, and therefore have only been recorded in the conflict category in Table 6.1. The Swahili language paper, Mtanzania, had the highest proportion of articles on trophy hunting. Most of these articles were negative (see Table 6.2), and related to corruption in the industry. There is some overlap in the content categories, with 11% of articles overlapping.

Table 6.1: Breakdown of number of articles and content in different newspapers in 2008.

Newspaper	Articles (n = 201)	Lion (big cat) conservation (%)	Lion (big cat) & tourism (%)	Lion (big cat) conflict^{+} (%)	Trophy hunting (%)
Guardian	41	39	49	20	7
Daily News	93	10	29	66	8
Mtanzania	37	24	35	8	57
Nipashe	30	30	37	33	17
Mean ± StDev		26 ± 12	37 ± 8	32 ± 25	22 ± 23

Lion conflict^{+} refers to human-wildlife conflict with lions and other big cats.

Of the four content categories of articles (see Table 6.1), human-lion conflict and lions and tourism were the most numerous (see Table 6.2); with almost double the amount of articles than the other two categories. A typical example of the lion and tourism articles in 2008 would relate the importance of wildlife to Tanzania's tourism economy, include a picture of a lion, and be positive in outlook. The human-lion conflict articles were perhaps not surprisingly usually negative in outlook (Table 6.2). In 2008, there were serious problems with man-eating lions in Singida region, and most papers ran stories relating to fear of these lions, described people being killed by the lions, and finally the capture and killing of one of the lions by game scouts. As mentioned earlier the articles relating to trophy hunting were predominately negative in outlook, an example of this is an article by the Daily News on the 24th April 2008 which quotes Dr Mzindakaya, an MP, as stating that the government was losing $60 million annually in shady allocations of hunting blocks and paltry fees being charged for trophy hunting. The article goes on to say that only $9 million was collected by government annually and that 12 foreign companies owned 57 of the prime hunting blocks. Contrasting with these trophy hunting newspaper stories, articles on lion conservation were generally of a positive outlook (Table 6.2), for example, the Guardian newspaper on 9th August 2008 described the Ngorongoro Crater as having the highest density of lions in the world and therefore was a good place to visit. The lion conservation and wildlife tourism articles also tended to be longer and have more pictures than the trophy hunting and human-lion conflict articles (Table 6.2).

Table 6.2: Content of four Tanzanian daily newspapers; outlook, length and photograph.

Content	Number of Articles (n)	Outlook$^+$ (+) (%)	(-) (%)	Unk (%)	Length (page)* ≥ 1 (%)	< 1 (%)	≤ ¼ (%)	% with picture (%)
Trophy hunting	36	25	58	17	3	30	67	25
Lion* conflict	82	12	87	1	1	61	38	12
Lion* conservation	43	79	16	5	19	44	37	44
Lions* & tourism	71	89	10	1	23	42	35	62

Lion(s)*- includes articles on other big cats (e.g. leopards). **Outlook**$^+$ - refers to the outlook of the article; (+) is positive, (-) is negative, and Unk is unknown. **Length (page)*** - is the page length of the article.

6.4.2 Questionnaires:

Almost half of all respondents had over ten years experience of working in SGR. It is of note that individuals working in a management role for the photographic lodges had in general spent the least amount of time in SGR (80% had less than five years experience of working in SGR), while 50% of hunting respondents had spent more than ten years in SGR. The WD staff questioned had the most experience of working in SGR (50% had over 15 years). After establishing the experience and background of respondents and reassuring them of the confidentiality of the questionnaire data, the perceived population trend data of elephant, buffalo, lion, and leopard was looked at. There is very little information on wildlife population trends in SGR. Based on responses, it seems that elephant and leopard populations are doing well, but there are concerns about the health of buffalo and lion populations (see Table 6.3). In terms of lion data, it is of interest that 50% of hunters thought the lion population was increasing, while another 50% thought it was decreasing. Nobody in the photographic industry thought it was decreasing (30% thought it was increasing, 40% thought it was staying the same, and the rest did not know). Detailed questions on lion sightings in SGR revealed that lions were mostly seen in small groups of less than five individuals (34% of respondents); and when male lions were seen, 70% of respondents said they had no manes. Only 15% said they had slight manes, and a further 15% said they had incomplete manes. No respondents said the male lions of SGR had a full mane.

Table 6.3: Perceptions of wildlife population trends.

	Increasing (%)	Decreasing (%)	Same (%)	Do not know (%)
Elephant population	51	28	13	9
Buffalo population	38	34	17	11
Lion population	28	49	11	13
Leopard population	40	17	28	15

In terms of illegal resource use or poaching, only 12% of respondents said that there was no poaching within their areas; and 42% of respondents said poaching was on the increase (while 21% said it was decreasing, 19% said it was staying the same, and 17% did not know). Most of the respondents saw illegal activities or signs of these activities in the reserve on a monthly basis (47% of respondents saw signs monthly, 17% saw it weekly, and 9% saw it on a daily basis). Just over 40% of respondents reported seeing people in the reserve illegally on a monthly basis, and the people tended to be in medium size groups of 5-15 individuals (62% of respondents). Almost 75% of respondents attempted to estimate what illegal activities were the most prevalent in their area. These illegal activities, in order of prevalence were (average % in SGR ± standard deviation in brackets): illegal fishing (35.1% ± 17.3); elephant poaching (32.2% ± 26.6); bushmeat poaching (28.3% ± 20.4); crocodile poaching (21.4% ± 16.9); illegal logging (10.2% ± 7.5); and, honey harvesting (5.5% ± 6.4).

Looking at other general wildlife management concerns, the majority of people questioned thought human-wildlife conflict around the SGR was increasing (38% of people said that it was increasing, 12% said it was decreasing, 32% said it was staying the same, and 17% did not know), but believed that communities living around the reserve were also benefiting from their proximity to SGR (68% agreed with statement, 13% disagreed, and the rest did not know). On general questions on whether an increase in the number of tourists visiting SGR would have a negative impact, the number of people that agreed with the statement was equal to those that disagreed (47% agreed and disagreed, while 6% did not know). However, there was an overall consensus that the amount of area set aside for photographic tourism in SGR should increase (83% said it should be increased, 8.5% said it should stay the same, and a further 8.5% did not know; nobody said it should be decreased), which would probably lead to more tourists visiting SGR.

The last section of the questionnaire dealt with lion trophy hunting in SGR. The majority of respondents thought trophy hunting in SGR was sustainable (57% agreed, 17% did not think it was sustainable, and 26% did not know), but perhaps surprisingly the vast majority of respondents (78%) thought that the lion quota should be reduced (14% thought it should stay the same and 8% did not know). Nobody thought the lion quota should be increased. However, just over half of respondents (53%) thought the quota system for lions could be abandoned, to be replaced with an age based system where only older lions should be shot (51% thought this should be restricted to seven year old lions, 11% thought six year olds would be fine, 6% thought five year olds, and 32% did not know). When asked whether nose colour was a good means to aging lions, 68% of respondents did not know (21% agreed and 11% disagreed), and just over 53% suggested other means of aging lions in the field. In terms of what proportion of male lions were shot when hunting, 51% did not respond to the question, but worryingly 6% said they shot all males seen in hunting situations (17% said 1 out of 5 males is not shot, 2% said 2 out of 5 males is not shot, 4% said 3 out of 5 males not shot, and 20% said 4 out of every 5 males seen is not shot). With regards to fees earned from trophy hunting, the majority of respondents, perhaps unsurprisingly as they were predominantly government officials, thought both the block and trophy fees should be increased (see Table 6.4). Nonetheless more people thought the trophy fee should be reduced than the concession/block fee (Table 6.4). However, looking at only trophy hunting operators the majority thought concession fees (75%) and trophy fees (50%) should stay the same (although 25% thought trophy fees should be decreased).

Table 6.4: Should trophy and/or concession fees be increased, decreased or stay the same?

	Trophy Fee (%)	Concession/Block Fee (%)
Decrease	18	3
Increase	58	62
Stay the same	18	26
Do not know	5	10

6.4.3 Interviews:

Ten key informants were interviewed, all in relatively senior positions, four currently working in the trophy hunting industry, two formerly worked in the industry, and another four working for the government managing the protected areas that form the basis of the industry. All had at least ten years experience of working in the industry. It was felt that the most informative individuals were those that were no longer involved in the trophy hunting industry. The confidentiality of the interviewees was assured prior to the interview (trophy hunters will be referred to as H01-H04; government officials as WD01-WD04; and, former hunters as F01-F02).

The trophy hunting industry in Tanzania is a close-knit community, with two main hubs, one in Arusha and another in Dar es Salaam. The hunting companies in Arusha meet on the first Tuesday of every month, while many of the individuals working in Dar es Salaam have worked for or with each other. For example, the former owner of Miombo, Michel Mantheakis, trained under Luke Samaras (Luke Samaras Safaris Ltd.), who in turn trained under Gerald Pasanisi (Gerald Pasanisi Safaris Ltd.). These three individuals controlled over 60% of SGR. Within the trophy hunting industry, there is a clash as to how to go forward which seems to be spread along generational lines, with the older generation much less inclined to talk to outsiders. "There is a clear knowledge as to who the good companies are and who are the bad companies, luckily most of the blocks in Tanzania are owned by the good companies" (H04). Yet there is reluctance to name or comment on the bad companies or other companies for that matter; all four hunting informants (H01-H04) stated that *their* companies did a good job and hunted sustainably, but there were other companies that were hitting their blocks too hard, but would not be drawn into naming them. It seems underpinning this reluctance to talk to outsiders is a fear of how unsustainable the hunting practices of the bad companies are, and a fear of being tainted by association. We (H02, H03, & F01) all know that many of these unsustainable practices are carried out by politically connected individuals who know next to nothing about hunting, but have used their political connections to acquire blocks which they sublease to professional hunters for short-term profits (described in detail in previous chapter). Both H03 and H04 said that trying to deal with these politically connected individuals would have a negative impact on their own companies, and it was best to focus on making sure that their own practices were sustainable.

In terms of making lion trophy hunting sustainable, all interviewees accepted that if they only hunted older animals, especially post-reproductive males, it would be sustainable. However, there was disagreement on what age this would be (as highlighted in the questionnaire section) and questions on whether lions could be accurately aged in the field in hunting situations. All the interviewed hunters (H01-H04 & F01-F02) suggested ways to age lions in the field, but the government officials (WD01-WD04) were not able to suggest a means to age lions. There were two key differences in approaches between hunting companies to make hunting sustainable; the first involved selling the opportunity to hunt, and the second involved selling suitable lions that the company had within a given block. The second approach involved having detailed knowledge of the lions of a given block (H01) or baiting extensively with camera traps to see if there were any suitable lions prior to selling the hunting safari to clients (H02). The first approach, however, is the norm, with hunting clients paying large sums for the chance to hunt lions, and if they find any lions the professional hunter (PH) has the final say as to whether the lion can be shot (H03, H04, F01 & F02). However, tourist hunters pay large sums of money to hunt lion (in most cases up to US$ 80,000, and in some cases over US$ 120,000); at such sums it would be very difficult to disappoint (F01 & F02). The clients tend to be cash rich, but time poor, and finding the 21 days needed to hunt lion is the main restricting factor (H02). In many cases the clients are almost 'guaranteed' a lion prior to coming, and that is the nub of the problem (F01).

The majority of lions are shot at baits. F01 said he had hunted lions for 12 years, and had guided 72 lion hunts, an average six lions a year. Of these 72 lions, 66 were shot at baits and only six were shot free-standing. H03 paints a similar picture; he said that over the last seven years, he has shot about 25 lions, and only 15% (four lions) have been free standing, the rest have been at baits. "Both leopards and lions are shot at baits; it is nonsense if people tell you they are not" (F02). H04 said that hunting the big cats is boring; it was something that he enjoyed in his younger days, now he only gets excited at the prospect of a buffalo or elephant hunt. Both F02 and H02 said the challenge to hunting lions and leopards was to get them to come to the baits during the day, and both expressed concern that they felt that there was an increase in hunting at night with spot lights. While F01 described a baited lion hunt he was involved in that went wrong; "we stuck a wildebeest in a tree as bait, got two lions, a male and a female, I asked the client if he was ready for the shot and that he should take it when he was ready, he shot and the lioness fell out of the tree dead." In Tanzania only male lions are available to hunt under licence. All current hunters (H01-H04) said baiting was a good thing as it allowed them more time to observe the lion and age them, and both H02 and H03 said that they had fined a PH for shooting an under-aged lion. H02 said "trophy assessment was the way forward; if a trophy does not meet the required standard it is not exported and the operator fined – be it buffalo or lion, or whatever."

The government focus (WD01-WD04) in relation to trophy hunting and game reserves was to make more money for Tanzania. All four (WD01-WD04) felt that it was in Tanzania's interest to increase the number of visiting photographic tourists by creating a viable southern circuit involving SGR. This would involve converting several hunting blocks to photographic tourism. H01 accepted that improved access to some hunting blocks made them now more suitable for photographic tourism, while F02 said that the whole of SGR should be now given over to photographic tourism – with hunting restricted to the blocks surrounding SGR. F02's main reason for suggesting an increase in photographic tourism was corrupt practices were more likely to have a negative impact on wildlife populations in a hunting scenario, and gave the example of a tourist hunter shooting more than s/he was allowed and then bribing officials to keep quiet about it. WD01 said corruption was a serious problem largely as a result of the disparity in what the game guards who are responsible for policing the hunting activities earn and what the tourist hunter pay (a game guard earns around \$350 a month, while a tourist hunter can pay up to \$120,000 for a 21 day safari). WD02 said high level corruption was a much more serious problem, focusing on the allocation of hunting blocks. H03 noted that some people own a huge number of blocks, but most do not. There are 4-5 companies that own most of the blocks, while the other 40 or so companies own 2-3 blocks (some only one block), and there are few opportunities for new companies to get more blocks (H03). When asked whether competitive bidding for blocks would free up blocks, both H03 and H01 said that they thought that this was a bad idea even if it could be done in an open and transparent way, which they thought highly unlikely. They (H03 & H01) said that Tanzanians would be squeezed out of the market, and foreigners would own everything, with HO3 stating; "it would mean people like Bill Gates would own blocks and ban hunting, or wealthy Arabs would get all the blocks." F01 went further than most and had a different vision of the future, stating that trophy hunting in Tanzania was in need of *massive* reform; stating that the future was increased privatization, as you have in South Africa.

Reforms to Tanzania's wildlife policy designed to lead to increased participation of communities in the management of wildlife areas and allow them to accrue some of the benefits of living in these areas (WMA scheme) received no support from any of the informants. The government officials (WD01-04) did not trust the people to stop poaching and manage their areas for wildlife, and seemed extremely reluctant to devolve or surrender power to the local level from central government. Similarly, the hunters and ex-hunters thought dealing with local communities increased the complexity and costs of their hunting operations. H04 stated that instead of dealing with just one body (e.g. the WD), agreements had to be made with each village within the WMA, and then you would still have to pay all the fees to the central government. H03 also noted that in the WMAs piloted by international development organisation (e.g. GTZ; Organization for German Technical Cooperation) the communities had unrealistic monetary expectations, and observed, "it would be really good if some of these international donor organisations tried to run their WMA schemes like a business and did not just throw money at the communities, it makes it impossible for companies to follow after them." These sentiments may explain why many WMAs are being quietly shelved and replaced with OAs.

6.5 DISCUSSION

Through looking at articles in four daily newspapers throughout 2008, the results have highlighted for the first time the perceptions of the Tanzanian press to big cat conservation and trophy hunting. The articles in the newspapers have a bearing on attitudes and perceptions of the Tanzanian people; and can broadly be divided into positive stories on lion conservation and the importance of lions (and other wildlife) to Tanzanian tourism, and negative stories on human-lion conflict. Most of the stories were related to human-big cat conflict (82 articles), closely followed by stories related to big cats and tourism (71 articles). Trophy hunting, on the other hand, had the least number of stories (36 articles) and the articles were largely negative (58% of the time) and tended to be linked to corruption, with the Swahili Mtanzania daily having the most stories on trophy hunting. The experiences of carrying out the questionnaires and key informant interviews with people working in the trophy hunting industry did portray an insular community wary of the negative opinions of outsiders. This contrasted with individuals working in the photographic tourism industry, who were much more open. Tanzanians working for the WD, the government management authority, were most concerned with increasing the revenue earned by the country from its wildlife. The newspaper, questionnaire and interview data are used in the following discussion of: i) wildlife population trends; ii) human-lion conflict; iii) community benefits; and, iv) sustainable lion trophy hunting. Most of the examples are from SGR, as the reserve has been the focus of this research, but the results are applicable to other parts of Tanzania or Africa, and other parts of the world where a multiple-use approach to wildlife management is being attempted.

6.5.1 Wildlife population trends:

The four species chosen for the population trend survey in the questionnaires were elephant, buffalo, lion and leopard. Elephant were chosen as they have been used to highlight the success or failure of wildlife management efforts particularly in relation to ivory poaching, and their large size make for accurate aerial surveys of their numbers (Seige & Baldus, 2000); elephants numbered more than 100,000 individuals in 1976 in SGR, which decreased due to poaching to under 30,000 individuals by 1989, the population has since recovered to 60,000 in 2000. This recovery was reflected in the results of the questionnaire survey, with 51% of people saying they thought the elephant population was increasing in SGR in 2008/9, although 32% of people thought elephant poaching was the most widespread illegal activity in SGR. This supports recent suggestions that elephant poaching is occurring at high levels across East Africa and the SGR has been shown to be the source of recent shipments of ivory seized in the Far East (Wasser *et al.*, 2009). The most recent elephant census results of Selous ecosystem highlight a dramatic decline in elephant numbers of ~31,500 elephants or a decline from 74900 to 43500 elephants between 2006 and 2009 (Damm, 2010). Although such dramatic declines should be tempered by the soon to be published Tanzania National Elephant Management Plan 2010-2015, which suggests that elephant figures in 2006 may represent an over estimate of populations (Sarah Durant, pers. comm.). Nonetheless, it would seem that there has been a decline and perceptions of population trends suffer from a lag effect.

Buffalo, lion and leopard were chosen as these three species are the three most important to the trophy hunting industry in Tanzania, accounting for 24% of the WD's total income in 2003 (Baldus, 2004). Buffalo can be counted using aerial surveys, but leopard and lion are very difficult to census accurately without expending considerable effort in ground based surveys (see Chapter 2 on monitoring lions in SGR). The highest number respondents perceived that lions were decreasing in number (almost 50%); the picture was less clear-cut for buffalo (38% thought increasing and 34% decreasing) and leopard (40% thought increasing and 17% decreasing). The general perception that leopard populations are doing well in SGR and Tanzania is reflected in more leopards being hunted than lions since 2004 across Tanzania, and the fact that leopard have not experienced the same large declines in trophy hunting off-take as lions over the last decade (Packer *et al.*, 2009; Packer *et al.*, 2010). The adult sex ratio in lions has also changed in parts of SGR from 1997 to 2009, an indication of over-hunting (1 male : 1.3 female in 1997, to 1 male : 3 females in 2009; see Chapter 2). Buffalo are an anomaly; the hunting quota appears to be sustainable (Caro *et al.*, 2009), yet there is a general perception that they are being overhunted (Baldus & Cauldwell, 2004) as they are the preferred species of tourist hunters (Lindsey *et al.*, 2006) and the buffalo is a highly sought after meat species by communities (Arcese *et al.*, 1995). Nonetheless, despite concerns for buffalo populations there has been no evidence of large decreases in population. However, should wildlife conservation be successful and reverse some of the downward trends in populations (e.g. sustainable lion trophy hunting practices leads to an increase in lion numbers), this would undoubtedly lead to increased conflict with neighbouring human communities as there are no fences separating people from wildlife in Tanzania.

6.5.2 Human-lion conflict:

In stories in the Tanzanian press on big cats the highest number related to conflict with people, and the majority of people questioned in SGR thought human-wildlife conflict was increasing (38%) or staying the same (32%) in areas around the reserve. Tanzanian districts with the highest number of lion attacks on humans have the lowest abundance of natural prey (Packer *et al.*, 2005b), and villages with the most lion attacks on humans have lower richness of prey species than neighbouring villages without attacks (Kushnir *et al.*, 2010). Between 1989 and 2004, at least 871 human attacks by lions have been recorded in Tanzania, with over 563 fatalities and two-thirds of these recorded attacks have been from districts neighbouring the SGR (Packer *et al.*, 2005b). This high level of human-lion conflict has led to reduced tolerance for dangerous carnivores outside the protected areas, and revenge killings of 'problem' lions are likely to have further consequences on the lion population. Studies of human-lion conflict from Southern Kenya (Hazzah *et al.*, 2009) and Botswana (Hemson *et al.*, 2009) emphasize the importance providing economic benefits (from wildlife tourism activities) to local people who engage in positive conservation activities, or benefits might usefully be distributed in relation to the costs of coexisting with wildlife, or used as incentives to better protect livestock or other human resources. Two things seem to be important when dealing with human-lion conflict: i) reduce the amount of conflict by removing the problem animal quickly or improve the safety of people and their livestock (Packer *et al.*, 2005b); and, ii) communities must benefit from coexisting with wildlife and engaging in positive conservation activities (Hazzah *et al.*, 2009; Hemson *et al.*, 2009).

6.5.3 Community benefits:

Since the 1990s the paradigm of 'conservation with development' has attracted support from conservation organisations and international development agencies in Tanzania and around SGR (Gillingham & Lee, 1999), whereby rural communities would participate in, benefit from, and support the sustainable management of natural resources (Leader-Williams *et al.*, 1994). Furthermore, wildlife based tourism is often seen as effective mitigation for human-wildlife conflict by conservation authorities and organisations, however, its scope as such has been questioned (Walpole & Thouless, 2005). Nonetheless, there were 71 articles, predominantly of a positive nature (89%), on the benefits Tanzania accrues from big cat conservation through tourism, and 68% of respondents to the questionnaires thought people in the communities around SGR benefited from the proximity to the reserve. In Tanzania, community-based management of wildlife was to be fostered through WMAs, and five pilot WMAs around SGR were designated in the 1990s (Baldus, 2006). Hunting was seen as one of the main money-earners for the WMA scheme (Baldus & Cauldwell, 2004). However, these WMAs have been a failure with little sharing of benefits from wildlife with the communities, and power, income and decision making all still remain with the central authorities (Nelson *et al.*, 2007; Baldus, 2009). The detailed interviews with informants involved with trophy hunting highlighted the government's lack of trust of communities and reluctance to surrender power, while the hunters and ex-hunters thought dealing with local communities increased the complexity and costs of their hunting operations, and could go some way to explaining the lack of success of the WMA scheme.

6.5.4 Sustainable lion trophy hunting:

There is a lack of consensus among conservation NGOs and African governments concerning the acceptability and effectiveness of trophy hunting as a conservation tool (Lindsey *et al.*, 2007a); this was reflected in the proportion of negative articles (58%) in the Tanzania press in 2008 dealing with trophy hunting. In Tanzania, there have been two major international donor funded projects to try to improve trophy hunting: i) Planning and Assessment for Wildlife Management from1990 to 1995 (PAWM; Leader-Williams *et al.*, 1996), and, ii) the Selous Conservation Project from 1987 to 2003 (SCP; Baldus & Cauldwell, 2004; Baldus, 2006). Both projects and the subsequent suggestions of reform (discussed in more detail in the following sub-sections) have been largely driven by organisations and individuals from outside the country (although in collaboration with Tanzanian government officials); but in 2006, the Minister of Natural Resources and Tourism set up a Special Committee of MPs to look at the trophy hunting sector to make suggestions to improve it (MNRT, 2006). The MPs focused on improving the revenue generated for Tanzania from trophy hunting and increasing the number of Tanzanian citizens in the industry. The trophy hunting industry in Tanzania and particularly in SGR is 'big business,' and when *properly* managed, it is totally sustainable and provides the funds necessary to manage and protect the Selous (Rohwer, 2009; Lindsey *et al.*, 2007a). The question is how much of the trophy hunting industry is well managed. In Tanzania, there are examples of widespread corruption in the conduct of trophy hunting (Leader-Williams *et al.*, 2009) and over-hunting of lions leading to population declines (Packer *et al.*, 2010). There have been many suggestions to make trophy hunting more sustainable, lions are the focus here and used as an example, and the various suggestions are discussed in more detail in the following sub-sections.

<u>Quota system:</u>

Hunting in Tanzania is based around a quota system, where each hunting block is issued a number of animals that can be shot under licence through educated guesswork (Severre, 1996). Based on data from 1989 to 1994, when lion trophy hunting in SGR was at comparatively low levels, Creel & Creel (1997) concluded that "the current intensity of lion hunting in Selous is sustainable, but the quota cannot be filled sustainably." Since then lion trophy hunting has increased, peaking with 115 lions shot in 1998 in SGR, and decreasing subsequently (Baldus, 2004). Recent research shows lion harvests declined by 50% across

Tanzania between 1996 and 2008, and hunting areas with the highest initial harvests suffered the steepest declines; and suggests that the annual hunting quotas be limited to 0.5 lions per 1000 km^2 of hunting area across Tanzania, except hunting blocks in the SGR, where harvests should be limited to 1.0 lion per 1000 km^2 (Packer *et al.*, 2010). This would represent at least a 50% decline in most cases of the lion hunting quota. It is encouraging that 78% of respondents to the questionnaire survey thought the lion quota should be reduced in SGR, and that nobody thought that the lion hunting quota should be increased.

Age-based approach:

An age-based system for lion trophy hunting has been developed in Tanzania (Whitman *et al.*, 2004) and a guide to aging lions for trophy hunters produced (Whitman & Packer, 2007). Serengeti demographic data strongly suggest that tourist hunting of lions would be sustainable if only males over five years are hunted, as this would allow males the opportunity to remain resident in a pride long enough to rear a cohort of young (Whitman *et al.*, 2004). These results imply that strict adherence to off-take of only old animals would make quotas for lion obsolete, and highlights the importance of being able to age lions in hunting situations. Nose colour has been suggested as a means to accurately age lions (Whitman *et al.*, 2004). The Tanzania Hunters and Outfitters Association (TAHOA) accepts the notion of only hunting older male lions, and set a minimum age requirement of six years on lion trophies in 2004, yet pictures of under-aged males (as young as two years old) that have been shot in Tanzania could still be found on hunting company web-sites in 2008 (see Packer *et al.*, 2009). Many of the advocates of sustainable resource use as a tool in conservation have raised doubts as to the validity of using nose colour as a means to age lions (Baldus, 2004; Mesochina *et al.*, 2010) and applying Serengeti data across Tanzania. It is therefore not surprising that the results of the questionnaires highlight confusion as to what age lions could be hunted and a means to aging lions. An age-based quota system, whereby the quota is increased or decreased depending on the quality or age of the lion trophies, as implemented in Mozambique (Begg & Begg, 2007), offers the best potential for long-term sustainability in the lion trophy hunting industry in Tanzania. The use of baits in hunting lions should further facilitate the opportunity to age lions in hunting situations.

Certification system:

As there is a significant market among US clients for conservation-friendly hunting (Lindsey *et al.*, 2006), a certification system would allow clients to select hunting operators on the basis of their commitment to conservation. A certification system has been suggested based on the following (Lindsey *et al.*, 2007b): i) conservation criteria of adherence to quotas and requirements for sex, age, and minimum size of trophies; ii) governance and landowner benefit criteria whereby local communities are empowered and benefit; iii) adherence to national legislation and agreed upon ethical standards. A certification system for Tanzania was suggested six years ago (Baldus & Cauldwell, 2004), but has yet to be accepted by the trophy hunting industry. It is abundantly clear from the detailed interviews with key informants, that within the industry, outfitters know which companies hunt responsibly. Therefore, hunters could deflect opposition to trophy hunting and adopt a consumer-based policy of no-tolerance of unethical practices (Leader-Williams *et al.*, 2009). Similarly, researcher or conservationists, who have a good knowledge of hunting companies, also have a duty to highlight companies that are performing well; with this in mind, the new Tanzania Wildlife Corporation (TAWICO), a hunting company in SGR, has been totally transparent and may provide a model for sustainable/ethical trophy hunting of lions.

Competitive block bidding:

A key output of the PAWM project was the Revised Draft Management Plan for Tourist Hunting dated January 1995, which was accepted by the Wildlife Division but has never been implemented. The management plan outlines a detailed reform of the tourist hunting industry and implementing these reforms would most certainly solve many of the problems inherent in the industry (Baldus & Cauldwell, 2004; Leader-Williams *et al.*, 2009). The management plan emphasises the allocation of hunting blocks through public tender for a 5-year lease. A system is outlined that would realize the market value of hunting blocks while also encouraging the continuity of lease by companies that occupy concessions. However, the detailed informant interviews of trophy hunters highlight scepticism in the transparent and corruption-free implementation of this block allocation process. Most also felt that their hunting company would be priced out of the market. Such sentiments go some way to explain why the 1995 Management Plan for Tourist Hunting has yet to be implemented. However, there have been recent increases in hunting block fees from $12,000 to $27,500 per annum as a result of the government's Special Committee on reform of the trophy hunting sector

(MNRT, 2006). Although this still represents a one size fits all approach to setting block fees, competitive bidding for blocks is back on the agenda as it offers the possibility of increased revenue for the government (Tender and auction method in block allocation; MNRT, 2006).

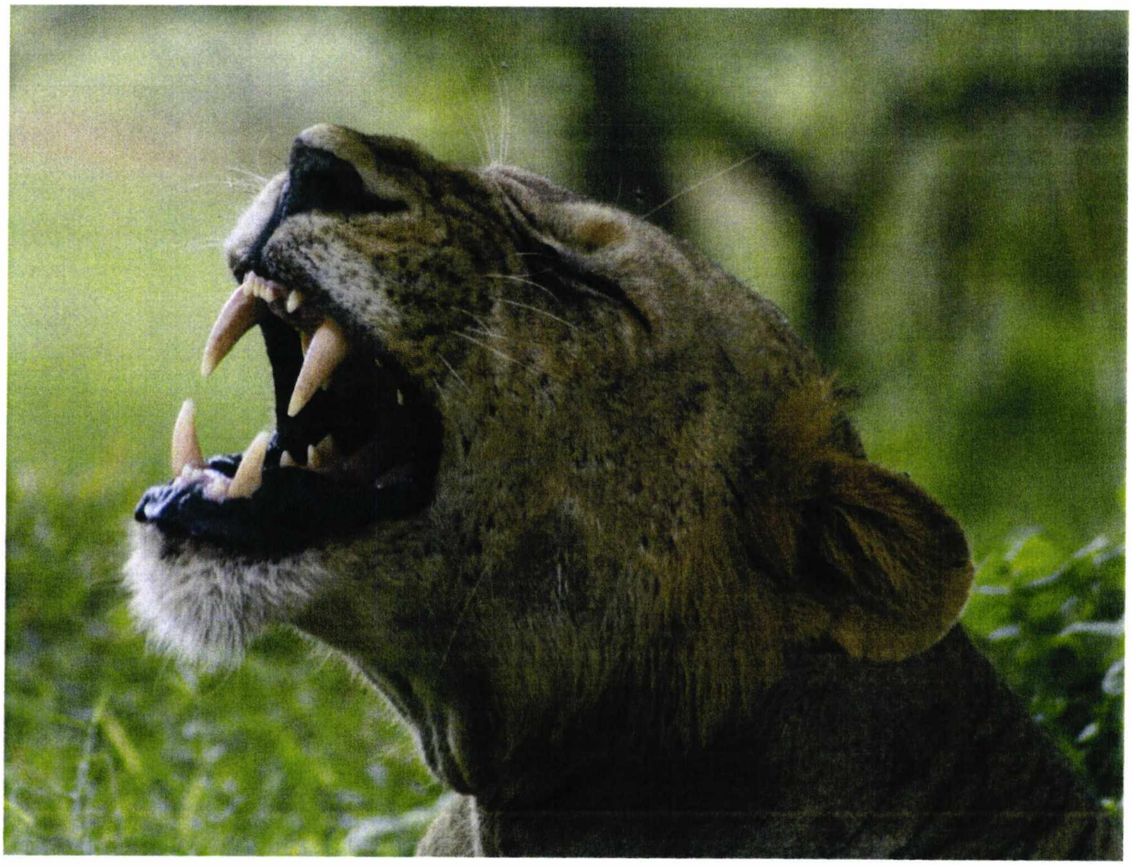
6.5.5 Photographic/ adventure tourism & a southern circuit:

There was an overall consensus in the interviews and questionnaires that the area set aside for photographic tourism in SGR should increase. Government officials expressed a desire to create a viable southern circuit by converting several hunting blocks to photographic tourism. The argument that trophy hunting generates revenue for conservation in areas not suitable for other forms of tourism (Leader-Williams & Hutton, 2005; Lindsey *et al.*, 2006) is less applicable when access to areas is improved, and there is a market for adventure or photographic tourism in those areas. Wealthy individuals have converted two hunting areas in Tanzania to photographic/adventure tourism by purchasing the hunting rights of the area and not utilizing them. Within SGR the amount of revenue generated by photographic tourism per km^2 far outstrips the amount brought in by hunting tourism per km^2, but hunting tourism still brings in much more money overall and requires many fewer visitors to make a profit (see Baldus & Cauldwell, 2004). There are large areas within SGR that will never be suitable for photographic tourism, and trophy hunting will be the best option in these areas. A less polarised and more pragmatic debate is clearly needed, and statements such as "without hunting, wildlife would disappear" or hunting is "slaughter on safari" are not very helpful (Lindsey *et al.*, 2007a).

6.5.6 Conclusion:

There is much that is good about the trophy hunting industry in Tanzania, but there is clearly scope for reform and improvement. Many of the necessary reforms are not new; from competitive block bidding, to certification, to only hunting older animals. Yet there seems to be reluctance to embrace these reforms, and there is a danger of continued negative publicity. In terms of lion trophy hunting, all the tools required to make it sustainable are available; some hunting companies have readily adopted them, others have not.

7 Discussion



7. Discussion: A wake-up call for the hunting industry in Tanzania.

7.1 THESIS OVERVIEW

Modern conservation paradigms hold that extractive use of natural resources, such as trophy hunting, can be beneficial. This thesis has examined lion trophy hunting in Selous Game Reserve (SGR) as a tool in conservation. Firstly, methods to monitor lion populations in SGR were carried out to suggest a total population of 4300 (range 1700-6900), representing Africa's largest lion population. The ecology of lions in an 800 km^2 area of northern SGR (Matambwe) was studied from 2006-2009, and lion distribution in this area was best explained by lean or dry season prey biomass.

Lion trophy hunting in SGR and Tanzania was shown to have a negative impact on the lion population (see also Packer *et al.*, 2010; Appendix 14.b). Therefore using several different methods a sustainable lion quota for each hunting block of SGR is suggested, and all data showed the need for the lion quota to be reduced in SGR. Further study into the main cause of unsustainable lion hunting practices determined that blocks in SGR with the highest lion hunting pressure (i.e. the most lions shot per 1000 km^2 per year) were also the blocks that experienced the steepest declines in trophy offtake from 1996 to 2008 and tended to be under short-term lease from the government, but brought the government the most revenue.

Lastly, the perception of people involved in the hunting industry in SGR to lion trophy hunting was investigated. The highest number of respondents (49%) thought the lion population was decreasing in SGR, and 78% of respondents thought the lion hunting quota should be reduced. The detailed interviews with key informants, highlighted many different possible ways to reform lion trophy hunting; all accepted that if they only hunted older lions it would be sustainable. Although this thesis has been largely negative about the impact of trophy hunting on lion populations in SGR, it is important to remember two things: i) lion trophy hunting brings in large sums of money for Tanzania and conservation in areas not particularly suitable to other land-uses (Baldus, 2004; Lindsey *et al.*, 2006); ii) lions show high population growth and as long as their habitat and prey base remain intact they have the capacity to bounce back from large population losses (see Packer *et al.*, 2005a; Kissui & Packer, 2004). The tools to make lion trophy hunting sustainable are available, it is hoped that they will be applied.

7.2 MONITORING LIONS

The Selous is thought to contain Africa's largest population of lions making it a popular destination for trophy hunters and tourists. However, little is known about their current population status and so a range of data were collected from 2006 to 2009 to provide this important information. Individual lions were identified in an 800 km^2 study area in the northern photographic part of SGR (Matambwe); where 112 lions were recorded in August 2009, giving a density of 0.14 lions km^{-2}. This density has remained relatively constant from 2006 to 2009 and from 1997 to 1999, but the adult sex ratio has decreased from roughly 1 male : 1.3 female in 1997 to 1 male : 3 females in 2009. Although these results are worrying and have been used in other areas to highlight unsustainable hunting practices (e.g. Loveridge *et al.,* 2007), a drop to 1 : 3 should not affect breeding success (Rodgers, 1974). Audio playback response surveys using buffalo distress call-ups were also carried out for a rapid census of lions in three hunting sectors in the west, east and south of SGR, and one photographic area in the north of SGR. Estimated adult lion densities varied from 0.02 to 0.10 km^{-2}, with the north and western areas having a higher density of adults. The results here highlight the value of call-ups in surveying cryptic hunted carnivores but stress the importance of long term projects for measuring population trends.

7.3 LION DISTRIBUTION IN SELOUS GAME RESERVE

Carnivore species are threatened with extinction due to a reduction in distribution and abundance. The conservation of the lion in SGR will ultimately depend on the accurate assessment and understanding of their distribution and abundance to allow for informed management decisions. Other studies have used habitat or soil type (or amount of rainfall) as surrogate proxies for resource availability or measured prey availability directly in the field (see Loveridge & Canney, 2009; Van Orsdol *et al.,* 1985). Both methods were used here to determine what factors influence the distribution of lions in the photographic part of SGR. These methods can then be combined with anthropogenic variables (e.g. distance to villages) to allow for a clearer picture of what factors influence lion distribution. The study was focused on an 800 km^2 study site in northern SGR. Lion distribution in northern Selous was best explained by lean or dry season prey biomass (r^2=0.33; y=0.0005x + 0.1336). The mean dry season prey biomass for the study site was 1436 kg km^{-1}, suggesting a lion carrying capacity for the study site of 164 lions (0.21 lions km^{-2}), which was above the observed number of lions (112 lions or 0.14 lions km^{-2}). However, another method based on the transect sightings of the lions' preferred prey suggested a carrying capacity of 104 lions for this area (0.13 lions km^{-2}). Based on prey transects and field observations of lions on kills, lions in northern Selous showed a preference for buffalo, zebra, giraffe and wildebeest and an avoidance of warthog and impala. However, no relationship was noted between lion distribution and buffalo sightings. Environmental and anthropogenic factors that best explained lion distribution in northern SGR were distance to the reserve boundary and villages and soil type of an area.

7.4 LION TROPHY HUNTING IN SELOUS AND TANZANIA

Trophy hunting has provided important economic incentives for conserving large predators (Baldus, 2004), but using trophy hunting can be a risky strategy because carnivore populations are difficult to monitor and some species, like the lion, show a propensity for infanticide that is exacerbated by removing adult males (Packer *et al.*, 2009). In Tanzania only male lions can be hunted, and Tanzania's lion population is subjected to sizable harvests by trophy hunters: an average of 243 wild lion trophies were exported annually between 1996 and 2006. Harvest trends for lions were analysed across Tanzania's 300,000 km^2 of hunting blocks, and lion harvests declined by 50% across Tanzania between 1996 and 2008, and hunting areas with the highest initial harvests suffered the steepest declines (see Packer *et al.*, 2010). The management of hunting in SGR and Tanzania is driven by a quota system, which is set through educated guesswork. Quantitative analyses suggest that annual hunting quotas be limited to 0.5 lions 1000 km^{-2} of hunting area, except hunting blocks in the SGR, where harvests should be limited to 1.0 lion 1000 km^{-2} (see Packer *et al.*, 2010). Two other approaches were used to examine the setting of the lion hunting quota in SGR, namely: i) a Normalized Difference Vegetation Index (NDVI) and expert opinion approach to estimate lion populations per block; ii) an individual-based stochastic model to examine three different lion population sizes hunted at current quota levels, where the impact of male breeding commencing at under three years of age or five years was investigated. A quota was suggested for each block based on a figure below ten percent of the adult male population. The results of the model showed that larger starting populations were better able to sustain high trophy hunting off-takes and populations where males reached a reproductive maturity at a younger age were also more robust. All data showed the need for the lion quota to be reduced in SGR, and it is expected that such suggestions will be resisted by the hunting industry in Tanzania. The hunting industry in Tanzania is well established, influential, and nervous that any suggestions of a reduction to the hunting quota is a small but irreversible step to banning trophy hunting in Tanzania (as happened in Kenya in the 1970s and Botswana recently). So it should be made absolutely clear that there is no suggestion of a ban of lion trophy hunting, merely a plea to reduce quotas to more sustainable levels. An age-based quota system, whereby the quota is increased or decreased depending on the quality or age of the lion trophies, as implemented in Mozambique (Begg & Begg, 2007), offers the best potential for continued long-term success in the lion trophy hunting industry in Tanzania.

Hunting companies in SGR, as in the rest of Tanzania, lease one or several hunting blocks from the government, and the company, as mentioned earlier, is allocated a species-specific quota for each block for the hunting season (July-December). The impact that length of block tenure has on trophy hunting of lions in SGR was investigated. The blocks in SGR with the highest lion hunting pressure (i.e. the most lions shot 1000 km^{-2} per year) were also the blocks that experienced the steepest declines in trophy offtake from 1996 to 2008 and tended to be under short-term tenure. These high hunting pressure blocks, however, brought in the greatest amount of revenue for the government km^{-2} of area. A move towards a competitive market-based approach for block allocation with a long-term tenure, of up to ten years, is strongly advocated here, away from the current over reliance on pay-as-you-use trophy fee per animal shot approach.

7.5 PERCEPTIONS OF TROPHY HUNTING IN TANZANIA

The important factor in the long-term survival of the lion will be human attitudes and actions. Tanzania supports most of the world's remaining free-ranging lions, and SGR has the largest lion population. Lion trophy hunting occurs in Tanzania and SGR. By looking at articles in four daily newspapers throughout 2008, the perceptions of the Tanzanian press have been highlighted, for the first time, to big cat conservation and trophy hunting. The articles can broadly be divided into positive stories on lion conservation and the importance of lions to Tanzanian tourism, and negative stories on human-lion conflict. Most of the stories were related to human-big cat conflict (82 articles), closely followed by stories related to big cats and tourism (71 articles). Trophy hunting, on the other hand, had the least number of stories (36 articles) and the articles were largely negative (58% of the time) and tended to be linked to corruption. The perceptions of wildlife managers and key players in the lion trophy hunting industry in SGR were sought through questionnaires (n= 47) and detailed interviews (n=10). The highest number of respondents (49%) thought the lion population was decreasing in SGR, and 78% of respondents thought the lion hunting quota should be reduced. The detailed interviews with key informants, highlighted many different possible ways to reform lion trophy hunting; all accepted that if they only hunted older lions it would be sustainable. There was, however, disagreement or confusion on how to age lions, but the fact that the majority of lions are shot at baits would allow for more time to observe and age lions. Most suggested reforms or changes to the trophy hunting industry in Tanzania were perceived in a negative light by the hunting respondents.

There is much that is good about the trophy hunting industry in Tanzania, but there is clearly scope for reform and improvement. Many of the necessary reforms are not new; from competitive block bidding, to certification, to only hunting older animals. Yet there seems to be reluctance to embrace these reforms, and there is a danger of continued negative publicity. The wildlife photographic industry now brings in much more revenue than the wildlife hunting industry for the government of Tanzania (US$ 70 million to US$ 20 million in 2006; Tarimo, 2009), and employs more people. There is a danger that continued negative publicity generated from trophy hunting will lead the government to ban trophy hunting to protect the image of the country's other wildlife based tourism industries, as has recently happened in both Botswana and Uganda. In terms of lion trophy hunting, all the tools required to make it sustainable are available; some hunting companies have readily adopted them, others have not. The government has a role in demanding and enforcing such changes.

Joseph Conrad is buried in Canterbury, near the University of Kent. Many of his arguments for and against colonialism in the early 1900s in "*The Heart of Darkness*", have some resonance around the current "use it or lose it" debate of trophy hunting in so far as comparing the detail to the big picture. On a broad scale, colonialism had the potential to bring development and trade to areas. However, this was very different to the reality of the abuse of power encountered by Marlow, Conrad's character in the Congo. Furthermore, many of Conrad's assertions on colonialism are, now in 2010, politically unacceptable. The big picture of trophy hunting is that it provides much needed capital for wildlife conservation in areas that may struggle to raise funds through other activities (Lindsey *et al.*, 2006), the detail is the possibility of corrupt practices (Leader-Williams *et al.*, 2009) and over-hunting (Packer *et al.*, 2009) funded by a group of people willing to pay large sums of money to shoot animals for pleasure. It will be interesting to see how future generations judge today's actions and arguments.

7.6 LIMITATIONS OF THE RESULTS

As repeated several times, SGR is the size of Switzerland. An attempt to cover as much ground as possible was made, but there is clearly a limit to how much ground two cars can cover. Furthermore any research into trophy hunting in Tanzania is politically sensitive. The government of Tanzania kindly gave me permission to work in the hunting areas of SGR, but understandably only with the hunting concession leaser's permission. As almost half of SGR blocks (~22,000 km^2) are leased to one person, it was felt that his support would be important to the success of the project. Three attempts were made to meet him to try and develop a working relationship and gain permission to visit his areas. However, after the third visit in June 2007 all our research permits were cancelled. It took three months of negotiation to be allowed to carry on with the project. I had to agree to focus on a lion population study in the photographic area of SGR (Matambwe), and to accept that trophy hunting was a government affair not open to independent research.

From September 2007 to January 2009, the project was based at Matambwe and I focused on a lion population and ecology study there. It was felt that the results of Chapter 3 would have been more useful had there been more detailed data from other parts of SGR. In 2009, during the non-hunting season (January-June) I was given permission to visit the hunting areas again. This was also the rainy season, so the logistics of this exercise was challenging, but census data from three different hunting areas in SGR were collected. More research on lions is certainly needed from the hunting areas of SGR.

In December 2007, a new Director took over at the Wildlife Division, which led to access to lion and leopard trophy hunting data in late-2008, which probably represents the project's biggest success. Six weeks were spent collating and inputting this data onto databases and checking the data against earlier records (e.g. Selous Conservation Project records). Some of filing was poor, and data were missing for many blocks for several years. The SGR had the most complete records with 87% available.

The sample size of interviews and questionnaires in Chapter 6 is a limiting factor, but it is difficult to talk to people if they do not want to talk to you. Furthermore, little attempt was made to look at the economics of trophy hunting, which would be an important factor when considering the sustainability of the activity. Both the government and hunting companies are extremely sensitive to allegations of corruption.

7.6.1 Further work:

"The Selous is remote, difficult to access, little explored and still poorly documented" (Rodgers, 2009). It has been a privilege to study lions in SGR for three years. There has been very little research work in SGR, and I feel it would be important to carry on working in SGR. While I was working there, the only other full-time project in the area was a rhino conservation project, which was suspended in 2008. There is enormous scope for further work in SGR on lion trophy hunting and related topics and future research should focus on the following topics:

- **Lion aging in SGR:** I have over 130 lion individual identification cards and would want to continue to monitor these lions, especially the known aged lions born during the period of this project. This could highlight that nose colour could be used to age lions in SGR and thus potentially in other areas of Tanzania, or develop other methods to age lions.
- **Mane study:** In lions, tourist hunting targets large males with large manes. Studies of four year old big-horn sheep (*Ovis canadensis*), where trophy hunting targets large animals with large horns has shown that body weight and horn size significantly decreased over the period 1972 to 2002 (Coltman *et al.*, 2003). In the Selous, the males are well known for having small manes (there is even talk of two types of lions in SGR, one that grows a mane and one that does not). Whether this is a result of tourist hunting selection or environmental considerations (e.g. the climate is too hot to support males with large manes, as is the case in Tsavo, Kenya; West & Packer, 2002) would be interesting to investigate.
- **Genetics study:** I have begun collecting lion tissue samples and am collaborating with Goran Spong at University of Umea on this. We have over 160 samples from across SGR and would be interested in looking at changes in gene frequencies, dispersal, or population structure.
- **Monitoring of trophy quality:** In Tanzania, all trophies are exported from either Arusha or Dar es Salaam. If a process of independent verification of trophies could be developed that hunting companies would agree to, this would represent a considerable achievement in making trophy hunting sustainable in Tanzania.

7.7 SUMMARY

This thesis has established that lion trophy hunting in Selous Game Reserve (SGR) peaked in 1998, and since then has decreased by 50%, but the number of trophy hunters has increased over this period. Investigation into the main cause of unsustainable lion hunting practices determined that blocks in SGR with the highest lion hunting pressure (i.e. the most lions shot per 1000 km^2 per year) were also the blocks that experienced the steepest declines in trophy offtake from 1996 to 2008 and tended to be under short-term tenure/lease from the government, but these blocks brought the government the greatest revenue. The lion population of SGR was established as 4300 (range 1700-6900), representing Africa's largest lion population. The ecology of lions in an 800 km^2 area of northern SGR (Matambwe) was studied from 2006-2009, and lion distribution in this area was best explained by lean or dry season prey biomass. All data showed the need for the lion quota to be reduced in SGR. Lastly, the perception of people involved in the hunting industry in SGR to lion trophy hunting was investigated. The detailed interviews with key informants highlighted many different possible ways to reform lion trophy hunting; all accepted that if they only hunted older lions or reduced the quota it would be sustainable.

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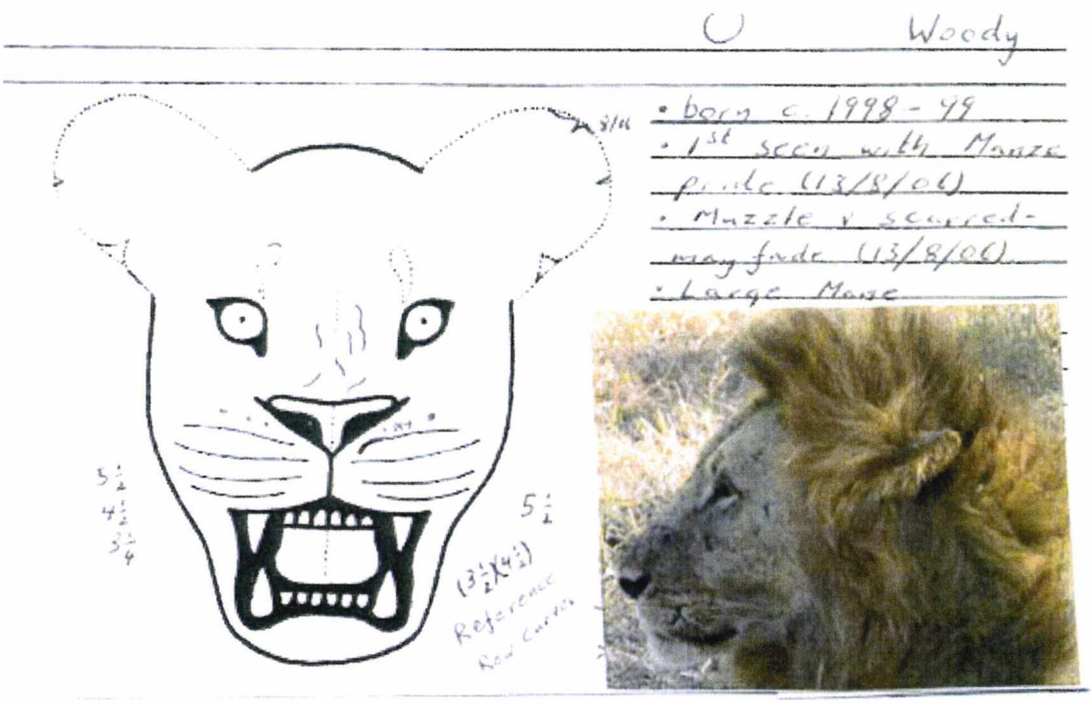
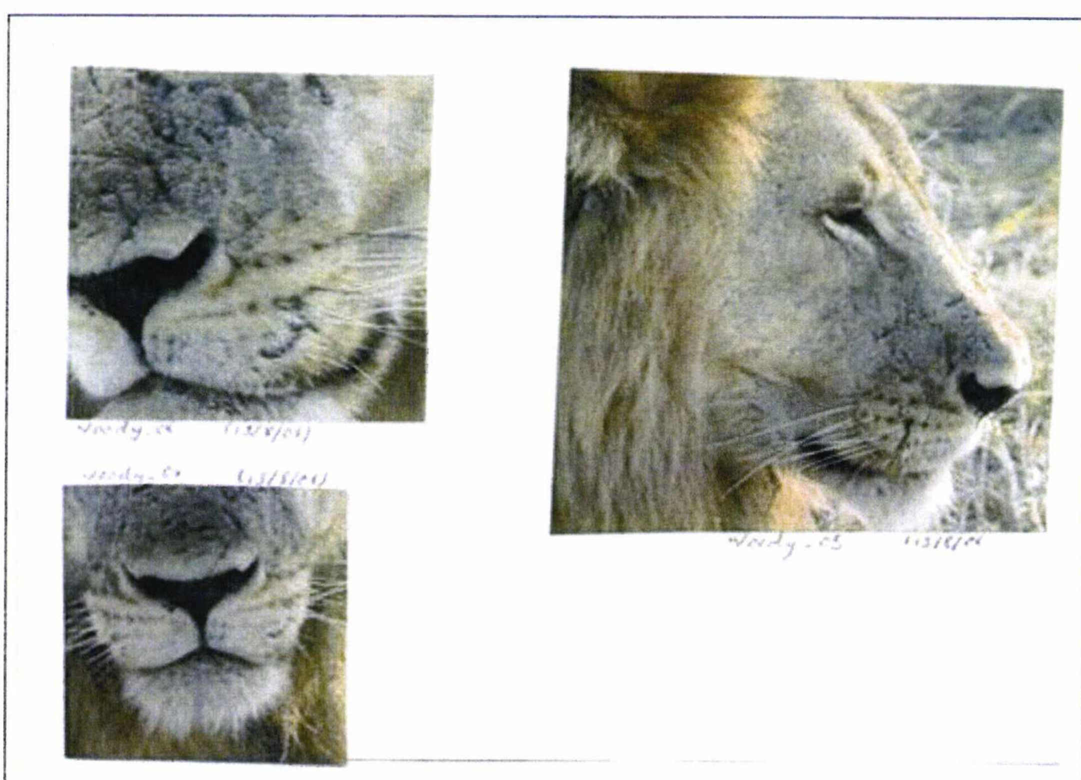
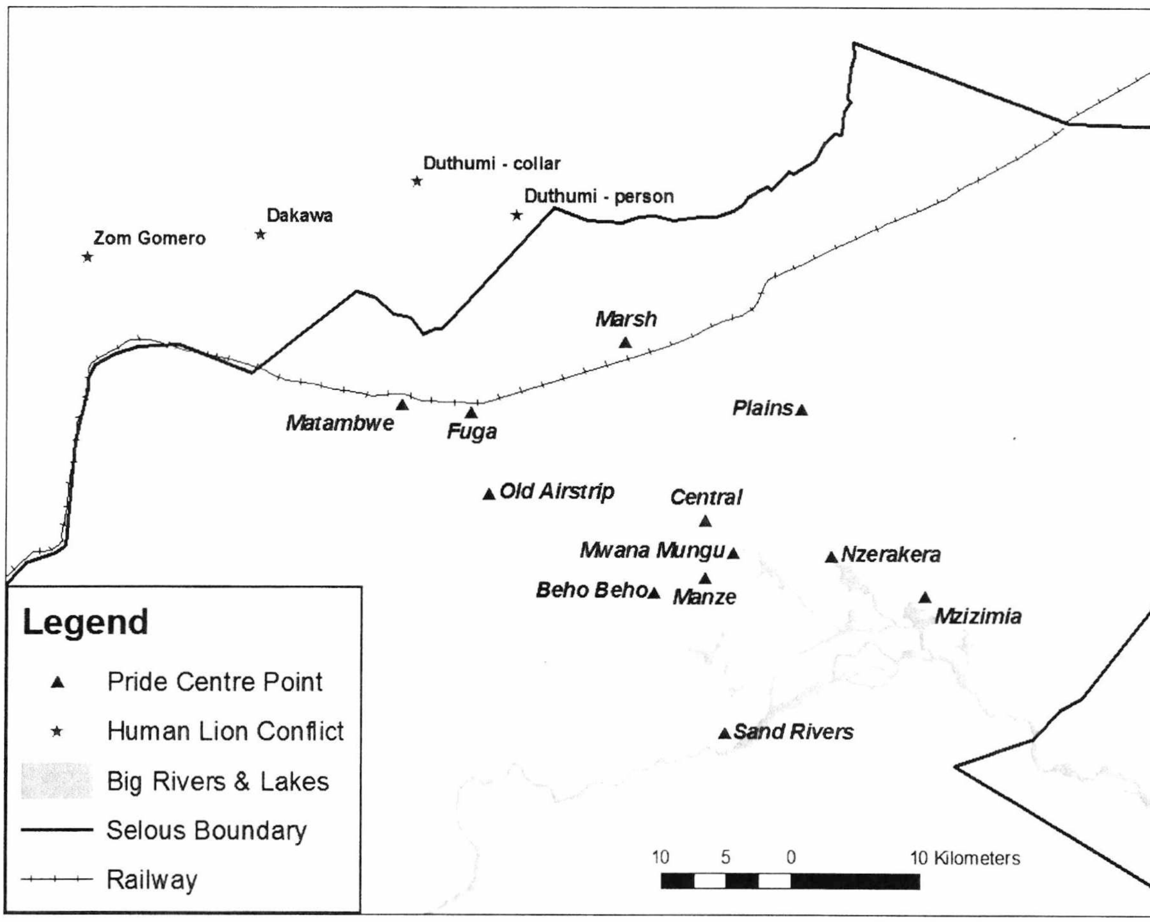
Appendices

APPENDIX 1: Lion Identification Cards. Front and back of a card shown below. Individual identification cards have been made for 124 lions in the study area. These cards have been scanned, and are available on CD on request.



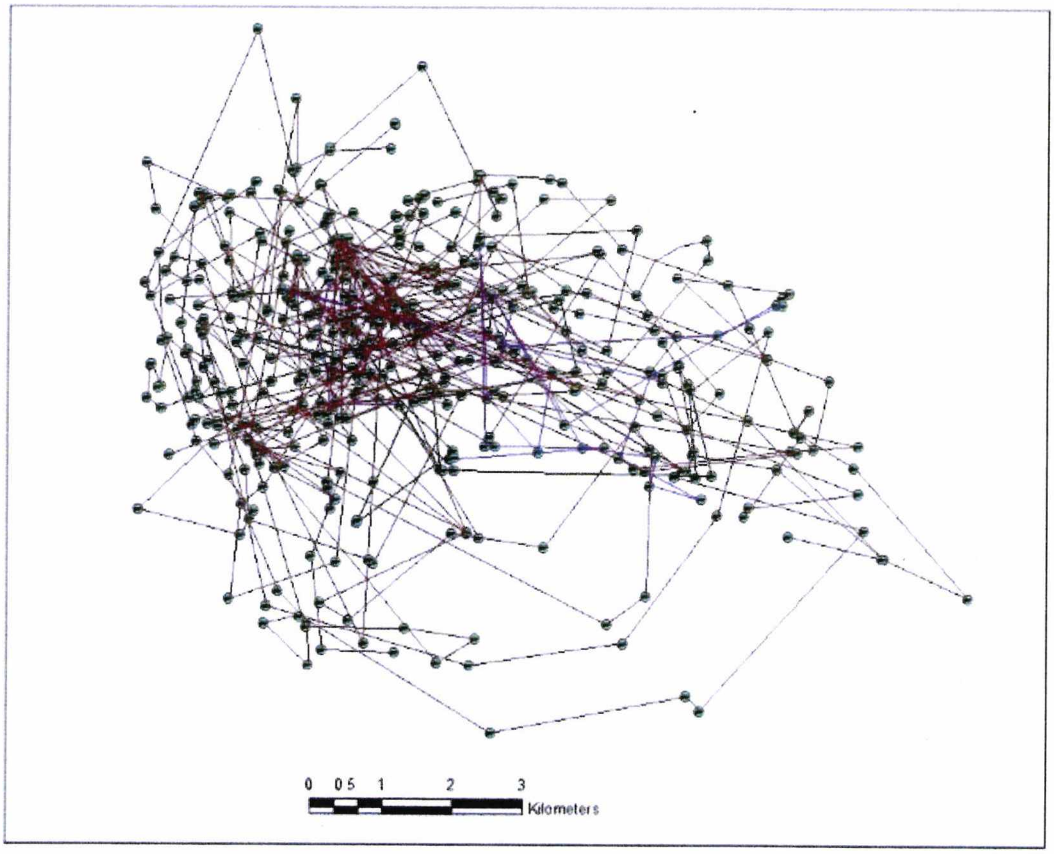


APPENDIX 2: Centre point of pride territories of lions in Matambwe sector of SGR from 2006-2009, and points marking human-lion conflict in areas bordering SGR during the same period.



Two of the three lions collared by the project were lost and their collars subsequently found in villages bordering the Matambwe sector. One collar was found near the village of Duthumi in August 2008 and the other near the village of Dakawa in August 2009. It could not be established how the collars got to their final locations, but a sub-adult male lion was killed near the village of Zom Gomero on 3rd September 2008 and a person was killed by a lion near Duthumi on 6th June 2008.

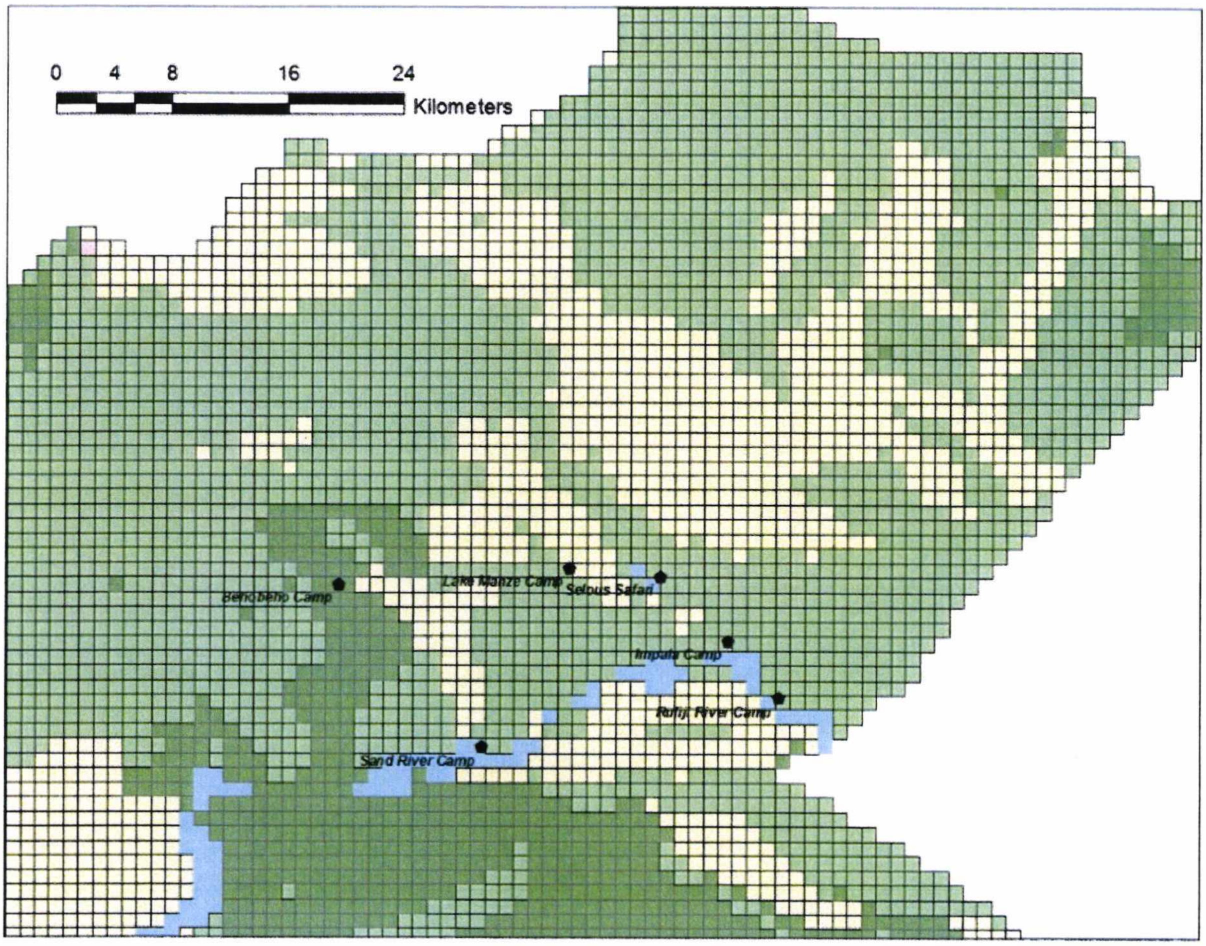
APPENDIX 3: Lion Movement Patterns; visual representation of the source of Table 2.3.



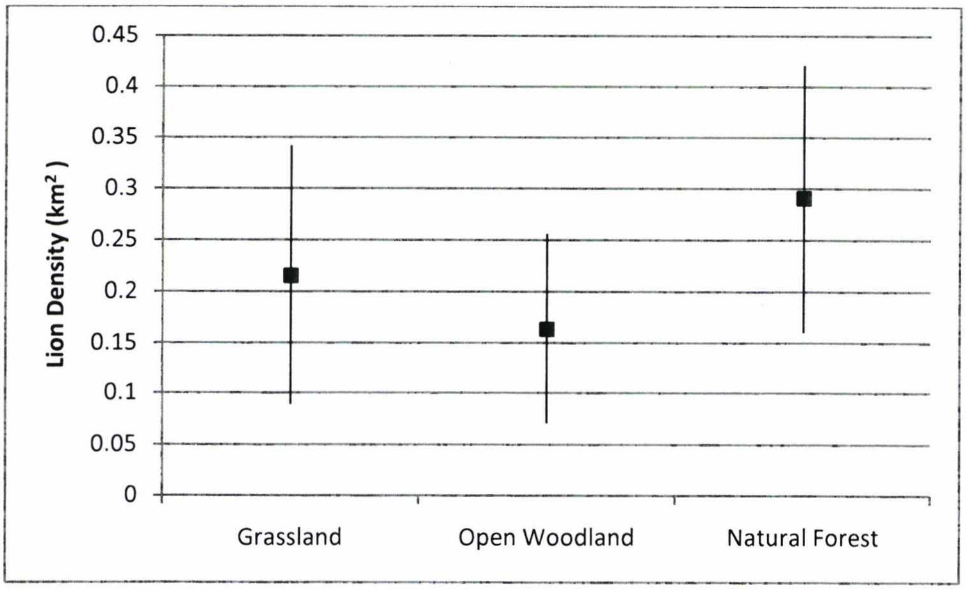
APPENDIX 4: Comparison of Lion Demographic Between Different Populations.

Location	Average Density	Average Group Size	Average Pride Territory	Author
Selous 2006-2009 (Matambwe; North)	0.14 per km^2 All 0.09 per km^2 Adult	3.3 Female 1.7 Male 3.4 Cub	12.7 km^2 50% 48.4 km^2 90%	This study
Selous 1996-1999 (Matambwe; North)	0.16 per km^2 All 0.10 per km^2 Adult	3.4 Female 2.4 Male 5.3 Cub	11.7 km^2 50% 52.4 km^2 90%	Spong, 2002
Selous 1967-1972 (Kingupira; East)	0.08 per km^2 All	3.2 Adult	-	Rodgers, 1974
Serengeti 1966-2006	0.10 per km^2 Adult	4.6 Female	62 km^2 75%	Mosser *et al.*, 2009
Ngorongoro 1962-2006	0.30 per km^2 All But has varied from 0.04 to 0.40 per km^2 over this period.		30 km^2 75%	Kissui & Packer, 2004
Tarangire 2003-2007	0.07 per km^2 All (Highest was 0.1 per km^2)			Kissui, 2008
Manyara 1966 & 2004	0.1 per km^2 All			Schaller, 1972 & recent unpublished survey (Ikanda, D. pers com.)
Katavi 1999 & 2008	0.07 per km^2 adult. 0.04 per km^2 adult (range 0.02 – 0.1 per km^2 adult).			Caro, 1999 Kiffner, 2009
Masai Mara	0.2-0.3 per km^2	22 All 9.2 Female 2.4 Male		Ogutu & Dublin, 1998
Kruger	0.1 per km^2 adult.	11.8 All		Funston *et al.*, 2003

APPENDIX 5: Habitat map for northern SGR; reduced to three habitat types.



Grassland: light brown. **Open woodland:** light green. **Closed Woodland/natural forest:** dark green.



Grassland (n=123), Open woodland (n=380), and Natural Forest (n=38). Lion density figures from Figure 3.2. Mean ± standard deviation.

APPENDIX 6: All prey preference data.

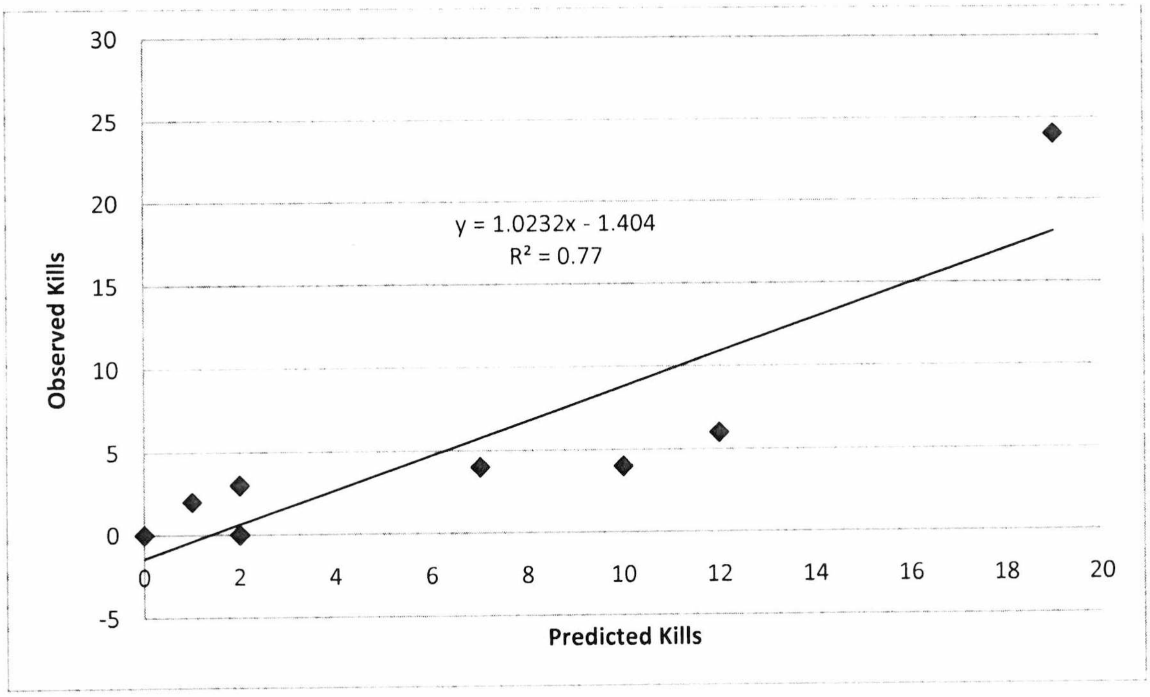
$$D = \frac{r - p}{r + p - 2rp}$$

Species	**Seen**	***p***	**Kills**	***r***	***D***
Buffalo *Syncerus caffer*	446	0.034	10	0.179	0.719
Bushbuck *Tragelaphus scriptus*	1	0.000	2	0.036	0.996
Eland *Tragelaphus oryx*	62	0.005	0	0.000	-1.000
Elephant *Loxodonta africana*	67	0.005	1	0.018	0.557
Giraffe *Giraffa camelopardalis*	586	0.045	7	0.125	0.504
Hippopotamus *Hippopotamus amphibius*	1	0.000	0	0.000	-1.000
Impala *Aepyceros melampus*	7701	0.591	2	0.036	-0.950
Kongoni (Hartebeest) *Alcephalus buselaphus*	7	0.001	2	0.036	0.971
Greater Kudu *Tragelaphus strepsiceros*	4	0.000	0	0.000	-1.000
Warthog *Phacochoerus africanus*	374	0.029	1	0.018	-0.239
Waterbuck *Kobus ellipsiprymnus*	9	0.001	0	0.000	-1.000
Wildebeest *Connochaetes taurinus*	2716	0.209	19	0.339	0.322
Zebra *Equus burchellii*	1046	0.080	12	0.214	0.515

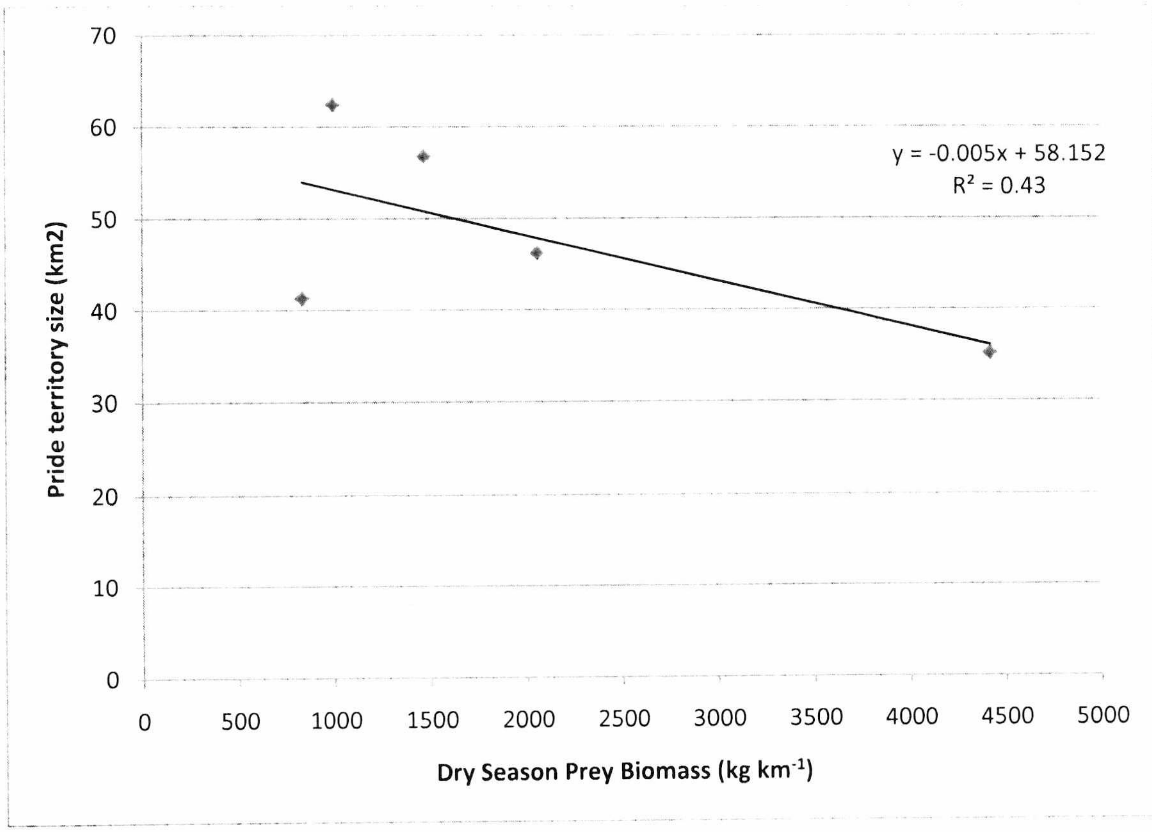
APPENDIX 7: Observed kills versus predicted kills (based on Hayward & Kerley 2005; Hayward et al. 2007a).

Linear regression: $r^2 = 0.77$, $\beta = 1.02$, $P < 0.01$

Prey	Observed Kills	Predicted Kills
Buffalo	10	4
Zebra	12	6
Giraffe	7	4
Wildebeest	19	24
Warthog	1	2
Bushbuck	2	0
Eland	0	0
Impala	2	3
Total	**53**	**43**

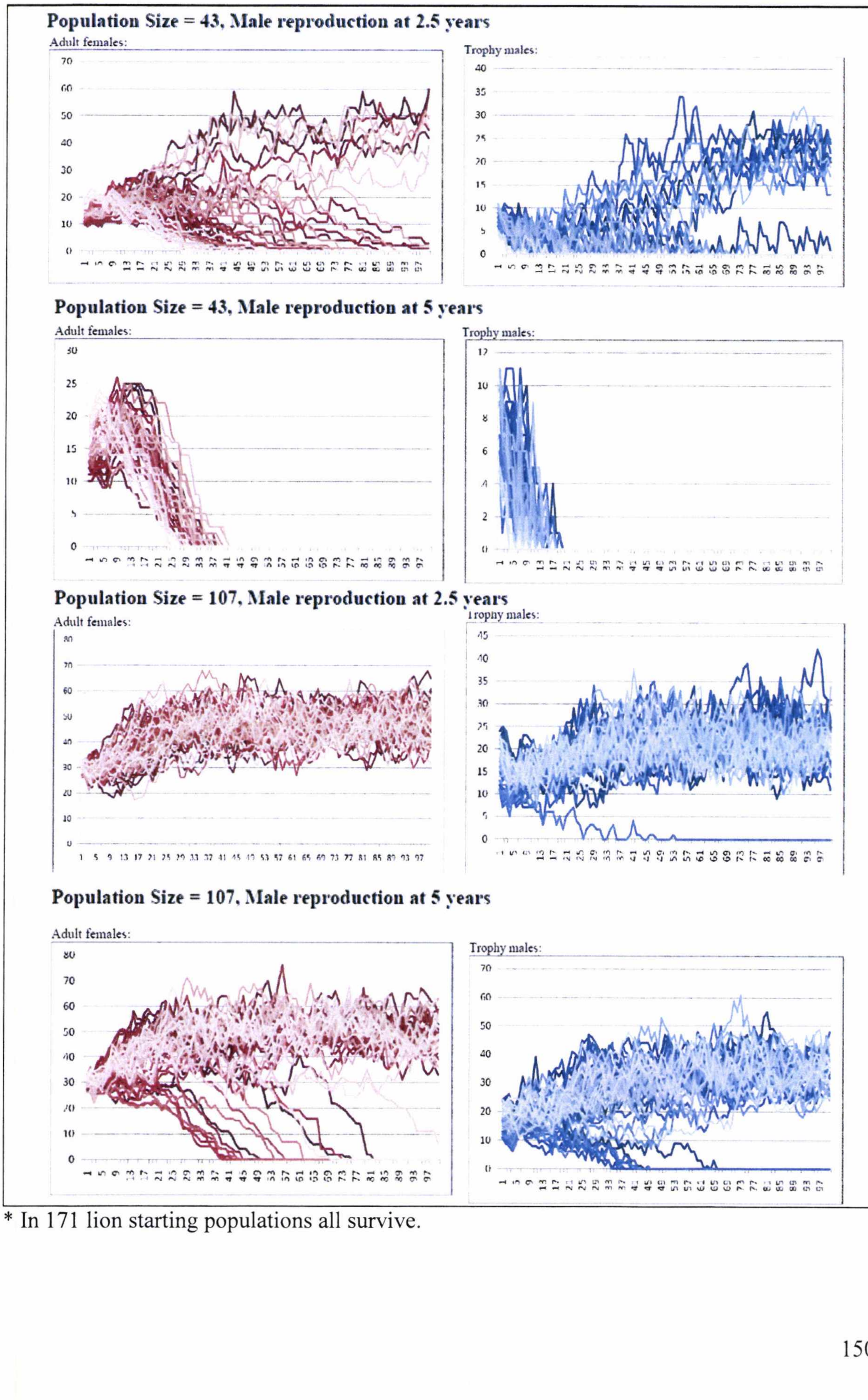


APPENDIX 8: Lion pride territories versus dry season prey biomass



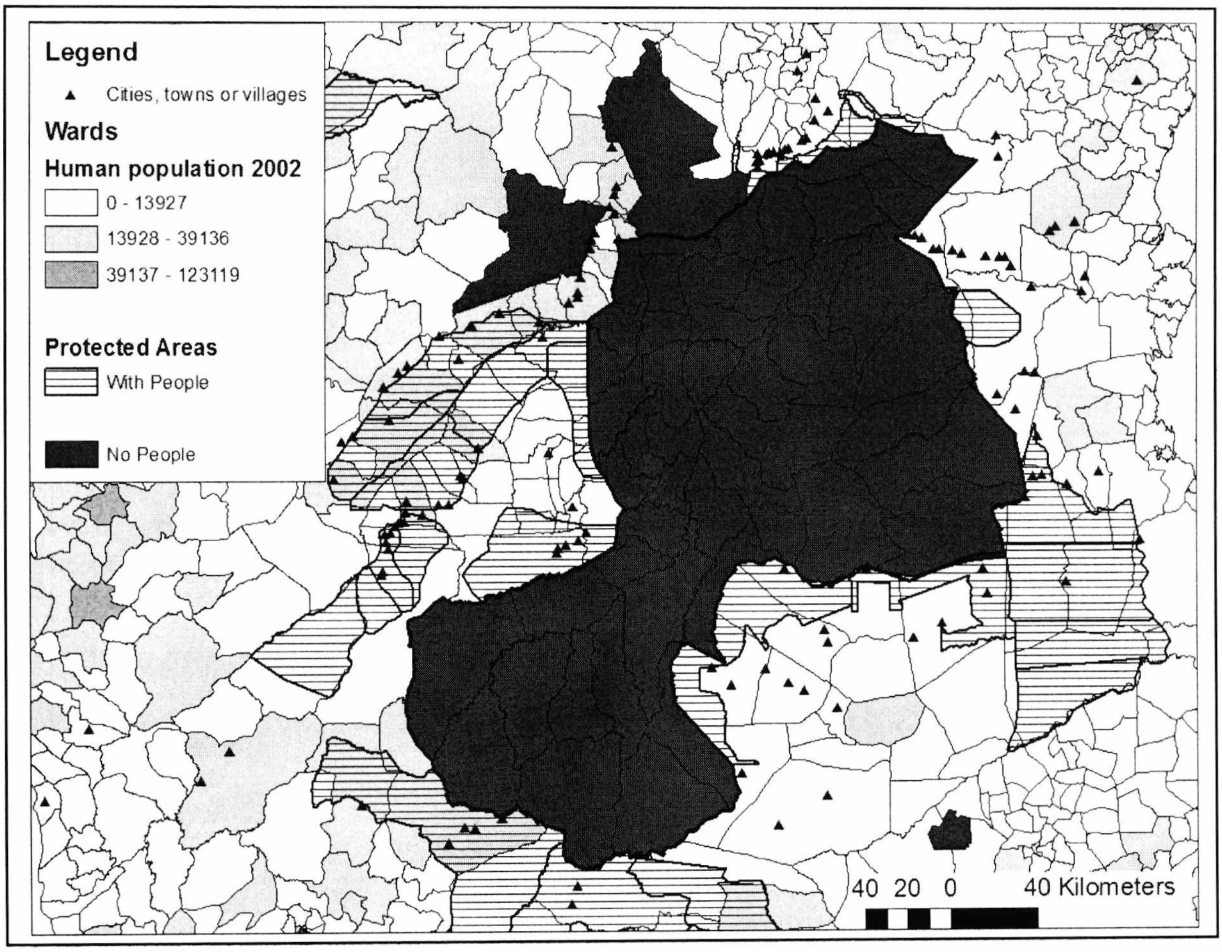
Result not significant due to small sample size.

APPENDIX 9: Results of simulation model



* In 171 lion starting populations all survive.

APPENDIX 10: Human population by ward surrounding SGR.



Appendix 11: Newspaper Data

Newspaper Name:		
Is the story in: Swahili or English		
Date when article published:		
Article Content:		**Please use this space to write any comments:** (For example if the article does not fit into any of the topics).
1) Trophy Hunting: Y / N	1a) Hunting companies Y / N	
	1b) Corruption Y / N	
	1c) Lion Y / N	
	1d) Other: Please State Below	
2) Lion human conflict: Y / N	2a) Man-eating Y / N	
	2b) Livestock killing Y / N	
	2c) Lions near towns Y / N	
	2d) Other: Please State Below	
3) Lion conservation: Y / N	3a) Populations / Biology Y / N	
	3b) Habitat Loss Y / N	
	3c) Research / TAWIRI Y / N	
	3d) Other: Please State Below	
4) Lions and tourism: Y / N	4a) National Parks Y / N	
	4b) Game Reserves Y / N	
	4c) Tourist attraction Y / N	
	4d) Other: Please State Below	
Article Length / Location:		
5a) More than one page 5b) One Page 5c) Less than one page 5d) Less than half page 5e) Less than quarter page		
Are there photographs / pictures with the article? Y / N		How many pictures?
Article is on what page?		
Total number of pages in Newspaper:		
Where in Tanzania is the article about? All (general) or please state region / district:		
Do you feel the article is **positive** or **negative** about lions / hunting?		

Appendix 12: Questionnaires

General Information.			
I) Do you work for:	1) Wildlife Division	2) Hunting tourism company	3) Photographic tourism company / Lodge
	4) Other; Please state:		
II) How long have you been involved with/ worked in Selous Ecosystem?			
1) 0-5 years	2) 5-10 years	3) 10-15 years	4) + 15 years
III) Over the last year, how long were you in Selous Ecosystem?			
1) less than 1 month	2) 1-3 months	3) 3-6 months	4) + 6 months.
IV) Where were you? Please circle the Blocks that you have been to, and also tick the boxes for Sectors/Areas you feel you have good knowledge of:			
1) Matambwe Sector	☐	Blocks: B1 KY1 LA1 MK1 R3 Y1 Z1	
2) Msolwa Sector	☐	Blocks: K4 K5 M1 M2 R1 R2 R4 U1 U2	
3) Kingupira Sector	☐	Blocks: LL2 LL3 MA1 MS1 RU1 U3 U4	
4) Ilonga Sector	☐	Blocks: IH1 K1 K2 K3 L1 LU1 LU2 LU3 LU4 LU5	
5) Miguruwe Sector	☐	Blocks: LL1 MJ1 MT2	
6) Liwale Sector	☐	Blocks: MB3 MH1 ML1 MT1	
7) Likuyu Seka Sector	☐	Blocks: LU6 LU7 LU8 MB2	
8) Kalulu Sector	☐	Blocks: MB1 N1 N2	
9) Wildlife Management Areas	☐	Please state which WMA in Selous area (and state if visited):	
10) Game Controlled Areas	☐	Please state which GCA in Selous area (and state if visited):	
11) Open Areas	☐	Please state which Open Area (and state if visited):	
12) Other/Comments. Please write any other comments here:			
V) Are you a:	1) Tanzanian Citizen	2) Tanzanian Resident	3) Other, please state:

Perceptions of Populations:			
I) Is the population of elephant:	1) Increasing	2) Decreasing	3) Staying the same
	4) Don't know		
II) Is the population of buffalo:	1) Increasing	2) Decreasing	3) Staying the same
	4) Don't know		
III) Is the population of lion:	1) Increasing	2) Decreasing	3) Staying the same
	4) Don't know		
IV) Is the population of leopard:	1) Increasing	2) Decreasing	3) Staying the same
	4) Don't know		
V) Any other comments on population trends:			

Information on Lions:
I) How often do you see lions (or signs of lions; e.g. footprints)? 1) Weekly 2) Monthly 3) Every 3 months 4) Yearly 5) Never
II) If you see lions, what is their general group size? 1) Don't see lions 2) Small groups; 1-5 lions 3) Medium groups; 5-15 lions 4) Large groups; +15 lions
III) If you see male lions, in general how big are their manes? 1) Don't see male lions 2) No manes 3) Slight mane[A] 4) Incomplete mane[B] 5) Full mane[C] A: On front of neck and chest, ridge along back of neck. B: Mane forms a complete ring around face, but there is a space between the central tuft of hair on the head and the ears. C: Heavy manes with long hair on throat and chest, no space between central tuft and ears.
IV) Do you have any data on lion numbers in your area? 1) Yes 2) No
V) If yes, please complete table below, if no, write N/A here:

Area/Block	Pride Name	No. of Adult Females	No. of Adult Males	No. of Cubs	Comments

Illegal Resource Use in Protected Areas
I) Is there illegal resource use in your area? 1) Yes 2) No
II) If yes, what is the main form of illegal use? 1) Elephant poaching 2) Bushmeat poaching 3) Fishing 4) Timber/wood extraction 5) Other; Please state:
III) If there is illegal resource use, what proportion is accounted for by each of the categories below? For example, 40% accounted for by elephant poaching, 40% accounted for by fishing, 15% accounted for by timber extraction, 5% by other (e.g. honey harvesting). If this question is not applicable, write N/A here:

Illegal Resource Use	Proportion (%)	Please write any comments here:
1) Elephant poaching		
2) Bushmeat poaching		
3) Fishing		
4) Timber/wood extraction		
5) Other; please state:		
5) Other; please state:		

IV) How often do you see signs of illegal resource use? 1) Daily 2) Weekly 3) Monthly 4) Every 3 months 5) Yearly 6) Never
V) How often do you see people illegally in the protected area? 1) Daily 2) Weekly 3) Monthly 4) Every 3 months 5) Yearly 6) Never
VI) If you see people illegally in the protected area, what size groups are they in? 1) Don't see people 2) Small groups; 1-5 people 3) Medium groups; 5-15 people 4) Large groups; +15 people

Perceptions of Management of the Selous
I) Illegal use of natural resources (poaching) in the Selous is: 1) Decreasing 2) Increasing 3) Staying the same 4) Don't know
II) An increase in tourist numbers will have a negative impact on the Selous. 1) Strongly agree 2) Agree 3) Don't know 4) Disagree 5) Strongly Disagree
III) In the Selous, areas used for photographic tourism should: 1) Decrease 2) Increase 3) Stay the same 4) Don't know
IV) In the Selous, hunting by tourists is good for conservation. 1) Strongly agree 2) Agree 3) Don't know 4) Disagree 5) Strongly Disagree
V) Human-wildlife conflict around the Selous is: 1) Decreasing 2) Increasing 3) Staying the same 4) Don't know
VI) Communities living around the Selous are benefiting from living near the Selous. 1) Strongly agree 2) Agree 3) Don't know 4) Disagree 5) Strongly Disagree

Tourist / Trophy Hunting. For Wildlife Division and hunting company personnel only.
I) Tourist hunting in Selous is sustainable. 1) Strongly agree 2) Agree 3) Don't know 4) Disagree 5) Strongly Disagree
II) The hunting quota for lion should be: 1) Decreased 2) Increased 3) Stay the same 4) Don't know
III) The hunting quota for lion is not necessary, only older lions should be hunted. 1) Strongly agree 2) Agree 3) Don't know 4) Disagree 5) Strongly Disagree
IV) If lion hunting is restricted by their age, it should be restricted to males over: 1) 4 years old 2) 5 years old 3) 6 years old 4) 7 years old 5) Not applicable
V) The colour of the lion's nose is a good indicator of the lion's age. 1) Strongly agree 2) Agree 3) Don't know 4) Disagree 5) Strongly Disagree
VI) Please list other methods that you use to age lions in the field:
VII) In hunting situations, what proportion of males that you come across do you leave? 1) None, shoot all males seen 2) 1 out of every 5 males seen is not shot 3) 2 out of every 5 males seen is not shot 4) 3 out of every 5 males seen is not shot 5) 4 out every five males seen is not shot 6) Question is not applicable.
VIII) If you do not shoot males in hunting situations, why do you leave them? 1) Male is too young 2) Male is with females and cubs 3) Male is mating with female 4) Conditions are not right for hunting 5) Other, please state: 6) Question is not applicable.
XI) Concession / block fees should be: 1) Decreased 2) Increased 3) Stay the same 4) Don't know
X) Trophy / Game fees should be: 1) Decreased 2) Increased 3) Stay the same 4) Don't know
XI) Any other comments on trophy hunting:

Thank you for completing this Questionnaire. Please return to: Henry Brink, Selous Lion Project, Box 34514, Dar es Salaam.

Appendix 13: Semi-Structured Interview

Date:	Start time:	End time:	Nationality:
Job:		Age: 20-30 30-40 40-50 50-60 +60	Sex: M / F

Interviews should last between one to two hours, and will take the following format. First, assure the interviewee of the confidential nature of the interview, and then carry out above questionnaire with the individual, which will be followed by questions on the following themes:

• Establish the Interviewee's Area of Expertise, and focus on that.
Where in the Selous/Kilombero have they worked? How long have they worked there? (Covered in questionnaire – but expand here, if necessary).
Have they been to the field recently? Where? When?

• Knowledge of Lion in their Block/Selous
What knowledge do they have of lions in their blocks/area? (Covered in questionnaire – but expand here, if have detailed knowledge). Have there been any censuses in their block/area? Where do they generally see the lions? Specific area (GPS?) or general habitat types (e.g. near water, dense woodland, open areas). What population of lions do you think Selous supports?
What do the lions feed on in their blocks/area?
Do they see females more often than males? Get group composition in more detail.

• Perceptions of Lions
Are lions important to the hunting industry? Why or why not?

• The Process of Tourist Hunting for Lions.
Describe in detail how you hunt lions. Tracked versus baited? What are the advantages of each system? How do you track lions/bait lions? How much bait? What used as bait? How much time do you have to observe the lion prior to shooting it?
How many male lions do you choose not to shoot? What is this decision based on?
How do you deal with a client who is keen to shoot a lion, but you've said no?
What sort of support/authority do you have to uphold your decision?
Discuss Tanzania wildlife policy and lions.
Is tourist hunting of 'problem' lions in areas around Selous feasible (HWC reduction method?)?

• Aging Lions in the Field.
Can lions be aged accurately in the field? Why or why not?
If they can be aged, how do you age a lion? Have you tried to age a lion using nose colour?

• Management Concerns in the Selous.
Are there any concerns for the management of Selous? What? Why?

• Suggestions for Improving Conservation in the Selous.
Based on previous question, what can be done to improve conservation in Selous (only ask if problems are identified)?
What do you think of competitive block bidding?

APPENDIX 14:

Appendix 14.a: Packer, C., Kosmala, M., Cooley, H.S., Brink, H., Pintea, L., Garshelis, D., Purchase, G., Strauss, M., Swanson, A., Balme, G., Hunter, L. & Nowell, K. (2009) Sport Hunting, Predator Control and Conservation of Large Carnivores. PLoS One **4 (6)**: e5941.

Appendix 14.b: Packer, C., Brink, H., Kissui, B.M., Maliti, H., Kushnir, H., & Caro, T. (2010) Effects of trophy hunting on lion and leopard populations in Tanzania. *Conservation Biology*. In Press.

Sport Hunting, Predator Control and Conservation of Large Carnivores

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Abstract

Sport hunting has provided important economic incentives for conserving large predators since the early 1970's, but wildlife managers also face substantial pressure to reduce depredation. Sport hunting is an inherently risky strategy for controlling predators as carnivore populations are difficult to monitor and some species show a propensity for infanticide that is exacerbated by removing adult males. Simulation models predict population declines from even moderate levels of hunting in infanticidal species, and harvest data suggest that African countries and U.S. states with the highest intensity of sport hunting have shown the steepest population declines in African lions and cougars over the past 25 yrs. Similar effects in African leopards may have been masked by mesopredator release owing to declines in sympatric lion populations, whereas there is no evidence of overhunting in non-infanticidal populations of American black bears. Effective conservation of these animals will require new harvest strategies and improved monitoring to counter demands for predator control by livestock producers and local communities.

Citation: Packer C, Kosmala M, Cooley HS, Brink H, Pintea L, et al. (2009) Sport Hunting, Predator Control and Conservation of Large Carnivores. PLoS ONE 4(6): e5941. doi:10.1371/journal.pone.0005941

Editor: Michael Somers, University of Pretoria, South Africa

Received March 7, 2009; **Accepted** May 7, 2009; **Published** June 17, 2009

Funding: Simulation modeling was supported by funding by NSF Biocomplexity grant BE-0308486. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

Management agencies typically skew harvests toward males in order to protect adult females. However, in species with extensive paternal investment such as African lions (*Panthera leo*), trophy hunting can increase the rate of male replacement (and associated infanticide) to the point of reducing population size unless offtakes are restricted to males old enough to have reared their first cohort of dependent offspring (≥5–6 yrs of age) [1–3]. Solitary felids have none of the "safety nets" provided by the cooperative cub rearing strategies of African lions [4–5], and Fig. 1ab illustrates the greater vulnerability of solitary species by examining the effects of trophy hunting on a hypothetical population of "solitary lions" while leaving other demographic parameters from ref. [1] unchanged (Supporting Information Table S1, also see ref. [6]). Leopards (*Panthera pardus*) may be more sensitive to sport hunting than solitary lions (with a safe minimum age of 6–7 yrs of age, Fig. 1c), whereas cougar (*Felis concolor*) males can be safely harvested as young as 4 yrs of age (Fig. 1d).

We tested whether infanticidal species are vulnerable to over-hunting by focusing on four large carnivore species with sizable markets for sport-hunted trophies, comparing three infanticidal felids (lions, cougars and leopards) to American black bears (*Ursus americanus*). We used black bears as a control case because males do not kill cubs in order to increase mating opportunities (sexually-selected infanticide – SSI), so rates of infanticide are not increased by male-biased trophy hunting; in fact, among ursids, SSI has been documented in only one population of European brown bears (*U. arctos*) [7–9].

We extracted data from the UNEP World Conservation Monitoring Centre (WCMC) CITES trade database (See Materials and Methods). Data on total trophy harvests of lions and leopards are not available, so we used CITES-reported exports, which in cougars and black bears were highly correlated with domestic sport-hunting totals (Supporting Information Fig. S1); likewise CITES-reported trade in Tanzania's lion trophies showed a close match between imports and exports. Given sustained market demand, harvest trends should provide a reasonable proxy of population trends since sport hunters use intensive methods such as baits and hounds to locate these animals, and quotas on annual offtakes are either too high to limit harvests or (for black bears) reflect the management agency's perception of population trend [10].

Results

Fig. 2 shows the annual CITES exports for lions and leopards and US offtakes of cougars and black bears (See Materials and Methods). The reported number of trophies increased rapidly across all four species as markets grew during the 1980's and 1990's [11–12]. Offtakes have continued to increase for black bears, reflecting the sustained growth of bear populations

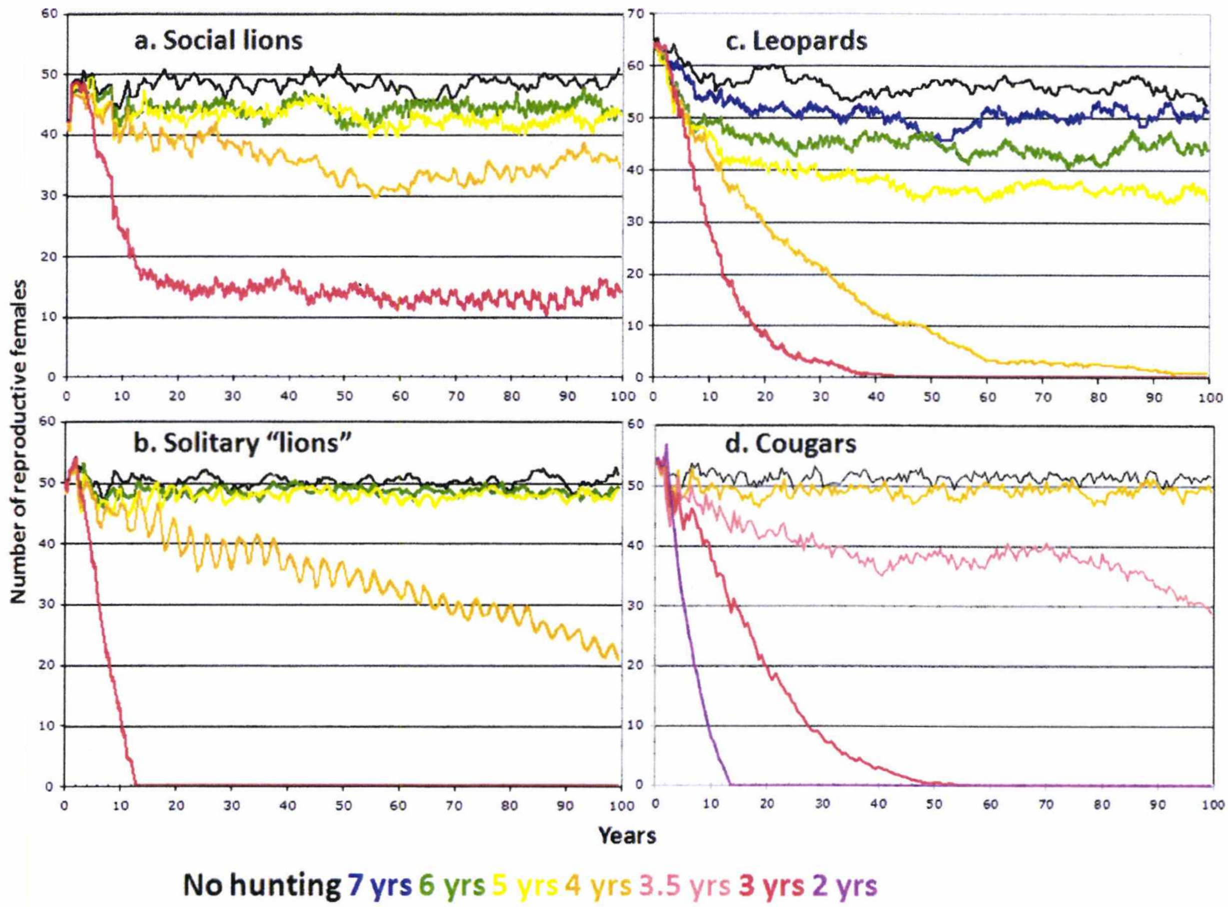

Figure 1. Average number of adult females in population simulations where all eligible males are removed during a 6-mo hunting season each year for 100 yrs. Colors indicate outcomes for different age minima for trophy males; each line indicates average from 20 runs. **A.** Population changes for "social lions" follow the assumptions and demographic variables in ref. [1] except to restrict hunting to 6-mo seasons and to incorporate additional details of dispersal, survival and reproduction [44–46]. **B.** Population changes for a hypothetical lion population where males and females are solitary and each territorial male controls one female. **C.** Population changes for leopards based on long-term data from Phinda Private Game Reserve [33,47] and other sources [37,48]. **D.** Population changes for cougars based on demographic data from refs. [27,49–53].
doi:10.1371/journal.pone.0005941.g001

throughout North America [13]. Leopard offtakes reached an asymptote in most countries, except for declines in Zambia in the 1980's and Zimbabwe in the 1990's and a recent CITES-granted increase to Namibia. In contrast, lion offtakes peaked then fell sharply in the 1980's and 1990's in Botswana, Central African Republic, Namibia, Tanzania, Zambia and Zimbabwe. Cougar offtakes showed similar peaks and declines in the 1990's in Arizona, Colorado, Idaho, Montana and Utah (Fig. 2).

The downward harvest trends for lions and cougars (highlighted in Supporting Information Fig. S2) most likely reflected declining population sizes: success rates (as measured by harvest/quota) have fallen for both cougars and lions (Supporting Information Fig. S3). Demand for lion trophies (as measured by total imports from across Africa) has grown in the US and held stable in the EU since the mid-1990s, sustained in recent years by imports of trophies of captive lions from South Africa [12,14] (Supporting Information Fig. S3). Several countries instituted temporary bans on lion trophy hunting (Botswana in 2001–2004, Zambia in 2000–2001 and western Zimbabwe in 2005–2008) or banned female lions from quota (Zimbabwe, starting in 2005), but these measures were implemented well after the major decline in lion offtake in each country. The harvest trends are also consistent with recent surveys suggesting a 30% continent-wide population decline in African lions [15] and declining cougar populations in several US states [16–17]. Conversely, black bear populations appear to be increasing across their range [13], even in states where cougar populations have declined (Fig. 2). Although not apparent from most hunting offtakes, leopards have undergone an estimated range decline of 35% in Africa [18] and were recently listed as Near Threatened by IUCN due to habitat loss, prey depletion, illegal skin trade and problem animal conflicts [19].

Trophy hunting is likely to have contributed to the declines in lion and cougar populations in many areas. Over the past 25 yrs, the steepest declines in cougar and lion harvests occurred in jurisdictions with the highest harvest intensities (Fig. 3a). Similarly, hunting blocks with the highest lion offtakes per 1000 km^2 in Tanzania's Selous Game Reserve showed the steepest declines between 1996 and 2008 ($r^2 = 0.26$, n = 45 blocks, P = 0.0004). The Selous is the largest uninhabited hunting area in Africa (55,000 km^2) and has long been the premier destination for lion trophies. Across jurisdictions, declining harvests were unrelated to habitat loss for either lions or cougars (Fig. 3b) or to snow

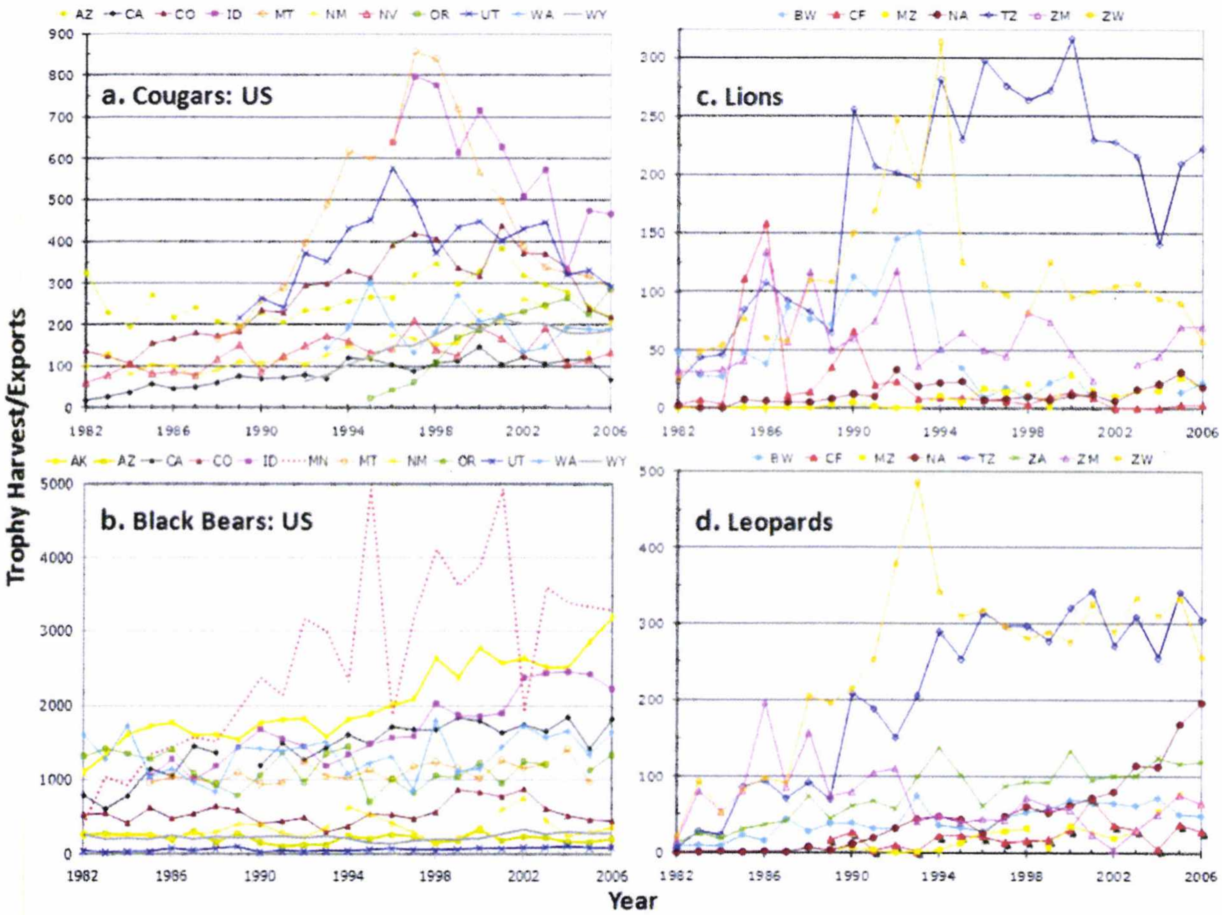

Figure 2. Domestic offtakes of a) cougars and b) black bears and CITES-reported trophy exports of c) lions and d) leopards. For US states: AK = Alaska, AZ = Arizona, CA = California, CO = Colorado, ID = Idaho, MN = Minnesota, MT = Montana, NM = New Mexico, NV = Nevada, OR = Oregon, UT = Utah, WA = Washington, WY = Wyoming. For CITES data: BW = Botswana, CF = Central African Republic, MZ = Mozambique, NA = Namibia, TZ = Tanzania, ZM = Zambia, ZW = Zimbabwe.
doi:10.1371/journal.pone.0005941.g002

conditions for cougars. We modified our population simulation models to estimate impacts of sport hunting in a changing environment and found that habitat loss only imposes an additive effect on the impact of trophy hunting (Supporting Information Fig. S4). Note that habitat loss in many African nations has been so extensive (Fig. 3b) that lion offtakes have failed to recover for 10–20 yrs following the peak harvest years except in Namibia.

Although trophy hunting of lions and cougars is often portrayed as an economic strategy for increasing support for carnivore conservation, local communities often seek extirpation of problem animals [15,20–22]. Thus, sport hunting quotas may sometimes reflect pressures to control carnivores rather than to conserve them. Across Africa, countries with the highest intensity of lion offtake also had the highest number of livestock units per million hectares of arable land ($P = 0.047$, $n = 7$). In the US, Oregon announced plans in 2006 to reduce its cougar population by 40% to decrease depredation on livestock, pets and game mammals [23], Washington altered its cougar quotas in response to human-wildlife conflicts in the 1990s–2000s, and recent offtakes have exceeded government-sanctioned eradication programs in several states. For example, Utah's sport-hunting cougar harvests averaged 500/yr in 1995-7 compared to peak culls of 150/yr in 1946–1949 [24], and Montana sport hunters harvested 800/yr in 1997–1999 vs. 140/yr in the peak "bounty" years of 1908-11 [25]. Likewise, South Africa exported 120 leopard trophies per year in 2004–2006, similar to the cull of 133 leopards per year in Cape Province (which covered most of the country) during 1920–1922 [26].

Fig. 4 shows the potential consequences of coupling a 40% cull of cougars with intensive sport hunting if the control program only targets males (reflecting traditional trophy hunting), removes males and females in proportion to their abundance, or only removes adult females. Fig. 4adg show population trends for the maximum fixed offtakes that never resulted in population extinctions during 20 simulations, whereas Fig. 4beh show the minimum fixed harvests that caused extinction in all 20 runs (often within 10 yrs of an initial decline). Fig. 4cfi show the consequences of applying the maximum "safe" offtakes if the population were inadvertently culled by 50% because of inaccurate population estimates. Consistent with population viability analyses [27–28], a female-only harvest comes closest to maintaining a persistent population reduction; a mixed male-female strategy allows the largest number of trophies to be harvested; a male-only harvest never maintains a

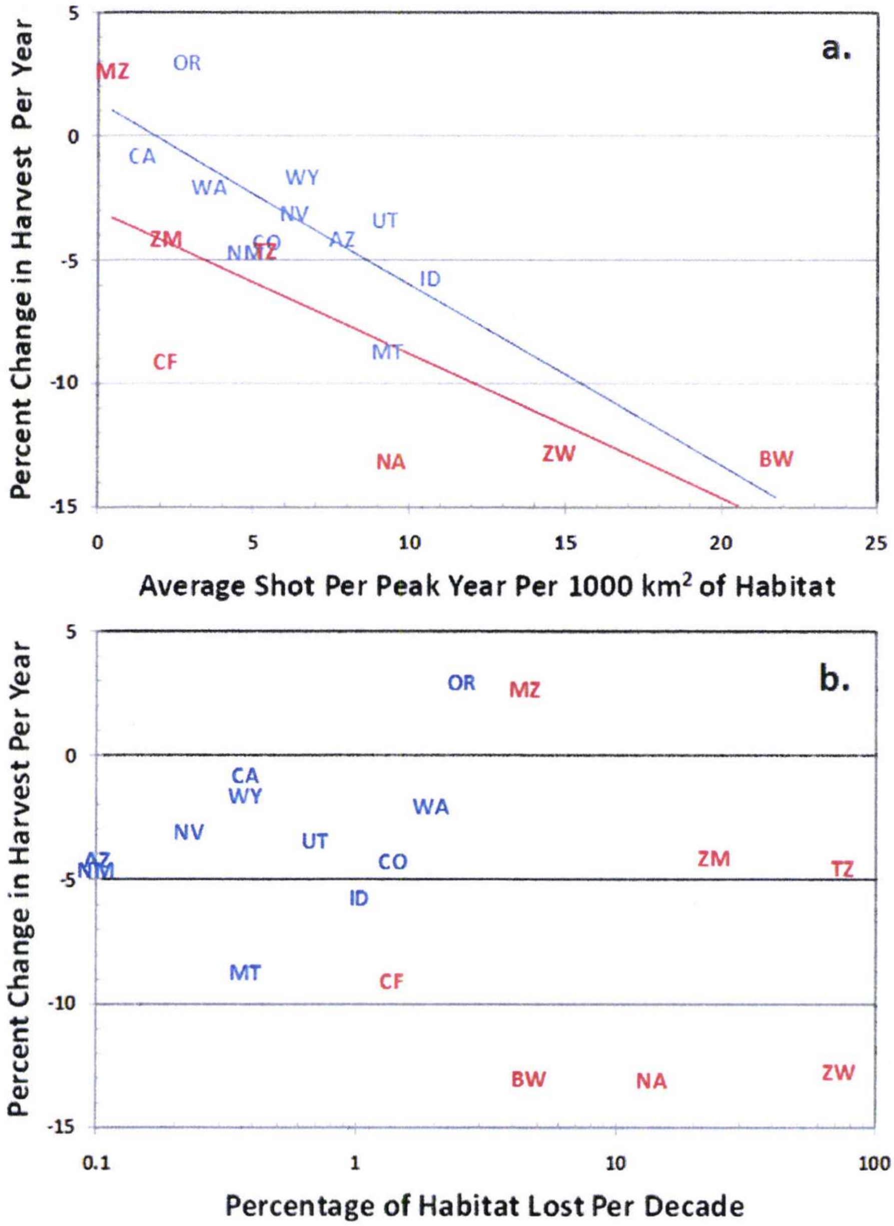

Figure 3. Recent trends in cougar offtakes (blue) and lion offtakes (red) as functions of a) harvest intensity and b) habitat loss. Jurisdictions with the highest harvest intensity showed the greatest decline in cougar offtakes ($r^2 = 0.5151$, $P = 0.0129$) and lion offtakes ($r^2 = 0.5796$, $P = 0.0468$). Habitat loss is plotted on a log scale to allow comparison between the African countries and the US states.
doi:10.1371/journal.pone.0005941.g003

40% reduction in population size and has the smallest margin of error (male-only harvests can have catastrophic effects even in non-infanticidal species [29]).

These simulations assume a fixed harvest whereas many wildlife agencies reduce their quotas in response to lowered offtakes (Supporting Information Fig. S3 also see ref. [30]). However, offtakes may often be maintained at constant levels through compensatory increases in hunting effort, running the risk of an "anthropogenic Allee effect" [31–32]. Hunters in Zambia, Zimbabwe and Tanzania maintain their lion harvests by shooting males as young as 2 yrs of age (Fig. 5). In Zimbabwe, high lion offtakes were sustained from 1995 until 2005 by allowing females on quota [3], and the duration of lion safaris increased by nearly 18% from 1997 to 2001 (Supporting Information Fig. S3). Similarly, hounds have been used to hunt leopards in Zimbabwe since 2001, potentially masking a continued population decline.

Discussion

Mortality from state-sanctioned and illegal predator control likely contributed to the overall population declines of cougars and lions; while leopards are also killed as pests, the leopard's CITES Appendix I status requires international approval for national export quotas, potentially providing safeguards against overhar-

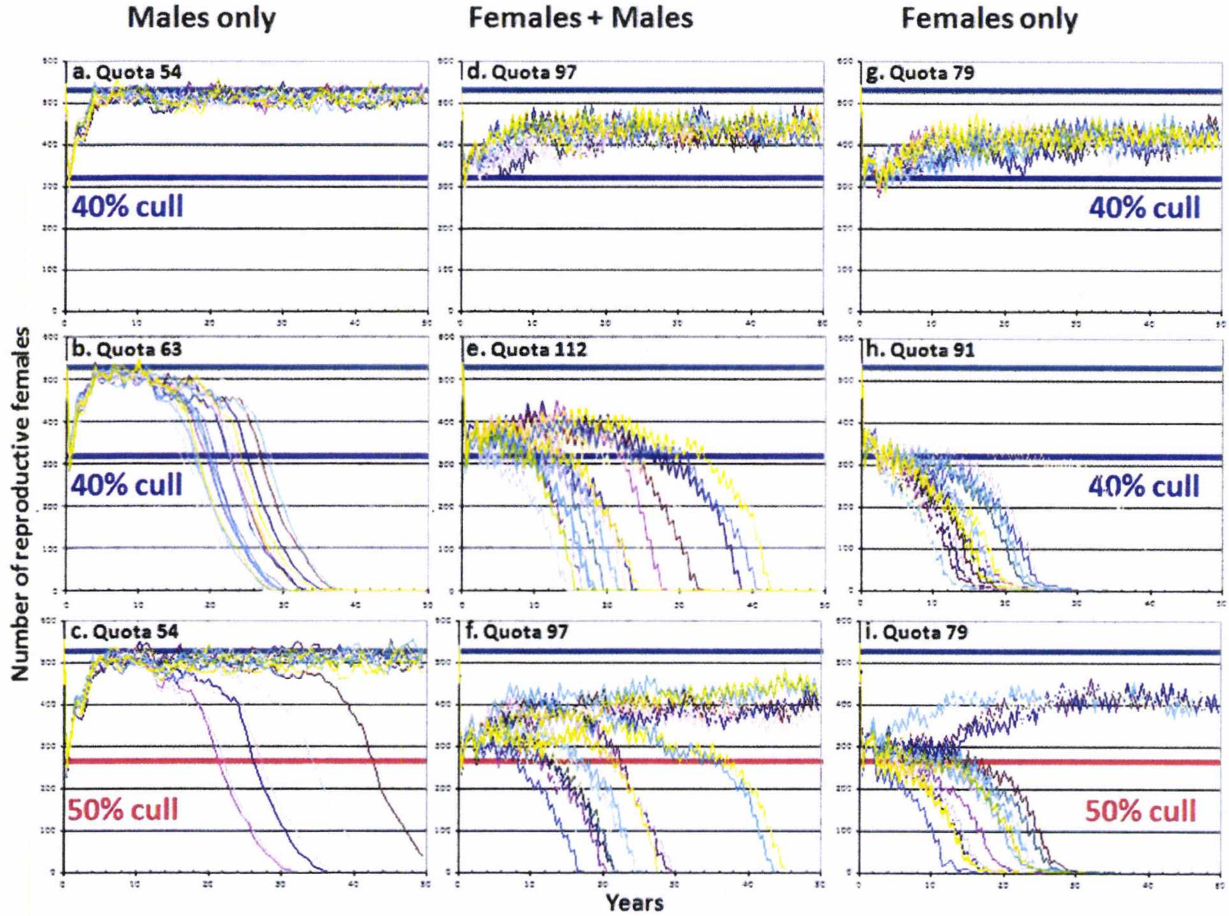

Figure 4. Simulated cougar populations subjected to an initial cull followed by fixed offtakes for 50 yrs. The initial cull is either 40% (top and middle rows) or 50% (bottom row), and the subsequent harvests are either the maximum offtake that incurred no extinctions in 20 runs following a 40% cull (top and bottom rows) or the minimum that produced 20 extinctions in 20 runs following a 40% cull (middle row). In the absence of sport hunting, the stable population size in these simulations is 527 reproductive females (indicated by the heavy black line in each graph); a 40% reduction in population size is indicated by blue lines, a 50% reduction by red lines. Each column represents a different harvest strategy: male only (left column), males and females (middle) and female only (right). Demographic parameters are set as in Fig. 1; quotas allow offtake of animals as young as 2 yrs; each graph shows outputs from 20 runs.
doi:10.1371/journal.pone.0005941.g004

vest. However, leopard exports have declined in some countries, quotas have risen in others, and concerns have been raised over the level of problem animal offtakes and the management of leopard hunting practices [33–35]. Further, leopard populations in many areas may have been "released" [36] by large scale declines in lion numbers: lions inflict considerable mortality on leopards [37]; consequently, hunting blocks in Tanzania's Selous Game Reserve with the highest lion harvest intensities showed the largest *increases* in leopard harvests ($P = 0.0059$ after controlling for declines in lion offtakes, $n = 45$ blocks). Thus the full impact of current trophy hunting practices on leopards may not be fully apparent for several more years.

Harvest policies for infanticidal species such as lions, cougars and leopards that relied on "constant proportion" or "fixed escapement" could help protect populations but require accurate information on population size and recruitment rates, which are virtually impossible to collect; a harvest strategy of "constant effort" can more easily be achieved by measuring catch rates and regulating client days [38–40]. Hunting efficiency could be reduced by banning or limiting the use of baits and hounds, but the absence of direct oversight in remote hunting areas would make enforcement difficult. Alternatively, the age-minimum harvest strategies illustrated in Fig. 1 could be implemented without risk of over-hunting, assuming that ages can be reliably estimated before the animals are shot [41] rather than afterwards [42]. Unsustainable levels of trophy hunting of lions and cougars appear to be driven by conflicts with humans and livestock: the intensity of lion hunting was highest in countries with the most intensive cattle production, and wildlife managers are under similar pressure from US ranchers to raise cougar offtakes. Thus an even more fundamental challenge for carnivore conservation will be to build community tolerance for predators by reducing the need for retaliatory predator control and by improving benefit sharing from well managed trophy hunting [15].

Materials and Methods

We analyzed trophy exports (http://www.unep-wcmc.org/citestrade/) by using the term "trophy" and restricting the analysis to countries that exported at least 25 trophies of a particular

Figure 5. Sample of under-aged male African lions shot by sport hunters in various countries from 2004–2008.
doi:10.1371/journal.pone.0005941.g005

species for at least 2 yrs from 1982 to 2006 (excluding captive-bred lion trophies from South Africa). Other types of exports (skins) were also analyzed for lions, since non-standard terms are sometimes used by reporting countries [43], but these did not alter overall export trends. Data on Tanzanian hunting quotas were provided by the CITES office at the Division of Wildlife headquarters in Dar es Salaam; data on duration of hunting safaris in Zimbabwe were from the head office of Parks and Wildlife Management Authority in Harare.

Offtake data for black bears and cougars were provided by the Alaska Dept. of Fish & Game, Arizona Game & Fish Dept., California Dept. of Fish & Game, Colorado Division of Wildlife, Idaho Fish & Game, Minnesota Dept. of Natural Resources, Montana Fish, Wildlife & Parks, New Mexico Game & Fish, Nevada Dept. of Wildlife, Oregon Dept. of Fish & Wildlife, Utah Division of Wildlife Resources, Washington Dept. of Fish & Wildlife, and Wyoming Game & Fish. Note that all cougar offtakes in California are due to predator control.

"Harvest intensity" is the average harvest of the three peak offtake years divided by the extent of habitat in that state/country. Regression coefficients were calculated across the time period beginning with the earliest of the three peak harvests and ending in 2006 for cougars or the last of the three lowest subsequent harvest years for lions (Supporting Information Fig. S3); percent change is the regression coefficient divided by the peak harvest. Limited lion and leopard offtake data were available from 1996–2008 in Tanzania's hunting blocks; trends were only calculated for blocks reporting ≥5 yrs of activity.

Cougar habitat is forest cover taken from the National Land Cover Database (NLCD) www.mrlc.gov/changeproduct.php; lion habitat is the extent of GLOBCOVER land classification categories 42, 50, 60, 70, 90, 100, 110, 120, 130, 134, 135, 136, 160, 161, 162, 170, 180, 182, 183, 185, 186 and 187 in each country, see http://postel.mediasfrance.org/en/DOWNLOAD/Biogeophysical-Products/. Habitat loss is based on change in forest cover in the US 1990–2000 and in woodland/forest habitat in Africa 1990–2005 from FAO Global Forest Resources Assessment 2005, http://www.fao.org/forestry/32185/en/. Snow conditions for cougars are taken from http://www.wrcc.dri.edu/Climsum.html and African livestock production is taken from http://www.fao.org/es/ess/yearbook/vol_1_1/pdf/b02.pdf, using production levels from years of peak lion offtake in each country.

Supporting Information

Figure S1 The number of CITES-reported exports of a) cougar trophies and b) black bear trophies from the US were highest in years when the most animals were harvested domestically in the western states ($P<0.001$ for each species).
Found at: doi:10.1371/journal.pone.0005941.s001 (0.69 MB EPS)

Figure S2 Trendlines for the population declines of a) cougars and b) lions. Individual states with statistically significant declines in cougar offtakes: MT, ID, AZ, UT and CO; individual countries with significant declines in lion offtakes: BW, TZ and ZW.
Found at: doi:10.1371/journal.pone.0005941.s002 (1.08 MB EPS)

Figure S3 Quotas, offtakes and catch rates each year since the peak harvests for cougars in Colorado, Montana and Utah and lions in Tanzania and Botswana; duration of lion hunts in Zimbabwe. Catch rates are (offtakes/quotas). Catch rates have generally declined because offtakes have fallen more quickly than quotas. Catch rates briefly improved in Utah and Botswana when quotas were adjusted downwards, but subsequently resumed an overall decline; Montana's adjustments in quotas are too recent to evaluate. For Zimbabwe, vertical lines indicate standard errors; numbers are sample sizes; duration of lion hunts became significantly longer between 1997 and 2001 ($P<0.01$). No other data are available on quotas or hunt durations from these or other countries/states. The bottom graphs show that declines in lion trophy exports are unlikely to reflect declining market demand; imports of lion trophies have increased, especially in recent years for captive-bred or "canned" lion trophies for South Africa. The declines in trophy exports are also unlikely to be caused by irregular reporting; adding additional exports of skins from Botswana, Tanzania and Zimbabwe would not significantly change the pattern of decline.
Found at: doi:10.1371/journal.pone.0005941.s003 (1.38 MB EPS)

Figure S4 Simulated impacts of trophy hunting in cougars for varying degrees of habitat loss. Solid lines are the same as in Fig. 1: all available males above the age minimum are harvested each year and available habitat remains unchanged over 100 yrs. Dashed lines show population sizes with the same harvest strategies but with 20% habitat loss in 100 yrs; dotted lines represent outputs with 40% habitat loss.
Found at: doi:10.1371/journal.pone.0005941.s004 (1.49 MB EPS)

Table S1
Found at: doi:10.1371/journal.pone.0005941.s005 (0.03 MB DOC)

Acknowledgments

We thank Colleen Begg, Tim Caro, Laurence Frank, John Fryxell, Markus Gusset, Andrew Loveridge, Alan Rabinowitz and Paula White for comments and discussion.

Author Contributions

Conceived and designed the experiments: CP MK KN. Performed the experiments: MK. Analyzed the data: CP MK HB LP KN. Contributed reagents/materials/analysis tools: MK HC HB LP DLG GP MS AS GB LH KN. Wrote the paper: CP DLG KN.

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Conservation Biology

Contributed Paper

Effects of Trophy Hunting on Lion and Leopard Populations in Tanzania

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Abstract: *Tanzania holds most of the remaining large populations of African lions (*Panthera leo*) and has extensive areas of leopard habitat (*Panthera pardus*), and both species are subjected to sizable harvests by sport hunters. As a first step toward establishing sustainable management strategies, we analyzed harvest trends for lions and leopards across Tanzania's 300,000 km² of hunting blocks. We summarize lion population trends in protected areas where lion abundance has been directly measured and data on the frequency of lion attacks on humans in high-conflict agricultural areas. We place these findings in context of the rapidly growing human population in rural Tanzania and the concomitant effects of habitat loss, human-wildlife conflict, and cultural practices. Lion harvests declined by 50% across Tanzania between 1996 and 2008, and hunting areas with the highest initial harvests suffered the steepest declines. Although each part of the country is subject to some form of anthropogenic impact from local people, the intensity of trophy hunting was the only significant factor in a statistical analysis of lion harvest trends. Although leopard harvests were more stable, regions outside the Selous Game Reserve with the highest initial leopard harvests again showed the steepest declines. Our quantitative analyses suggest that annual hunting quotas be limited to 0.5 lions and 1.0 leopard/1000 km² of hunting area, except hunting blocks in the Selous Game Reserve, where harvests should be limited to 1.0 lion and 3.0 leopards/1000 km².*

Keywords: harvests, *Panthera leo*, *Panthera pardus*, population trends, sport hunting

Efectos de la Cacería Deportiva sobre Poblaciones de Leones y Leopardos en Tanzania

Resumen: *Tanzania mantiene la mayoría de las poblaciones remanentes de leones Africanos (*Panthera leo*) y tiene extensas áreas de hábitat de leopardo (*Panthera pardus*), y ambas especies son sujetas a cosechas considerables por cazadores deportivos. Como un primer paso hacia el establecimiento de estrategias de manejo sustentable, analizamos las tendencias de cosecha de leones y leopardos en los 300,000 km² de bloques de cacería de Tanzania. Sintetizamos las tendencias poblacionales de leones en áreas protegidas donde la abundancia de leones ha sido medida directamente, así como datos sobre la frecuencia de ataques de leones sobre humanos en áreas agrícolas altamente conflictivas. Ubicamos estos resultados en el contexto de la población humana en rápido crecimiento en Tanzania rural y los efectos concomitantes de la pérdida de hábitat, el conflicto humanos-vida silvestre y las prácticas culturales. Las cosechas de leones han declinado 50% en Tanzania entre 1996 y 2008, y las áreas de cacería con las cosechas iniciales más altas sufrieron las declinaciones más pronunciadas. Aunque cada parte del país está sujeto a alguna forma de impacto antropogénico por habitantes locales, la intensidad de la cacería deportiva fue el único factor significativo en el análisis estadístico de las tendencias poblacionales de leones. Aunque las cosechas de leopardos fueron más estables, regiones fuera de la Reserva de Caza Selous con las cosechas iniciales de leopardos más altas también mostraron las declinaciones más pronunciadas. Nuestros análisis cuantitativos sugieren que las*

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Paper submitted July 14, 2009; revised manuscript accepted April 13, 2010.

DOI: 10.1111/j.1523-1739.2010.01576.x

cuotas anuales de cacería se limiten a 0.5 leones y 1.0 leopardo/1000 km² de área de cacería, excepto los bloques de cacería en la Reserva de Caza Selous, donde las cosechas deben limitarse a 1.0 león y 3.0 leopardos/1000 km².

Palabras Clave: cacería deportiva, *Panthera leo*, *Panthera pardus*, cosechas, tendencias poblacionales

Introduction

Although habitat loss and retaliatory killing are generally considered the primary threats to large felids across Africa (Ray et al. 2005; IUCN 2006; Bauer et al. 2008), hunting can also deplete animal populations (e.g., Milner-Gulland et al. 2003; Fryxell et al. 2010), especially in felids in which sexually selected infanticide is common (e.g.,Whitman et al. 2004; Caro et al. 2009). For example, excessive trophy hunting appears to have caused large-scale declines in African lions (*Panthera leo*), American cougars (*Felis concolor*), and possibly African leopards (*Panthera pardus*) (Packer et al. 2009). Across seven countries (lions) and 11 U.S. states (cougars), jurisdictions with the highest sport-hunting harvests per 1000 km² of habitat subsequently showed the steepest proportional declines in harvests. The growing use of dogs to hunt leopards in Zimbabwe, and declining leopard harvests in Zambia and Zimbabwe (Purchase & Mateke 2008; Balme 2009; Packer et al. 2009; Balme et al. 2010) have also raised concerns about leopard management and trophy hunting.

Tanzania has an extensive network of national parks (38,365 km², including Ngorongoro Conservation Area), game reserves (102,049 km²), and game-controlled areas (202,959 km²), and has more lions than any other country in Africa. Four of the continent's six largest remaining populations of lions occur in Tanzania in the Serengeti, Maasai Steppe, Selous, and western Tanzania (Fig. 1). Leopards are common throughout Tanzania, and the country has been granted one of the highest export quotas for leopard trophies by CITES. In addition, Tanzania is the most popular destination for sport hunting of lions and leopards (http://www.unep-wcmc.org/citestrade/) in the world. An average of 243 wild lion trophies were exported per year between 1996 and 2006. In Zimbabwe and Zambia 96 and 55 trophies/year, respectively, were exported, and no other country exported more than 20 per year (Packer et al. 2009). Tanzania also exported an average of 303 wild leopard trophies/year, whereas Zimbabwe exported 300 per year and no other country exported more than 100 per year.

Lions and leopards throughout Africa are subject to widespread loss of habitat, prey depletion, and human-animal conflicts that are associated with rapid human population growth (e.g., Ray et al. 2005; Woodroffe & Frank 2005; IUCN 2008). In Tanzania, human population growth has been particularly high along the borders of the wildlife areas (Fig. 2a), and deforestation has accelerated in the past 15 years (Packer et al. 2009) with concomitant declines in herbivore populations (Stoner et al. 2007). Thus, there is an urgent need for quantitative analysis to establish sustainable harvest practices, while taking care to disentangle the impacts of trophy hunting from these other anthropogenic factors. Trophy-hunting quotas for lions and leopards have never been based on rigorous quantitative analysis of harvest patterns in any country (Packer et al. 2009).

Data on lion population trends in Tanzania are available from long-term studies conducted in a small number of protected areas where trophy hunting is not permitted (e.g., Kissui & Packer 2004; Packer et al. 2005*a*), but no comparable population data exist for leopards. The population status of both species is unknown in all of the country's hunting blocks. Nevertheless, three factors allow Tanzania's trophy harvests to be used as indirect measures of population trends (Packer et al. 2009). First, hunting companies invest enormous effort into locating lions and leopards, and most animals are shot at baited stations. Male lions frequently scavenge (Schaller 1972) and are thus especially susceptible to baiting. Second, clients must purchase a "21-day safari package" to be granted permission to hunt lions or leopards in Tanzania. Sales have grown by 60% over the past decade, and overall quotas for lions and leopards have also risen (Fig. 2b). Third, a substantial proportion of Tanzania's lion trophies in 2006–2008 consisted of subadult males (see Fig. 5 in Packer et al. 2009), which is a sign of over-exploitation (e.g., Allendorf & Hard 2009). Therefore, any decline in harvest likely reflects declining population size.

We assessed whether trophy hunting has had measureable effects on the abundance of lions and leopards in Tanzania. We tested whether hunting areas with the highest harvest levels subsequently showed signs of overhunting. Additionally, we used data from long-term studies of lions conducted in Tanzania's phototourism areas to examine whether any of these largely unhunted populations have been affected by trophy hunting. We also evaluated the potential effects of other anthropogenic factors, such as conversion of natural vegetation to agriculture, human population density and growth, the presence of ritual and retaliatory killings, and proximity of wildlife habitat to human-occupied areas.

Methods

Continuous, long-term records of individual lions have been collected in 2700 km² of Serengeti National Park since 1966 (Packer et al. 2005*a*), in the 250-km² floor of

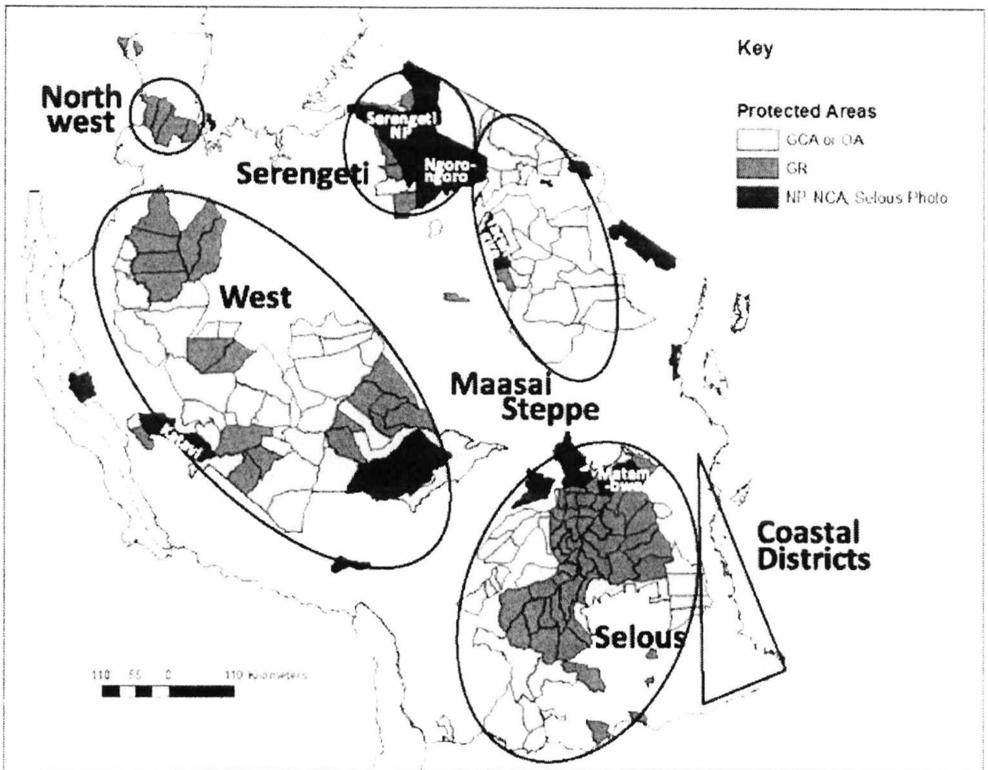

Figure 1. Map of protected areas and hunting areas in Tanzania (ellipses, major ecosystems within the country). No settlements are allowed in game reserves (GR) and national parks (NP); only pastoralist Maasai are allowed to reside in Ngorongoro Conservation Area (NCA); and settlements are permitted in game controlled (GCA) and open areas (OA). Trophy hunting is prohibited inside national parks and the Ngorongoro Conservation Area.

Ngorongoro Crater since 1963 (Kissui & Packer 2004), and in 2000-km^2 of Tarangire National Park since 2003. Comparable short-term studies of individual lions were conducted in 600–850 km^2 areas of the Matambwe Phototourism Area of Selous Game Reserve in 1996 and 1999 (Spong 2002) and in 2007–2008. We did not consider data from a 1992 study by Creel and Creel (1997) because of the small size of the area they covered (90 km^2 vs. 725 km^2 in subsequent studies) and because of atypically high lion density in their lakeshore study area.

Female lions in Serengeti, Tarangire, and Matambwe were fitted with radio collars and located and observed two to eight times per month. We used these data to determine the group membership of each pride. Ngorongoro Crater is primarily open grassland; thus, individual lions could be located opportunistically. Our estimates of lion density in Katavi National Park came from Caro (1999), who surveyed 80 km of ground-based transects twice annually since 1995 and controlled for variations in visibility along the width of each transect in his surveys. Cases of lion attacks on humans are reported to District Game Offices throughout the country (Packer et al. 2005*b*). We updated data from districts with the highest number of lion attacks in the country over the past two decades (Lindi, Masasi, Mkuranga, Mtwara, Ruangwa, Rufiji, and Tunduru districts) to extend the analysis to 2008.

The CITES office at the Division of Wildlife Headquarters in Dar es Salaam provided data on quotas and harvests of lions and leopards in each hunting block, as well as the national totals of clients and 21-day safaris. We analyzed the harvest data at two scales: individual hunting blocks and seven geographically discrete regions. Hunting blocks are leased by the Tanzanian government and range in size from 141 to 8440 km^2 (mean [SD] = 1695 km^2 [1339], $n = 168$). We restricted our block-level analysis to the 45 blocks in the Selous Game Reserve because the German Technical Assistance agency, Gesellschaft für Technische Zusammenarbeit (GTZ), had spent considerable development funds on record keeping in the Selous (Baldus & Cauldwell 2004; Caro et al. 2009; Leader-Williams et al. 2009) and because records were available from an average of 87% of the Selous blocks each year (vs. only 69% in the rest of the country). In the regional analysis, we considered seven discrete areas: Maasai steppe (22 blocks), northwestern Tanzania (4 blocks), greater Serengeti (8 blocks bordering Serengeti National Park), western Tanzania (42 contiguous blocks), Selous Game Reserve (45 blocks), a set of blocks near Selous Game Reserve first hunted in 2002 (14 blocks), and a set of

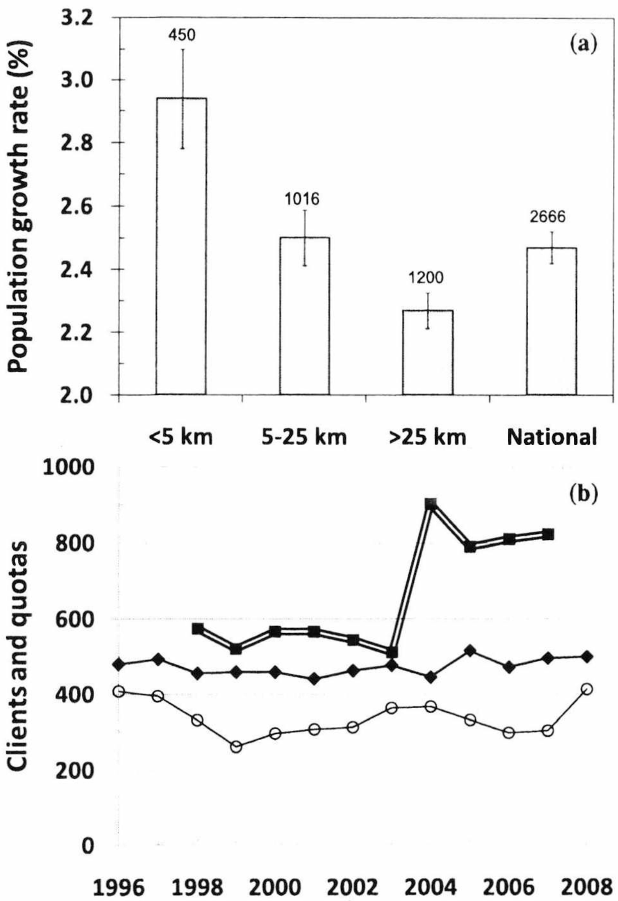

Figure 2. Human population growth and demand for lion and leopard trophies in Tanzania. (a) Annual population growth from 1988 to 2002 in wards located each distance from national parks and game reserves (numbers above bars, number of wards; lines, SE). Wards <5 km from protected areas grew faster than those 5–25 or >25 km away ($p < 0.001$*). (b) Total number of 21-day safaris (double line, solid squares) and total quotas for lions (solid diamonds) and leopards (open circles) across all of Tanzania's hunting blocks.*

blocks near Selous hunted since 1996 (7 blocks). For each hunted area, we defined the initial hunting intensity as the average annual number of animals harvested per 1000 km^2 in 1996–1999. We then calculated the harvest regression coefficient for 1996 through 2008. The annual rate of change in lion harvest was the regression coefficient divided by the initial intensity. Because the rate of change approaches zero at high initial intensities, we log-transformed all data sets where initial intensities exceeded 3 trophies$\cdot$1000 $km^{-2}\cdot year^{-1}$.

We estimated potential habitat loss with data from 1997 on land conversion to agriculture within or adjacent to each wildlife area (FAO 2002). We used data from the national census (Tanzanian National Bureau of Statistics 2002) to measure human population density in 2002 and the rate of human population growth in each ward between 1988 and 2002). Ward-level growth rates were calculated from photographs of 1988 ward-boundary maps stored at the National Bureau of Statistics in Dar es Salaam. For most areas, quantitative data were not available for prey loss, extent of retaliatory killing, ritual killing, or disease, so we noted only presence or absence of each factor (Table 1) and whether felids living in phototourism areas were affected by trophy hunting (e.g., Tarangire lions regularly move into hunting blocks from the national park). As a measure of overall exposure to anthropogenic effects of local people, we distinguished between hunting blocks that were completely surrounded by other hunting blocks and blocks that abutted non-wildlife areas and were thus located along an "edge." Proportion of edge is the total area of edge blocks in a particular ecosystem divided by the total hunted area in that ecosystem.

For the analysis of the regional trophy harvests, we constructed a priori candidate models to test the effects of hunting intensity, agriculture, human population density, human population change, and "edge effects" (Table 2). We sought the best model(s) to account for harvest trends in each species. Statistics were run in PROC REG in SAS (version 9.1, SAS Institute 2002). We performed model selection with Kullback-Leibler (K-L) information-theoretic approach with Akaike's information criterion corrected for small sample size (AIC_c) (Burnham & Anderson 2002; Anderson & Burnham 2002). For each candidate model, we used the residual sum of squares (RSS) to calculate the values for AIC_c: $\Delta AIC_c = (AICi - \text{min AIC})$, where min AIC is the minimum AIC value of all models, ω_i is the Akaike weight (weight of evidence that model i is the best approximating model given the data and the set of candidate models) (Burnham & Anderson 2002).

Mean harvest intensities and harvest trends were tested for normality by regressing the residuals against normal probability curves. We detected no significant deviations or evidence of kurtosis.

Results

Across the five long-term lion studies in nonconsumptive protected areas, lion numbers remained the same in one population (Matambwe), increased in one population (Serengeti), and decreased in three populations (Tarangire, Katavi, and Ngorongoro), and the frequency of lion attacks on humans also declined in the agricultural areas of coastal Tanzania (Fig. 3).

The Serengeti and Ngorongoro lions suffered from severe disease outbreaks (Table 1). Whereas the Serengeti population recovered quickly (Packer et al. 2005*a*), the

Table 1. Summary of threats to Tanzania's lion and leopard populations.

Ecosystem and site	*Type of area*	*Size of ecosystem (km^2)*	*Survey area (km^2)*	*Years*	*Lion population or harvest trend[a] (r^2, p)*	*Lion harvest/ 1000 km^2/ yr 1996-1999[b]*	*Leopard harvest trend[a] (r^2, p)*	*Leopard harvest/ 1000 km^2/ yr 1996-1999*	*Proportion agriculture in 1997 (%)*	*Human population density per km^2 in 2002*	*Human population growth 1988-2002 (%)*	*Prey loss[b]*	*Retaliatory lion killing[b]*	*Ritual lion killing*	*Disease*	*Proportion edge*
Greater Serengeti																
Ngorongoro Crater	photo tourism	250	250	1989-2009	−0.23 0.027	N			0	9.77	9.53	N	Y	N	Y	N
SE Serengeti National Park	photo tourism	25,000	2,700	1989-2009	+0.74 <0.001	Y			0.67	13.35	3.59	Y	Y	Y	Y	Y
Serengeti blocks (8)	trophy hunting	25,000	11,597	1996-2008	−0.44 0.026	2.06	−0.25 ns	2.30	6.89	11.14	3.72	Y	Y	Y	Y	100%
Maasai Steppe																
Tarangire National Park	photo tourism	52,836	2,000	2003-2009	−0.64 0.031	Y			0	15.52	2.95	Y	Y	N		Y
Maasai Steppe blocks (24)	trophy hunting	52,836	50,036	1996-2008	−0.04 ns.	0.54	−0.15 ns	1.36	16.9	9.04	4.96	Y	Y	N		69%
Greater Selous																
Matambwe Photo-Area	photo tourism	90,089[c]	725	1997-2009	−0.20 ns.	Y			0.02	2.95	1.26	Y	Y	N		Y
Selous game reserve blocks (45)	trophy hunting	90,089	44,244	1996-2008	−0.51 0.006	2.62	+0.05 ns	2.45	2.01	2.51	1.06	Y	Y	N		34%
Selous: old blocks (7)	trophy hunting	90,089	13,774	1996-2008	−0.10 ns.	1.36	+0.13 ns	0.64	17.1	13.05	2.40	Y	Y	Y		100%
Selous: new blocks (16)	trophy hunting	90,089	17,295	2002-2008	−0.41 0.119	2.00	−0.03 ns	1.72	12.5	7.60	1.43	Y	Y	Y		100%
Western Tanzania																
Katavi National Park	photo tourism	143,138	4,300[d]	1995-2009	−0.50 0.016	Y			0.40	4.35	2.97	Y	Y	Y		Y
Western blocks (54)	trophy hunting	143,138	121,551	1996-2008	−0.57 0.004	1.42	−0.10 ns	1.08	5.08	6.61	4.15	Y	Y	Y		76%
Northwest Tanzania																
Northwestern blocks (4)	trophy hunting	4,240	3,995	1996-2008	−0.45 0.034	2.26	−0.11 ns	4.11	2.45	28.43	4.34	Y	Y	N		100%
Southeast Tanzania																
Coastal districts	agriculture	58,704	58,704	1990-2008	±0.24 0.05[e]	Y			42.9	32.62	2.51	Y	Y	N		Y

[a] *Trends are based on annual lion surveys in the photo tourism areas and on lion and leopard harvests in the hunting areas over the years specified in each row.*
[b] *Abbreviations: N, no threat; Y, threat present.*
[c] *Total area of photo tourism areas: 2996 km^2.*
[d] *Area repeatedly surveyed (80 km of ground transects).*
[e] *Number of lion attacks on humans, r^2 and p are for the quadratic term.*

Table 2. Akaike information criterion (AIC) test of the contribution of each variable to lion-harvest trends and leopard-harvest trends in six sport-hunting areas.*

Model	K	AIC_c	ΔAIC_c	ω_i
Lion harvest				
lion trophy hunting	2	−46.64	0.00	0.922
null model	1	−39.31	7.33	0.024
proportion edge	2	−38.02	8.62	0.012
lion trophy hunting + proportion edge	3	−37.65	8.99	0.010
proportion agriculture	2	−37.43	9.21	0.009
Leopard harvest				
log leopard trophy hunting	2	−37.85	0.00	0.637
null model	1	−35.37	2.48	0.184
proportion agriculture	2	−33.29	4.56	0.065
log leopard trophy hunting + proportion edge	3	−31.93	5.92	0.033
Human population change	2	−31.81	6.04	0.031

**The model with the lowest AIC and highest Akaike weight (ω_i) values is the best model, although any model with a ΔAIC value of <2 would be considered a plausible alternative. Models with ΔAIC greater than the null model can be disregarded (Burnham & Anderson 2002) (K = df). All the same variables were tested for both species, but only the top five models for each are reported.*

abundance of Ngorongoro Crater lions remained below carrying capacity due to recurrent epizootics (Kissui & Packer 2004). This population also suffered mortality from Maasai herders (Kissui et al. 2009).

The Matambwe and Serengeti study populations were exposed to modest levels of trophy hunting, whereas the Tarangire population spent 4–6 months of the year outside the National Park, where they are subject to high levels of retaliatory killing in response to cattle depredation (Kissui 2008) and to trophy hunting. In contrast, Katavi lions were relatively sedentary, and their numbers were low as a result of high trophy harvests in the surrounding hunting blocks (Kiffner et al. 2009).

Lion harvests declined significantly in four of seven hunting areas across the country: the northwest, the west, around Serengeti National Park, and inside Selous Game Reserve (Fig. 4; Table 1). Record keeping was most thorough inside the Selous Game Reserve and provided the best opportunity for a block-by-block analysis. The "retention scheme" in Selous also provided higher levels of antipoaching and infrastructure development than any other hunting area in the country (Baldus & Cauldwell 2004; Leader-Williams et al. 2009), so we considered hunting trends in this area separate from other areas.

Lion harvests inside the Selous Game Reserve declined most steeply in blocks that experienced the highest legal harvest per 1000 km^2 in 1996–1999 (Fig. 5a). Human settlement is not permitted inside Tanzanian Game Reserves, so none of these blocks suffered any loss of habitat from agriculture or deforestation. Lion harvests did not decline more rapidly in the "edge" blocks of the Selous than in blocks that were completely surrounded by other hunting blocks. In the remaining six hunting areas, regions with the highest initial trophy harvests per 1000 km^2 again showed the steepest proportional declines in harvest (Fig. 5b). No other variable (e.g., agriculture, human population density, etc.) had a statistically significant effect (Table 2).

In contrast to lions, leopard harvests have not shown statistically significant harvest trends in any of the seven hunting areas (Fig. 4). Nevertheless, harvests in the northwest declined by about 10% per year since 1996, and harvests around Serengeti declined 5% per year. Within the Selous Game Reserve, hunting harvests declined more steeply in the blocks with the highest harvest level in 1996–1999, but this trend was not significant (Fig. 5c). Across the rest of the country, the proportional decline in leopard harvest was significantly higher in areas with the highest initial harvests (Fig. 5d), and trophy hunting was the only important variable (Table 2).

Reports by hunting operators and tour guides inside Selous indicate leopard abundance has increased in the past 5 years. Selous hunting blocks with the highest average lion harvests in 1996–2008 showed the largest increases in leopard harvests (Packer et al. 2009).

Discussion

Trophy hunting appears to have been the primary driver of a decline in lion abundance in the country's trophy-hunting areas and is likely affecting lion abundance in Katavi National Park and possibly Tarangire National Park. In contrast, lion abundance was unchanged in two of the three phototourism areas that are only minimally affected by trophy hunting; lion abundance has fallen in Ngorongoro Crater even though the area is protected from hunting. We lacked independent estimates for leopard population trends, but trophy hunting may have similarly driven a decline in leopard abundance in several areas outside Selous. In contrast to the conclusions of IUCN (2006) and Bauer et al. (2008), reports, we were unable to detect any consistent impact from habitat loss or human-carnivore conflict in hunting areas, although retaliatory killing was substantial in several of the protected areas.

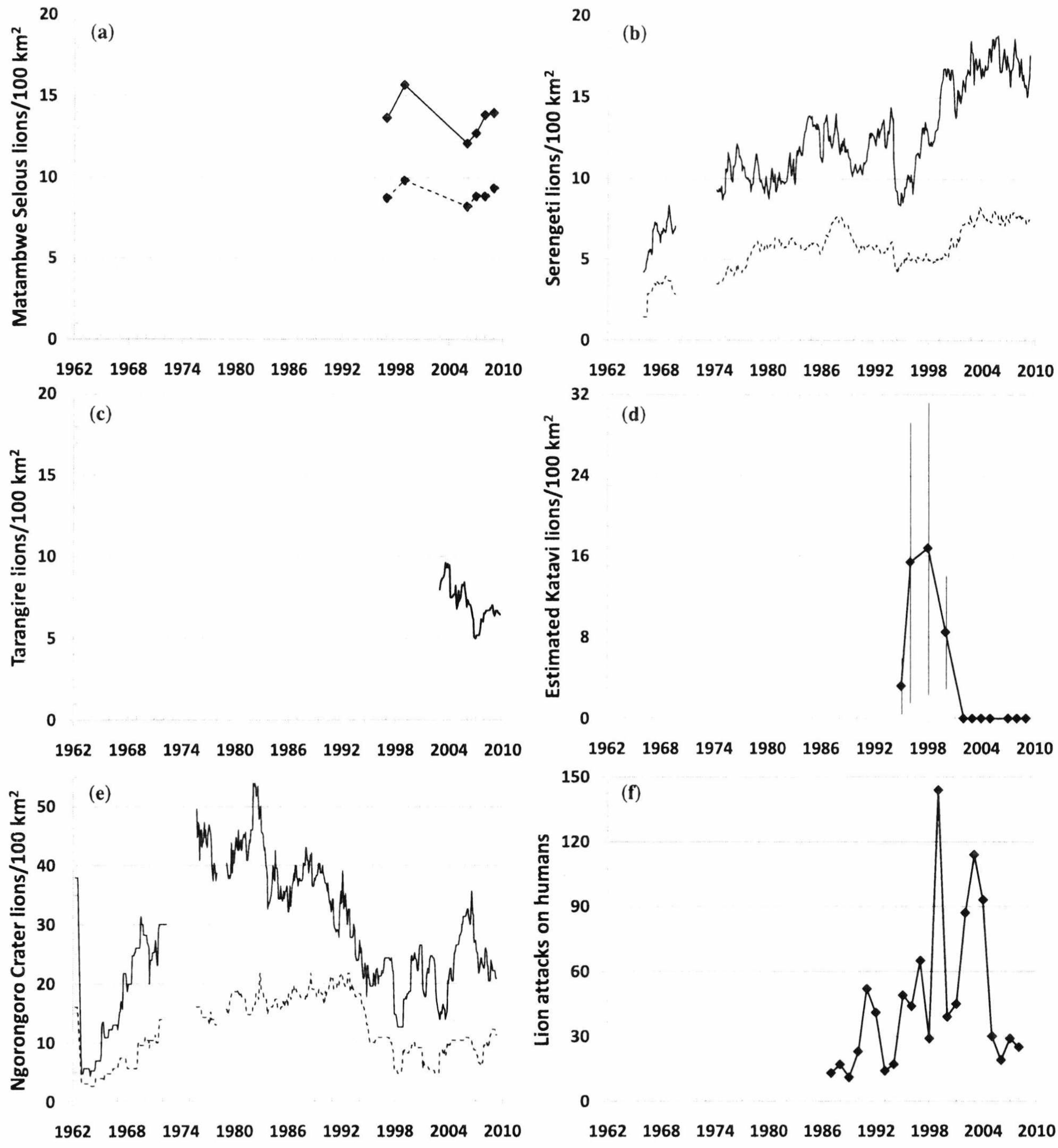

Figure 3. Long-term data on lion population density in (a) Matambwe Phototourism Area, Selous Game Reserve, (b) Serengeti National Park, (c) Tarangire National Park, (d) Katavi National Park (SE), and (e) Ngorongoro Crater and on (f) the number of lion attacks in Lindi, Masasi, Mkuranga, Mtwara, Ruangwa, Rufiji, and Tunduru districts (reported to the Tanzanian Wildlife Authorities) (solid lines, total population density; dotted lines, adult density; diamonds, annual surveys; lines without diamonds, continuous observations).

Trophy Hunting

In Tanzania the Selous Game Reserve is the largest contiguous hunting area uninhabited by humans and is thus the area most exclusively affected by trophy hunting (Caro et al. 2009). The simulation models of Whitman et al. (2004) predicted that removing 10% of ≥4 year-old-male lions each year would cause an eventual 50%

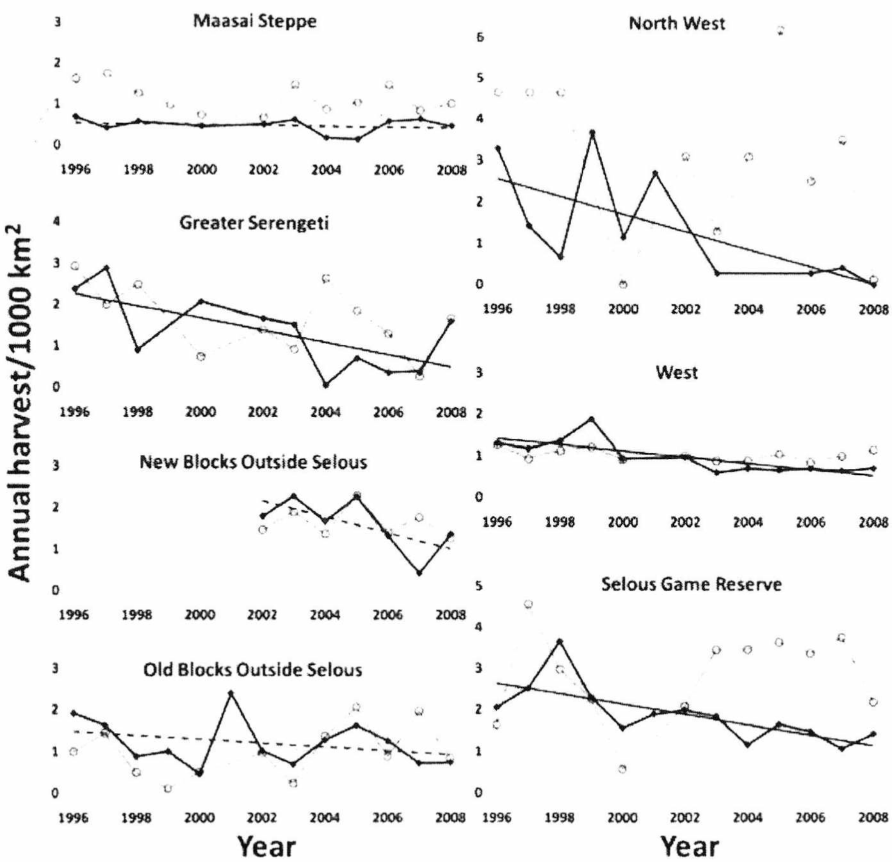

Figure 4. Average number of lions (heavy lines, diamonds) and leopards harvested (thin lines, circles) in major hunting areas (solid regression line, statistically significant declines between 1996 and 2008; dashed regression line, not significant).

decline in the total population. The average annual harvest in Selous was 2.62 males per 1000 km^2 in 1996–1999, which would have comprised 9.4% of 27.9 adult males per 1000 km^2 in the Matambwe phototourism sector. In the Katavi-Rukwa ecosystem, an average of 10.8 males were shot each year between 1996 and 2008, a period when an estimated average of 38 adult males occupied the entire area (Caro 2008; Kiffner et al. 2009), making annual harvests about 28.4% of males. Thus it is plausible that trophy hunting has reduced the lion population inside Katavi National Park, as suggested by Kiffner and colleagues (2009). High lion harvest around Zimbabwe's Hwange National Park has had measureable effects on the population inside the Park (Loveridge et al. 2007, 2009), whereas seasonal movements of lions originating from Tarangire National Park may have helped sustain harvests in nearby hunting blocks—an effect that counters extensive human population growth and habitat loss in the Maasai Steppe.

At least three factors may be responsible for stability of leopard harvests. First, widespread declines in lion abundance could have released leopards from interspecific competition (Crooks & Soulé 1999), and leopards seem to have benefited from declining lion numbers in Selous Game Reserve (Packer et al. 2009), although we have only anecdotal reports that leopards have increased in the Selous. Second, about 30% of Tanzania's documented leopard trophies are female (Spong et al. 2000). Packer et al. (2009) showed that cougar populations can theoretically withstand higher levels of harvest of females than males, and the same pattern should occur in any other polygynous species with sexually selected infanticide. Third, hunting companies might have put more effort into shooting leopards as lions became more difficult to locate in their hunting blocks.

Loss of Habitat and Prey

As seen elsewhere (Wittemyer et al. 2008), human population growth is highest in wards located <5 km from Tanzania's wildlife protected areas (Fig. 2a). Tanzania has lost >37% of woodland and forest habitat since 1990 (Packer et al. 2009), and bushmeat poaching has increased throughout the country (Jambiya et al. 2007), further reducing the prey base for lions and leopards. Bushmeat poachers operate within Katavi National Park (Caro 2008), the western edge of the Serengeti ecosystem (Sinclair et al. 2008), and in most hunting areas around the country (Caro & Andimile 2009). In northern Serengeti National Park, lions were largely extirpated in the 1980s by poachers setting snares for herbivores (Sinclair et al. 2003). Matambwe lions have died after eating poisoned carcasses set out to kill crocodiles in Selous. Conversion of rangeland to agriculture in the Maasai Steppe

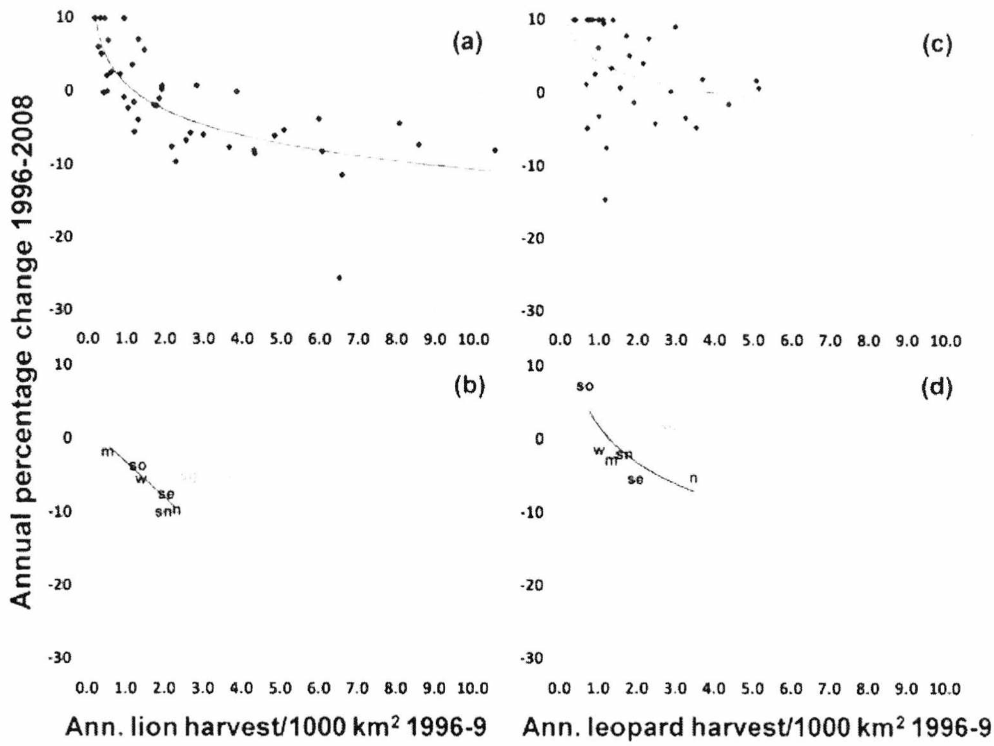

Figure 5. Proportional change in harvest of lions and leopards versus average harvest in 1996–1999: (a) lion harvest patterns in hunting blocks in the Selous Game Reserve ($r^2 = 0.57$, n = 44 blocks, $p < 0.0001$) and (b) lion harvests in the six ecosystems outside of Selous ($r^2 = 0.87$, n = 6 ecosystems, p = 0.0064) (M, Maasai Steppe, 24 blocks; n, northwestern Tanzania, 4 blocks; SE, Serengeti, 8 blocks; SN, new blocks outside Selous, 16 blocks; SO, old blocks outside Selous, 7 blocks; W, western Tanzania, 54 blocks; SG, Selous Game Reserve, 45 blocks [plotted for comparison]); (c) leopard harvest patterns in hunting blocks in the Selous Game Reserve ($r^2 = -0.11$, n = 32 blocks, p = 0.0600); (d) leopard harvests in the six ecosystems outside Selous ($r^2 = -0.71$, n = 6 ecosystems p = 0.0345) (Selous again plotted for comparison).

has blocked several migratory routes of Tarangire's wildebeest and zebra populations, which has likely forced lions to rely more on livestock when outside the park (Kahurananga & Silkiluwasha 1997). Tanzanian districts with the highest number of lion attacks on humans have the lowest abundance of natural prey (Packer et al. 2005*b*), and villages with the most lion attacks on humans have lower richness of prey species than neighboring villages without attacks (Kushnir et al. 2010).

Although rapid human population growth and high human population density in several areas would seem likely to have contributed to declining harvests (Table 1), lion and leopard harvests have been stable in the Maasai Steppe and in the older hunting areas around Selous, despite widespread conversion of land to agriculture and high human population density (Table 1). Thus, losses of habitat and prey do not explain changes in lion and leopard harvests in hunted areas (Table 2). These effects may be obscured, however, by the seasonal influx of lions from nearby National Parks (as for the Maasai Steppe) and by limitations in our data (data on agriculture were from 1997, and the last Tanzanian census was in 2002).

Retaliation

Retaliatory killing mostly affects lions; local communities seldom succeed in retaliating against stock-killing leopards (Kissui 2008). Retaliatory killing likely occurs in every area, but has been prominent in Tarangire, Ngorongoro Crater, and districts along the coast that have high levels of attacks on humans. Around Tarangire and in most of the Ngorongoro Conservation Area, Maasai kill lions in direct proportion to the number of cattle lost to lions (Kissui 2008; Ikanda & Packer 2008). Across the nation, the number of lion attacks on humans increased dramatically in the late 1990s (Packer et al. 2005*b*), possibly as a result of extensive flooding during the El Niño rains of 1998. Retaliatory lion killing in coastal districts intensified in 2004–2005, and few cases of attacks on humans have been reported in the past few years (Fig. 3f). Members of Tanzania's largest ethnic group, the agropastoralist Sukuma, kill lions in response to livestock depredation (Abrahams 1967). The Sukuma have recently settled in wildlife areas (Brandstrom 1985; Paciotti et al. 2005) and may have reduced lion abundance in several hunting areas. Sukuma poisoned 22 lions in 2005–2006 in one block near the Selous (R. Shallom, personal communication). Sukuma have also killed lions in Maswa Reserve (adjacent to the Serengeti) and in the Katavi-Rukwa ecosystem. Nevertheless, the number of lions killed by sport hunters has been stable in the Maasai Steppe, despite intensive retaliatory killing of lions from the Tarangire National Park. Thus, retaliation is unlikely to be the major cause of the overall decline in lion harvests in hunting areas (Table 2).

Ritual Killing

Leopards are not killed in rituals. Maasai kill lions for ritual purposes (*Ala-mayo*), but such incidents are uncommon in the Serengeti-Ngorongoro ecosystem ($\sim$2 per year) relative to retaliatory killing (3–4 per year) (Ikanda & Packer 2008) and trophy harvests (11.5 per year). Ritual killing appears to be rare in Tarangire compared with retaliatory killing (Kissui 2008). The Datoga rituals are similar to those of the Maasai (Wilson 1952; Klima 1965), and, like the Sukuma, they have recently settled in wildlife areas in central and western Tanzania. Lion killings by the Datoga have been documented north of the Selous and in the West, but precise impacts on lions are difficult to evaluate. Sukuma conduct ritual killings in western Tanzania, the extent of which is unknown.

Disease

Diseases of lions have been studied only in Serengeti and Ngorongoro Crater, and no quantitative data are available on diseases of leopards in Tanzania. Severe drought led to fatal infections of canine distemper virus and babesia in Serengeti lions in 1994 and Ngorongoro Crater lions in 2001 (Munson et al. 2008), and the Ngorongoro Crater lions also suffered from two undiagnosed epizootics in 1994 and 1998 (Kissui & Packer 2004) (Figs. 3b & e). The Ngorongoro Crater population appears to be immunocompromised by a high degree of inbreeding (Kissui & Packer 2004); a similar situation in South Africa's Hluhluwe iMfolozi Park was ameliorated by translocating unrelated animals into the park population (Trinkel et al. 2008). Thus, chronic vulnerability to disease largely results from inbreeding in small, isolated lion populations, and disease outbreaks are unlikely to have contributed to the persistent population declines in any of the hunting areas.

Harvest for Body Parts and Edge Effects

Although lion teeth and claws have long been sold in local markets and Sukuma use lion parts as medicine, there are so far no reports of lion bones being exported from Tanzania as substitutes for tiger bones in traditional Chinese medicines.

Hunting areas located adjacent to human-dominated areas did not have larger declines in lions or leopards than hunting areas that were buffered from human-dominated areas, suggesting that the overall effects of local people have been less severe than the effect of sport hunting.

Recommendations

Sport hunters are extremely efficient in locating their quarry, lion and leopard trophy hunting specifically targets adult males, and each male replacement has profound effects on the reproduction of multiple females. Tanzania currently allows about 500 lions and 400 leopards per year to be killed for sport in an area of 300,000 km^2 (1.67 lions and 1.33 leopards/1000 km^2). The proportion of male lions removed by trophy hunters in the mid- to late 1990s was unsustainable (28%/year in some areas).

Lion hunting should not exceed 1.0 lions/1000 km^2 in the Selous Game Reserve (Fig. 5a), whereas an upper limit of 0.5 lions/1000 km^2 should be imposed for the rest of the country (Fig. 5b). Within the Selous, leopard harvests increased 2%/year despite an annual average offtake of 2.9 leopards/1000 km^2 (Fig. 5c); thus, an upper limit of 3.0 leopards/1000 km^2 would be prudent. In the rest of the country, leopard quotas should not exceed 1.0 leopard/1000 km^2 (Fig. 5d). If these recommendations were adopted, national quotas would total about 180 lions and 400 leopards/year. These numbers still exceed current harvest levels, but, if they were adopted, hunting effort would be distributed more evenly across the country.

A strict age minimum would help ensure safe harvest levels despite uncertainties about local population sizes (Whitman et al. 2004, 2007). Restricting harvest to male lions that are $\geq$5 years old may be sufficient to minimize the population impacts of trophy hunting, even if every $\geq$5-year-old male was removed every year (Whitman et al. 2004, 2007). Lion ages can be reliably estimated in field conditions (Whitman & Packer 2007), and Mozambique's Niassa Reserve has successfully implemented a 6-year age minimum for hunted lions (Begg & Begg 2009), and a few Tanzanian hunting companies have voluntarily set a 6-year age minimum. A safe minimum age for leopards may be 7 years (Packer et al. 2009). Age-assessment criteria, however, are not yet available for leopards, and it is unknown whether leopard ages can be estimated reliably in the field.

Lions and leopards are CITES-listed species; thus, every precaution should be taken to prevent harvesting that could cause populations to decline. We therefore recommend, first, that Tanzania reduce quotas to 0.5 lion (or 1.0 in Selous) and 1.0 leopard (or 3.0 in Selous)/1000 km^2. Comparable statistical analysis should be performed in other range states, as sustainable offtake rates are likely to vary between countries. Second, professional hunters and clients in every range state should be educated as to how to estimate ages of lions (Whitman & Packer 2007). Third, the age of each trophy lion should be independently validated by post-mortem photographs illustrating physical features that indicate age (e.g., nose coloration) and tooth x-rays (pulp cavities enclose by year 4 in lions) and physical measurement of tooth wear (Whitman & Packer 2007). Fourth, underage trophy lions should not be exported. Fifth, similar age-assessment criteria and export policies should also be developed for leopards.

Trophy hunting has been considered essential for providing economic incentives to conserve large carnivores (e.g., Baker 1997; Hurt & Ravn 2000; Child 2004; Lindsey et al. 2006; Dickson et al. 2009). Nevertheless, successful conservation clearly requires that hunting harvests not exceed sustainable levels.

Acknowledgments

We thank the Wildlife Division of the Ministry for Natural Resources and Tourism for hunting-area data and authorization of our study; the Tanzanian Wildlife Research Institute, Tanzanian National Parks, Ngorongoro Conservation Area Authority, and Tanzanian Commission for Science and Technology for permission to conduct field research; G. Schaller for advice; and M. Borgerhoff Mulder and two anonymous referees for comments. Long-term research in the Serengeti and Ngorongoro is funded by NSF (National Science Foundation) Long Term Research in Environmental Biology grants DEB-9903416 & DEB-0343960; in Tarangire by African Wildlife Foundation, Wildlife Conservation Society (WCS), and Panthera; in Matambwe by National Geographic Society (NGS) and Panthera; in Katavi-Rukwa by Columbus Zoo, NGS, and University of California-Davis; and in the coastal agricultural districts of Tanzania by NSF Biocomplexity grant BE-0308486, WCS, Wildlife Protection Fund of Tanzania, and Panthera.

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