

The conservation status and dynamics of a protected African lion *Panthera leo* population in Kafue National Park, Zambia

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ABSTRACT

The abundance of African lions *Panthera leo* has declined rapidly in recent decades, largely due to competition for space with growing human populations. The future persistence of the species in the wild therefore depends heavily on viable populations in large protected areas, where lions play key ecological and economic roles. Zambia is one of nine countries estimated to have over 1000 wild lions, and Kafue, its largest national park, is a key refuge for the species. In this thesis I aimed to address the paucity of management and conservation relevant data on Kafue's lion population. I first used a track-based occupancy survey to determine the broad-scale drivers of lion distribution in the park. My results did not support my *a priori* expectations of anthropogenic edge effects driving lion occupancy; instead favourable habitat emerged as the best predictor of dry season lion distribution. The lack of edge effects is likely a result of the uniform suppressive effect on prey biomass of ubiquitous illegal bushmeat hunting in Kafue. After using my occupancy results to stratify my study area, I tested the effectiveness and efficiency of two well-established survey methods, track counts and call-up surveys, by comparing the resulting density estimates with that of a reference sample of GPS-collared lions in the study area. Accuracy of the two results was comparable, but the call-up estimate was more precise. However, call-up surveys are subject to variation in response rates that is difficult to quantify. I thus recommend that track count surveys are more suitable for monitoring lion population trends in Kafue. I further provide the first robust density estimate for northern Kafue of 1.83 lions (>1yr old) per 100 km². Understanding how animals use space is fundamental to their conservation. I therefore used GPS collars to investigate lion spatial ecology at a finer scale, and the effects thereon of the seasonal flooding of large parts of Kafue. Home range sizes were comparable to those of other lion populations in the region. However, seasonal inundation caused lions to expand home ranges, travel greater distances and shift away from favourable habitat in the wet season, potentially contributing to apparent high cub mortality rates. The combination of these factors may limit the resilience of the population in the face of identified local anthropogenic threats (i.e. illegal hunting of ungulates and lions, legal trophy hunting of lions and frequent, uncontrolled bushfires). I provide both direct and indirect evidence of such threats, and conclude that lion abundance in Kafue is limited primarily by the suppressed prey population, while the extent and regularity of bushfires may also have adverse effects. I recommend stronger enforcement of existing regulations pertaining to illegal hunting and fires, and the implementation of recently developed monitoring software to improve the efficiency and effectiveness of limited law enforcement resources. I further conclude that lion hunting quotas were excessive prior to the 2013 ban on hunting in Zambia, and suggest that the ban remain in place for at least three years to enable adequate recovery of the population. If the Zambian government elects to lift the ban, I propose a total combined quota of 5.25 lions per annum for the hunting concessions surrounding Kafue. I further recommend the implementation of strict age-based regulations within a robust adaptive management framework, based on the best available scientific data, to ensure the sustainability of harvest. To evaluate the effectiveness of such management interventions I propose long-term monitoring of lion abundance and distribution in Kafue using annual track count surveys. This study highlights that even the largest of Africa's national parks cannot ensure the survival of flagship apex carnivores. My findings and recommendations may be applicable to other wild lion populations in large protected areas where data paucity limits management effectiveness. Understanding and managing threats to these protected areas at the appropriate scale is critical if they are to meet their conservation objectives and ultimately ensure the persistence of wild lion populations.

DEDICATION

I dedicate this work to my dad who, from when I was a boy, instilled in me a love for adventure, wildlife and the outdoors, and my mom, who would have done anything for me, and, in her final years, taught me to make the most of all of mine. I know she would have been proud.

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CHAPTER 1

Introduction

General Introduction

In October 2011, Earth's estimated human *Homo sapiens* population exceeded 7 billion for the first time. One billion of these people resided in Africa, Asia was home to 4.2 billion and Europe, the Americas and Oceania hosted the remainder (UNFPA, 2011). This global population is projected to grow to 10 billion by the end of the twenty-first century, with Africa's numbers expected to increase to 3.6 billion inhabitants, a 360% expansion in less than a century (UNFPA, 2011). Growing human populations require additional space and resources, leading to increased transformation of natural habitat. For example, crop production increased by 47% between 1985 and 2005 and agriculture currently utilises about 38% of the earth's terrestrial surface area (Foley *et al.*, 2011). Such landscape modification and the resultant human-dominated environments have been identified as the primary drivers of species extinction on a global scale, resulting in plant and animal species currently being extirpated at a scale between 1,000 and 10,000 times greater than the 'background' rate (Lewis *et al.* 1990; May *et al.* 1995; Pimm & Raven 2000; Woodroffe 2000).

Large carnivores' wide-ranging habits, in addition to their propensity to kill domestic livestock and, occasionally, humans, mean they are amongst the genera most likely to experience escalating levels of conflict with people in regions of increased human density (Woodroffe & Ginsberg, 1998; Woodroffe, 2000; Treves & Karanth, 2003). For example, in 18 studies of human-wildlife conflict across four continents, large felids were responsible for livestock losses of up to 13% of herd size. These depredations resulted in widespread legal and illegal, often indiscriminate, retaliatory killing of eight different species of wild cats (Loveridge *et al.*, 2010). Such conflict is not limited to ecosystems with domestic livestock; carnivores are further persecuted for killing wild ungulates where these herbivores have an economic value to land owners through commercial hunting or meat production (Graham *et al.* 2005; Marker *et al.* 2010). The most aggressive retaliatory responses to carnivores occur when humans are physically attacked or killed by wild predators (Kruuk, 2002). The incidence of such attacks is by no means rare in the modern era, with, for example, lions *Panthera leo* estimated to have killed 563 people in Tanzania between 1990 and 2004 (Packer *et al.*, 2005b) and tigers *P. tigris* killing comparable numbers in India and Bangladesh over the last four decades (Siddiqi & Chroudbury, 1987; Karanth & Gopal, 2005; Khan, 2007).

These continuing and often escalating conflicts are almost invariably a consequence of human communities expanding into the few remaining natural areas that support large numbers of such carnivores, rather than these species increasing in numbers and expanding their distribution to include areas occupied by humans (Woodroffe, 2000). The net result has been the extirpation of

many large carnivores from significant tracts of their original distribution (Woodroffe & Ginsberg, 1998).

Although Protected Areas (PAs) alone may not be sufficient to conserve all biodiversity (Burkey, 1995; Soule & Sanjayan, 1998), rapid anthropogenic landscape transformation outside of these areas will increase their relative importance for the future survival of a multitude of species, particularly, large carnivores. The expansive ranging behaviour of these genera dictate that PAs must encompass vast extents of land if they are to provide sufficient refuge for populations to persist at sustainable levels (Brashares *et al.* 2001). Spatial requirements can be as high as 10,000 km² for a species such as African wild dogs *Lycaeon pictus* (Woodroffe *et al.* 1997) or almost 80,000 km² in the US state of Idaho for grizzly bears *Ursos arctos* (Noss *et al.*, 1996). In most developing countries, land of this scale could produce significantly higher short-term financial returns through resource extraction (e.g. logging, bushmeat harvesting, mining, etc.) than through protection and conservation (Wilkie & Carpenter 1999; Loveridge *et al.* 2006). This has led critics to argue that PAs designed exclusively for the protection of wildlife are neither realistic nor morally justifiable e.g. (Hilborn *et al.*, 2006). Their future existence in the face of concomitant increases in political pressure from disaffected communities will therefore depend on their ability to generate economic benefits that improve the livelihoods of neighbouring and/or displaced stakeholders (Bruner *et al.* 2001; Lindsey *et al.* 2006a).

It is in this context that the economic value of large carnivores to PAs becomes apparent. They are flagship species, their charismatic nature attracting the attention, empathy and subsequent financial support of the general public (Caro & O'Doherty, 1999; Caro *et al.*, 2004) through diverse avenues including donations for tiger conservation in Asia (Walpole & Leader-Williams, 2002), park fees to view grey wolves *Canis lupus* in Yellowstone National Park (NP; Montag *et al.* 2005) and trophy fees to hunt a leopard *P. pardus* in Zimbabwe (Lindsey *et al.* 2006b). Many large carnivores also function as umbrella species in that conservation of sufficient habitat to support them at sustainable levels simultaneously provides protection for a multitude of sympatric species (Caro & O'Doherty, 1999; Caro, 2003; Sergio *et al.*, 2006). This attribute has been utilised in the design of PAs as well as the evaluation of potential linkages between them (Lambeck, 1997; Roberge & Angelstam, 2004). Large carnivores also fulfill an important ecological role as apex predators in natural ecosystems, limiting both herbivore (Soule & Noss, 1998) and mesopredator populations (Crooks & Soule, 1999; Prugh *et al.*, 2009), and thereby enhancing both plant and animal biodiversity and maintaining essential ecosystem processes within PAs (Sergio *et al.*, 2006).

The mutually beneficial relationship between large carnivores and PAs accentuates the importance of research to ascertain the effectiveness of individual PAs at maintaining

sustainable populations of species in these genera. A number of long-term studies into species such as cheetah *Acinonyx jubatus* in Serengeti NP (Durant *et al.*, 2007) and grey wolves in Yellowstone NP (Smith *et al.*, 2011) have set the standard in this context, while others have highlighted that living within a PA does not guarantee immunity against the effects of anthropogenic persecution (Woodroffe & Ginsberg, 1998; Loveridge *et al.*, 2007).

Currently, however, a significant number of PAs, particularly in developing countries, have little to no data on the population dynamics and conservation status of, or threats faced by, their large carnivores (e.g. Bauer *et al.* 2003). Zambia's Kafue NP (Kafue), one of the world's largest PAs, is a prime example of such a park, and this thesis is a first step towards rectifying this knowledge gap through an investigation into Kafue's potentially globally significant population of African lion.

Lion ecology

The African lion is the largest African felid, and the largest terrestrial carnivore on the continent (Sunquist & Sunquist 2009). Lions occupy a broad range of habitat types across their distribution, with a preference for combinations of scrub, thick bush and grassland, or open woodlands (Nowell & Jackson, 1996) and only tropical rainforest and the Saharan interior naturally excluded from their historic distribution. Prey taken by lions ranges from rodents to elephants *Loxodonta africana* though they prefer medium to large ungulates, predominantly preying on the most locally abundant species in the 190-550kg range, with a mean weight of 201kg for preferred species (Hayward & Kerley 2005). Certain species in this range such as sable *Hippotragus niger* and eland *Taurotragus oryx* are, however, taken less often than expected (Hayward & Kerley 2005).

Female lions weigh an average of 126kg while males are significantly larger with a mean mass of 190kg (Sunquist & Sunquist 2009). Lion social structure comprises fission-fusion groups of, usually, 2-9 (range 1-18) related adult females (females may be unrelated in exceptional circumstances; Smuts 1978; Owens & Owens 1984) and their offspring (Packer *et al.*, 1991). Mean group size varies between regional populations and is positively correlated with prey abundance (Van Orsdol *et al.* 1985). Groups of females are called prides; each pride establishes a home range, which it defends against other prides (Schaller, 1972) with varying levels of spatial overlap (Spong 2002). Home ranges are intergenerational and typically inherited matrilineally through female philopatry (Spong *et al.* 2002; VanderWaal *et al.* 2009). New prides are typically formed by female dispersal, as in the Serengeti and Ngorongoro Crater, where up to 33% of females leave their natal pride by the age of 4 years (Pusey & Packer, 1987). Various theories have been developed to explain the evolution of sociality in

lions, including the benefits of cooperative hunting (Schaller, 1972), defense of cubs against infanticide (Packer *et al.* 1990) and, more recently, the ability of larger prides to colonise and retain more productive territories than smaller prides in a heterogeneous landscape (Mosser & Packer, 2009).

Male lions are either nomadic or territorial depending on their life stage (Schaller, 1972). Young males are evicted from their natal pride prior to reaching sexual maturity, and form nomadic coalitions with between 1 and 6 other related or unrelated males (Bygott *et al.* 1979; Pusey & Packer 1987), although individuals in coalitions of 4 or more animals are always related (Packer *et al.*, 1991). Distance dispersed from natal territories varies; male lions in the woodland environment of South Africa's Kruger NP remained closer to their natal ranges than their counterparts on the plains of the Serengeti (Funston *et al.*, 2003). Male coalitions begin challenging for territorial tenure when they are approximately 4-6 years old, although few ever attain this status (Schaller, 1972; Packer & Pusey, 1987). If successful, the new coalition's territory will encompass the home range(s) of one or more female prides and be vigorously defended against other males (Schaller, 1972). Coalitions remain resident for an average of two to three years (Packer *et al.*, 1988), though larger groups of 4-6 individuals can maintain their ranges for twice as long as 1-2 males (Bygott *et al.* 1979). Whilst holding tenure, males undertake territorial patrols, using scent marking (Schaller, 1972) and vocalisations to demarcate their territorial boundaries and communicate their whereabouts to conspecifics (Grinnell *et al.* 1995; Grinnell & McComb 1996). In their final life stage, male coalitions are evicted from their territories by younger challengers, and revert to being nomads (Schaller, 1972). During this period, as in the pre-tenure stage, coalition members are highly social, hunting and scavenging cooperatively (Bygott *et al.* 1979; Hanby & Bygott 1987).

Lions show no clearly defined breeding season across their distribution, although there are seasonal peaks in birth rates in certain regions (e.g., February to April in Kruger NP; Smuts *et al.* 1978). Females generally mate with resident adult males (Gilbert *et al.*, 1991), except in the rare instances where the resident male is related. Under these conditions females may leave the pride to avoid inbreeding (Packer *et al.*, 1988). Gestation is approximately 110 days (Cooper, 1942) after which litters of, on average, 2.3 cubs (range 1-6) are born (Schaller, 1972), although mortality rates can be as high as 73% (Van Orsdol *et al.* 1985). Mean inter-birth interval is 24 months (Packer *et al.*, 1988), but drops to 4-6 months if a litter is lost (Packer & Pusey 1983a). When a resident male coalition is expelled by challengers, the usurpers typically kill or evict all cubs under the age of two years, thus stimulating estrus in the females and maximizing the newcomers' opportunity for paternity during their limited reproductive tenure (Packer & Pusey 1983b; Packer *et al.* 1988). Females, however, exhibit reduced fertility during periods of male instability, with infanticide being the primary driver of increased interbirth

intervals (Packer & Pusey, 1983b). Takeover-induced infanticide may have indirect reproductive benefits by promoting birth synchronicity amongst pride females, which in turn allows for both communal suckling and defense of cubs (Pusey & Packer 1994; Packer *et al.* 2001). Nevertheless, more cubs are successfully raised in years of resident male stability than in years when takeovers occur (Packer *et al.* 1988).

Lion conservation status

Although lions once occurred in many parts of Eurasia, they became extinct in Europe around 2,000 years ago, and in Asia are restricted to a single isolated population of 300-350 individuals in India's Gir Forest (Breitenmoser *et al.* 2008). In sub-Saharan Africa, at the turn of the 20th century, lions occurred wherever suitable habitat was located (Mills 2004), but a hundred years later they had been extirpated from 6 of 42 original range states (Bauer *et al.* 2005). In total, lions have lost approximately 75% of their historical African distribution (Figure 1.1), and of the remaining 3,000,000 km², almost half has no official conservation status (Bauer, 2008; Riggio *et al.* 2013). The species is classified as Vulnerable by the IUCN, with east and southern Africa accounting for 75% of remaining lion distribution, and west and central regions of the continent only 25%, where lions are further classified as regionally endangered (Bauer *et al.* 2005; Bauer *et al.* 2008).

Lions are difficult to count (Ogutu & Dublin 1998; Stander 1998; Ogutu *et al.* 2006) and prior to the 1990's, few attempts had been made to estimate the size of the African population. Myers (1975) postulated that numbers had halved to as low as 200,000 in the preceding 25 years, and, 11 years later, the same author noted an ongoing and accelerating decline (Myers 1986). Ferreras and Cousins (1996) used GIS models to calculate an estimate of 75,800 lions in their 1980 base year, while Nowell and Jackson (1996) applied educated "guesstimates" to place the population between 30,000 and 100,000 individuals in the mid-1990's. In the twenty-first century, Chardonnet (2002), then Bauer and Van Der Merwe (2004), produced estimates of 39,000 (range 29,000 – 47,000) and 23,000 (range 16,500 – 30,000) respectively. The different methods used for the above range-wide surveys necessarily lead to large variation in population estimates. For example, 30% of Bauer and Van Der Merwe's (2004) calculation was based on scientific field surveys, whereas Chardonnet (2002) only used this method for approximately 12% of his count (for details of methodological differences see Bauer *et al.* 2005).

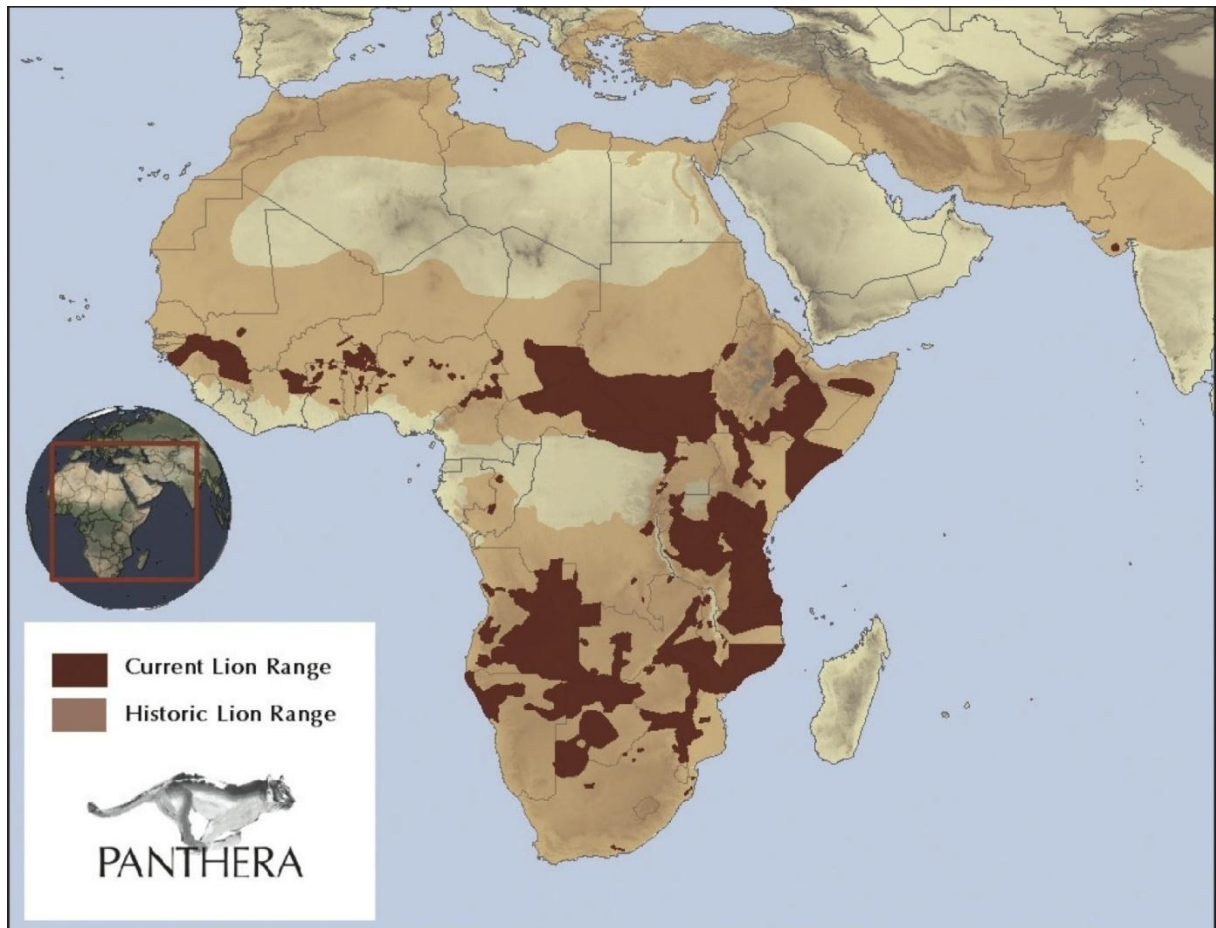


Figure 1.1. Lion distribution map (Online: http://www.panthera.org/sites/default/files/Lion_Current_and_Historic_Range_0.pdf, Accessed 26 November 2013)

Notwithstanding the inevitable uncertainty arising from estimates at a continental scale, most authors are in agreement that there has been a steady and significant decline in both lion numbers and range, with the consensus position indicating a 30-50% decline in abundance over 20 years, the equivalent of just three lion generations (Bauer *et al.* 2005; Bauer *et al.* 2008). The most recent range-wide analysis determined that there are likely less than 35,000 lions left in the wild, more than half of which are found in Tanzania, including three (Serengeti, Selous and Rungwa-Ruaha) of the remaining six populations numbering 1,000 or more, the others being Kruger NP, the Okavango-Hwange complex and Niassa National Reserve in Mozambique (Riggio *et al.*, 2013).

Lions face a multitude of anthropogenic threats with the greatest losses over the last 20 years being outside of PAs, where competition with humans for space and resources is greatest (Bauer *et al.* 2008; Loveridge *et al.* 2010). Frank *et al.* (2008) identified the rise in livestock depredation by lions and concurrent growth in persecution by humans as the primary drivers of this decline in lion numbers at a continental level. Lions are directly persecuted by people in retaliation for the killing of livestock and people. For example, Ogada *et al.* (2003) found a positive correlation between numbers of livestock lost to lions and number of lions killed in

Laikipia, Kenya. Historically, rural African communities employed people and dogs to guard their stock during the day, and corralled the animals in protective bomas (enclosures) by night, thus enabling coexistence with lions and other large carnivores (Ogada *et al.* 2003). However, increasing human numbers, growing reliance on a cash economy, political pressure, religious beliefs and, in some cases, poorly designed compensation schemes have all led to the weakening of animal husbandry standards, with subsequent increases in livestock depredations (Hazzah *et al.* 2009).

As a result of this conflict, lions are killed legally through Problem Animal Control (PAC) programs instituted by governments as well as illegally by communities (Woodroffe & Frank 2005). Documented methods of illegal killing include spearing (both as retaliation and initiation rites) in Tanzania (Lichtenfield 2005), shooting in Botswana (Hemson *et al.* 2009) and Namibia (Stander 1990) and poisoning in Kenya (Hazzah 2006). The indiscriminate nature of poisoning, and the low cost and availability of lethal poisons such as carbofuran (an agricultural insecticide banned in the European Union, Canada and the United States), makes this method of persecution a priority concern for the future of lions as well as other terrestrial and avian scavengers (Frank *et al.* 2008).

In addition to direct persecution, reduced prey biomass as a result of over-hunting by humans plays a significant role in declining lion numbers (Loveridge *et al.* 2010). Wild herbivores (and, occasionally, carnivores; Ndibalema & Songorwa 2007) are hunted by rural villagers as part of a subsistence lifestyle or to be sold to local and international consumers as a luxury food item (Davies 2002; Loibooki *et al.* 2002; Lindsey *et al.* 2011; Fitzgibbon *et al.* 2012). The quantity of bushmeat harvested and its impact on lion populations has yet to be quantified, but, as a potential indication, the Congo basin (not a lion stronghold) is estimated to lose between 1 and 5 million tonnes of wild animal biomass to the bushmeat industry per annum (Wilkie & Carpenter 1997; Fa *et al.* 2002). In addition to loss of prey, the widespread use of wire snares as a hunting method also leads to direct killing of lions and other carnivores (Noss 1998). Driven largely by poverty and unemployment, the scale of bushmeat extraction is unlikely to diminish unless the costs to poachers associated with law enforcement exceed the benefits obtained from the meat supply, or the exploited wildlife attains an economic value in its living state that exceeds its direct value as a source of protein, and its commercial value as a saleable good (Hofer *et al.* 2000).

Such challenges, their deleterious effect on lions and the associated expense of conserving the species in PAs led Packer *et al.* (2013a, 2013b) to investigate the cost and effectiveness of erecting fences around currently unfenced lion populations as a potential solution. These authors concluded that fenced lion populations can be maintained at 80% of their potential

densities for USD500 km⁻² per annum, whilst the cost of maintaining unfenced populations is more than USD2000 km⁻², and nearly half of these may decline to extinction in the next 20-40 years. These conclusions were, however, contested by (Creel *et al.*, 2013), who argue that lion density is not as important as lion numbers, and by this measure, large, unfenced populations are more important to lion conservation.

The consumptive utilisation of wildlife in the form of trophy hunting can provide some of the economic incentives required to encourage communities to conserve stocks in their areas (Lindsey *et al.* 2006a; Lindsey *et al.* 2007b; Treves 2009), and availability of lions on hunting quotas contributes to the financial viability of hunting operations (Lindsey *et al.* 2012b). Poorly managed trophy hunting of lions has, however, lead to population declines in predominantly hunting reserves such as Selous Game Reserve (GR) in Tanzania (Packer *et al.* 2010) and within National Parks adjacent to hunting concessions such as Hwange NP in Zimbabwe (Loveridge *et al.* 2007; Davidson *et al.* 2011). Photographic tourism is an alternative, non-consumptive tool that can assign value to wildlife, and lions are among the species most sought after by wildlife tourists (Lindsey *et al.* 2007a; Okello *et al.* 2008). However, photographic tourism is not considered to be economically viable in many areas of remaining lion range (Baker 1997).

Finally, lions also face a number of less pervasive, but potentially locally significant challenges, such as disease (Roelke *et al.* 1996), inbreeding (Bjorkland 2003; Kissui & Packer 2004), bushfires and habitat loss and conversion (Bauer 2008).

The host of threats described above attests to the complexity of conserving lions in the dynamic, heterogeneous and fluctuating landscape in which they still persist, and underlines the importance of ongoing research to determine local and regional management priorities.

Thesis outline

The overall objective of my thesis is to develop a baseline understanding of the conservation status of lions in Kafue, and the threats faced by the species in this PA.

In **Chapter 2** I provide an introduction to Kafue and outline methods used in the thesis that are common to more than one chapter.

In **Chapter 3** I use a track-based survey analysed in an occupancy model framework to investigate which areas of northern Kafue are most likely to be used by lions, and the likely drivers of such use.

In **Chapter 4** I compare the efficiency and effectiveness of two well established lion survey methods, call-ups and track counts, as tools to monitor Kafue's lion population. I also generate the first robust density estimate for lions in northern Kafue.

In **Chapter 5** I use data from GPS collars to investigate the spatial ecology of lions in northern Kafue, and consider the effects of the seasonal flooding of the landscape on this aspect of their behaviour.

In **Chapter 6** I identify the primary anthropogenic threats to lions in Kafue, use the results of the preceding chapters to provide direct and indirect evidence of these threats and recommend management interventions to mitigate them.

Finally, in **Chapter 7** I summarise my findings and place them in a broader context of lions in Africa, carnivore conservation in general and the importance of effective protected area management.

CHAPTER 2

General Methods

Study area

Zambia is a land-locked country in southern Africa with a surface area of approximately 752,000 km² and an estimated human population of 14,2 million, of which 39% is classified as urban (Online: <https://www.cia.gov/library/publications/the-world-factbook/>, accessed November 2013). Of the nine African countries estimated to hold more than 1000 wild lions (Riggio *et al.*, 2013), Zambia has the third-lowest human population density (Table 2.1). Given the well established negative relationship between human density and carnivore abundance (Woodroffe, 2000), Zambia's relatively low human density means that the country is of critical importance to carnivore conservation in the southern and East African region.

The Zambian government has allocated a significant portion of its land to wildlife-based land uses, and has a network of 20 national parks (IUCN Category II; ~64,000 km²), 36 Game Management Areas (GMAs; IUCN Category VI; ~167,000 km²) and 3 small wildlife and bird sanctuaries (34 km²; Figure 2.1). In total, this network covers approximately 40% of the country's land (Government of Zambia, 2010), and is mostly managed by the Zambia Wildlife Authority (ZAWA). National parks generate revenue primarily through photographic tourism, and no human settlement is allowed within these PAs. Many of them are, however, heavily impacted by illegal hunting, regular uncontrolled burning and, less commonly, informal mining (Simukonda, 2011; Watson *et al.*, 2013). GMAs were established to provide buffers between NPs and agricultural areas, and, in recent years, have primarily generated revenue through trophy hunting (Simasiku *et al.*, 2008). However, in January 2013 Zambia's government placed a temporary moratorium on all trophy hunting and an indefinite ban on hunting of lion and leopard (Online: <http://www.bbc.co.uk/news/world-africa-20969868>, accessed March 15 2013). Communities are allowed to live in GMAs and rely largely on trophy hunting for income. However, there is no guaranteed tenure of land and no enforcement of limitations to immigration by outside communities. Human density and habitat conversion is thus increasing in many GMAs, driving increased levels of illegal hunting and habitat loss (Lindsey *et al.*, in press.; Watson *et al.*, 2013).

Table 2.1. Human population data (Online: <https://www.cia.gov/library/publications/the-world-factbook/>, accessed November 2013) for nine countries estimated to hold more than 1000 wild lions (Riggio *et al.*, 2013).

Country	Surface area (km²)	Population (no. of people)	Population density (people/km²)	Rural proportion (%)	Rural population	Rural population density (people/km²)
Botswana	581,730	2,127,825	3.66	38.3	814,957	1.40
Ethiopia	1,104,300	93,877,025	85.01	83.0	77,917,931	70.56
Kenya	580,367	44,037,656	75.88	76.0	33,468,619	57.67
Mozambique	799,380	24,096,669	30.14	68.8	16,578,508	20.74
Namibia	824,292	2,182,852	2.6	61.6	1,344,637	1.63
South Africa	1,219,090	48,601,098	39.87	38.0	18,468,417	15.15
Tanzania	947,300	48,261,942	50.95	73.3	35,376,003	37.34
Zambia	752,618	14,222,223	18.90	60.8	8,647,112	11.49
Zimbabwe	390,757	13,182,908	33.74	61.4	8,094,306	20.71

Proclaimed a National Park in 1950, Kafue, at 22,319 km², is Zambia's largest PA and the second-largest NP in Africa. It is situated in western Zambia between 14°00'-16°40'S and 25°15'-26°45'E, and is adjoined by 43,692 km² of GMAs. Three main rivers, the Kafue, Lunga and Lufupa run the length of the park, which is split into northern (10,958 km²) and southern (11,361 km²) sectors by the M9, a major regional paved road (Figure 2.1). Due to the size of Kafue and the time constraints imposed by the wet season, I was unable to study the whole park and thus restricted my fieldwork to the northern region. I selected the north primarily as a result of my logistical support (Wilderness Safaris camps) being located in this sector, but also due to the reputation of the Busanga Plains being a key area for lions in the park.

The Kafue region experiences two distinct seasons, a wet season from December to May, and a dry season from June to November. Mean annual rainfall in the north is 1020 mm, dropping to 510 mm in the south (Fanshawe, 2010). The majority of this rain falls between December and March, and the park is largely inaccessible by vehicle from December to early May. My fieldwork was thus limited to the dry season only (i.e. May to November). I subsequently was not able to collect rainfall data for my study and those data that I was able to obtain from third parties were unreliable.

Collared lions

During the course of my study, I deployed 20 VHF/GPS (Vectronic Aerospace GmbH, Berlin, Germany) collars on 15 lions (seven adult females from six prides, eight adult males from seven coalitions). Lions were located opportunistically and all immobilisations were carried out by qualified wildlife veterinarians, duly authorised by ZAWA. No lions were adversely affected by the immobilisation and collaring process, and all collars were fitted with drop-off devices, programmed to release the collar two years after deployment. I programmed collars to record GPS fixes at 00h00, 06h00 and 18h00 each day, as lions are most active during the crepuscular and nocturnal hours, and generally do not travel far during daylight (Schaller, 1972). I retrieved the data from the collars via handheld UHF receiver (8 collars) or the Iridium satellite network (12 collars) from date of deployment to 31 May 2013 (Table 2.2). I collected lion demographic data through regular observation of collared groups during the dry seasons of this period.

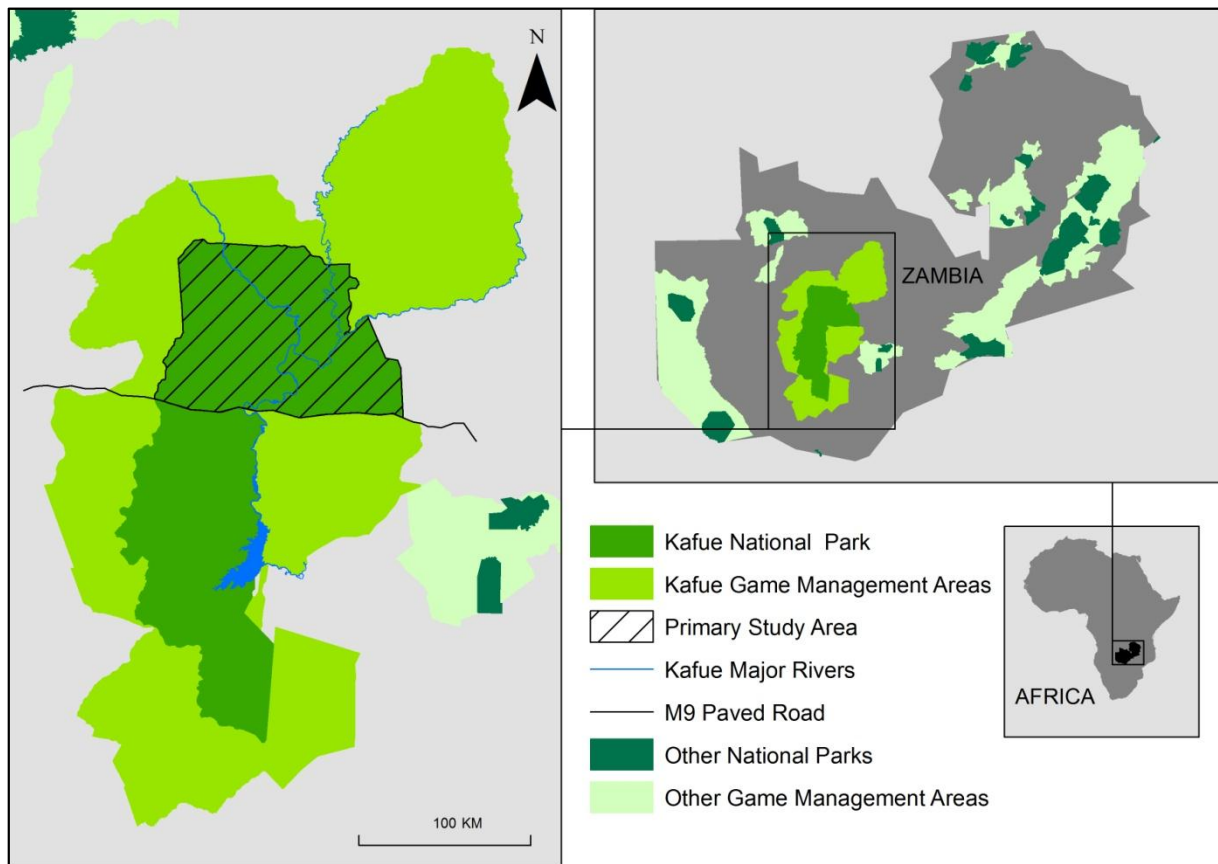


Figure 2.1. The location of Kafue National Park and adjacent Game Management Areas within Zambia, relative to Zambia's entire Protected Area network and within Africa.

Home range calculations

I used the adaptive kernel method in the HOME RANGE TOOLS extension (Rodgers *et al.*, 2007) of software ARCGIS v9.2 (ESRI, Redlands, California) for all home range calculations, and calculated home range (HR; 90% isopleth) and core area (CA; 50% isopleth) for each lion group that included a collared lion (Spong, 2002). To reduce the risk of spatial autocorrelation, I used one GPS fix per day, arbitrarily chosen at 00h00, for all home range calculations (*sensu* Davidson *et al.*, 2011). I calculated wet and dry season ranges for all groups for which I had a minimum of 60 seasonal locations (*sensu* Spong, 2002). Where lion locations indicated that a river formed a boundary for an individual, I clipped the home range accordingly. I assumed that data from a collared female or collared male were representative of the movements of the relevant pride or coalition respectively. However, I note that two females (F39 and F53) collared in one pride were <200m apart for only 62.7% of paired locations ($n = 1774$), and two collared males (M37 & M43) in one coalition (of three males) on only 28.4% of paired locations ($n = 846$). I used F53 to represent the Lufupa Pride as she was alone only once in 15 observations, while F39 was alone on five of 18 observations. I analysed M37 & M43 separately as the

composition of their coalition, which included a third male, was highly fluid. I used appropriate subsets of these data for analyses in Chapters 3, 4 and 5.

Table 2.2. Summary of lions collared from 1 September 2010 to 31 May 2013 including the individual identity of the collared lion, the name of the group the lion lived in and the total duration that each lion wore the collar while it was still active. ¹ Two females in the same group that were collared concurrently. ² Two males in the same coalition that were collared concurrently for ten months.

Lion	Group	Duration (months)
F18	Busanga pride	31.7
F21	Papyrus pride	29.5
F28	Treeline pride	33.3
F39 ¹	Lufupa pride	19.9
F53 ¹	Lufupa pride	19.9
F72	Moshi pride	10.9
F77	Kafwala pride	9.8
M06	Treetops coalition	8.0
M08	Papyrus male	2.2
M16	Busanga coalition	29.3
M31	Musanza coalition	2.0
M37 ²	Lufupa coalition	19.8
M43 ²	Lufupa coalition	9.8
M48	Lushimba coalition	10.0
M73	Kafwala coalition	10.9

Prey biomass

I utilise spatially explicit prey biomass estimates for various aspects of my analyses in Chapters 3, 5 and 6. I initially trialled distance-sampling techniques, counting ungulates along road transects (*sensu* Buckland *et al.*, 2004) to calculate prey biomass, but low encounter rates and a limited road network made this method unfeasible. I therefore used data from an aerial survey (Frederick 2011), which covered the entire park and the GMAs, for all prey biomass calculations. Aerial surveys can underestimate the abundance of smaller ungulates (Ferreira & Van Aarde, 2009), but as these species are out of the preferred prey range of lions (Hayward & Kerley, 2005), the effect is likely limited. The Kafue survey was carried out in the 2011 dry season, the middle year of my three years of fieldwork, which may limit its utility in 2012 analyses. However, the 2011 aerial survey found no significant changes in ungulate abundance from an earlier 2008 survey (Frederick, 2009, 2011), and I thus propose that, similarly, any change in overall prey biomass from 2011 to 2012 would not have been material. I also use a

kernel density estimator (see below) to smooth the data spatially, and account for some movement of ungulates both within and between dry seasons.

The aerial survey of Frederick (2011) was divided into transect subunits of 6.25 km², 12.5 km² and 25 km² depending on sampling intensity. I calculated prey biomass for each subunit using the formula

$$SB_j = \sum_{i=1, j=1}^n \frac{c_{ij}}{s_j} \times u_j \times m_i$$

where SB_j is prey biomass in subunit j , c_i is the number of individuals of species i observed in the count in subunit j , s_j is the aerial survey sample strip area (km²) for subunit j , u_j is the subunit area (km²) for subunit j and m_i is 75% of the female weight (kg) for species i (Table 2.3). I included only medium to large ungulates (Hayward & Kerley 2005) in the size range from bushbuck to buffalo in my analysis.

I split the analysis into three shapefiles, one for each subunit size, and used the POINT DENSITY ESTIMATOR tool in ARCGIS v10.1 (ESRI, Redlands, California) to create a smoothed prey biomass raster for each subunit size. Data were smoothed to reduce the effects of the use of subunit centre-points to represent aerial survey observations, as well as to account for animal movements. I set the raster cell sizes at 6.25 km², 12.5 km² and 25 km² respectively, and the neighbourhood as a circle with 10.0 km radius. The resulting raster was a prey biomass layer of smoothed biomass km⁻² for each raster cell.

Software used

All spatial analyses were conducted using either software ARCGIS v10.1 or GOOGLE EARTH (Google Inc., Mountain View, California) or a combination of both. I used software STATISTICA (Statsoft, Tulsa, Oklahoma) for all statistical analyses unless otherwise indicated.

Table 2.3. Calculation of mean of 75% of female mass (kg) estimates from Estes (1991), Skinner & Chimimba (2005) and Stuart & Stuart (2006). Species listed are medium to large ungulates recorded during aerial survey conducted by Frederick (2011). *Values used for prey biomass calculations.

Common name	Scientific name	Skinner & Chimimba	Stuart & Stuart	Estes	Mean*
Bushbuck	<i>Tragelaphus scriptus</i>	-	23	32	27
Buffalo	<i>Syncerus caffer</i>	345	413	432	397
Bushpig	<i>Potamochoerus larvatus</i>	52	48	53	51
Eland	<i>Taurotragus oryx</i>	222	338	-	280
Lichtenstein's					
Hartebeest	<i>Alcelaphus lichtensteinii</i>	125	124	-	124
Impala	<i>Aepyceros melampus</i>	31	30	34	31
Kudu	<i>Tragelaphus strepsiceros</i>	116	135	128	126
Puku	<i>Kobus vardonii</i>	-	47	45	46
Red lechwe	<i>Kobus leche leche</i>	46	60	59	55
Reedbuck	<i>Redunca arundinum</i>	29	31	36	32
Roan	<i>Hippotragus equinus</i>	-	195	195	195
Sable	<i>Hippotragus niger</i>	-	173	165	169
Warthog	<i>Phacochoerus africanus</i>	42	43	49	45
Defassa					
Waterbuck	<i>Kobus ellipsiprymnus defassa</i>	-	195	140	167
Wildebeest	<i>Connochaetus taurinus</i>	149	135	156	147
Plains Zebra	<i>Equus quagga</i>	227	236	165	209

CHAPTER 3

On tracks: a spoor-based occupancy survey of lion distribution in Kafue National Park

Summary

The African lion has lost more than 75% of its historic range and numbers of wild lions continue to decline. Protected areas are critical to the species' future, yet its conservation status in many of these reserves remains unknown. Zambia is one of nine countries estimated to hold over 1000 wild lions, and Kafue, its largest national park, is a key stronghold for the species. Understanding lion distribution and threats facing the species in the park are of particular relevance given the recent ban on lion hunting in Zambia and the uncertainty over this industry's future in the country. In this chapter, I used a single-season occupancy model based on detection of lion tracks to estimate proportion of area used and to derive a spatially explicit probability of lion use for northern Kafue, an area for which no previous empirical lion data exist. My top-ranking model predicted that lions use 72.1% of the study area, 23.3% greater than the naïve estimate. Contrary to my expectations, and possibly due to apparent ubiquity of illegal bushmeat hunting in the park, neither prey biomass nor anthropogenic edge effects emerged as important drivers of lion distribution, with habitat class instead the best predictor. My findings provide the management authority with relevant survey methods and identify focal areas for further lion research in the Kafue system. More broadly, I demonstrate the utility of track-based occupancy models in establishing the distribution of large carnivores within previously unsurveyed African protected areas.

Introduction

Protected areas play a key role in the continued existence of a multitude of threatened fauna and flora (Gaston *et al.*, 2008). However, human population growth rates in many developing countries are significantly higher on the borders of PAs than elsewhere (Wittemyer *et al.*, 2008; but see Joppa *et al.*, 2009). Illegal resource extraction from PAs (Brashares *et al.*, 2004) and human-wildlife conflict along the borders with densely populated areas (Graham *et al.*, 2005) have led to the decline and even extirpation of many species within the nominally secure boundaries of PAs (Caro & Scholte, 2007). Large carnivores, such as the African lion, are particularly vulnerable to such edge effects due to their wide-ranging behaviour, and the real and perceived threats they pose to human lives and livelihoods (Woodroffe & Ginsberg, 1998; Woodroffe, 2000). As one of only nine countries estimated to have more than 1000 wild lions remaining, Zambia is a critical contributor to the conservation of the species. The majority of the country's lions occur in PAs in three ecosystems, Kafue, the Luangwa Valley and the Lower Zambezi, but, barring the analysis of Becker *et al.* (2012), limited management and conservation-relevant data exist for these populations.

Legally protected within PAs, lions are nevertheless regularly killed as by-catch in wire snares set by illegal bushmeat hunters (Lindsey *et al.*, 2013a), whose activities simultaneously impose indirect pressure on the species by reducing available prey biomass (Lindsey *et al.*, 2013a). These twin threats persist in GMAs, where local communities have rights to the land but ownership of the wildlife vests with ZAWA and limited consumptive utilisation is permitted (Lewis & Alpert, 1997). Until recently, trophy hunting of lions was an additional source of anthropogenic mortalities in GMAs, but in January 2013, citing declining numbers, the Zambian government banned all trophy hunting of lion (and leopard; <http://www.bbc.co.uk/news/world-africa-20969868>, accessed March 15 2013). The current paucity of data on the country's lion population has left the issue of whether or not to reopen trophy hunting of the species unresolved and led to calls for additional research. This chapter will provide an initial understanding of lion distribution within northern Kafue, a key lion stronghold in Zambia, and thus contribute to an informed decision on the future of the country's lion hunting industry.

To determine the distribution of a species of interest, surveys are traditionally conducted in predetermined landscape units (natural e.g. ponds or abstract e.g. grids) within the study area wherein the presence or absence of the species is recorded (Mackenzie *et al.*, 2002; Mackenzie, 2005a; Hines *et al.*, 2010). However, these results may be biased by false absences (i.e. species present but not detected). This limitation can be overcome through the use of occupancy models, which use a detection history (a dataset generated by multiple spatial

and/or temporal survey replicates in each survey unit), to first calculate the probability of detecting the species given that it was present in the unit during the survey (the detection probability, p). Thereafter, p is used to adjust the naïve presence estimate to a probability of occupancy (ψ) by accounting for the effects of false absences in survey units with no detections (Mackenzie *et al.*, 2002; Mackenzie, 2005a; Hines *et al.*, 2010). The occupancy probability can be manipulated to represent the spatially explicit probability of an individual site being occupied, and can also be interpreted as the proportion of the study site that is likely occupied (the Probable Area Occupied, or PAO, (Hines *et al.*, 2010; Karanth *et al.*, 2011; Harihar & Pandav, 2012).

Various methods have been used to compile detection histories in carnivore occupancy surveys. For example, detection of spoor has been used to indicate tiger presence in India (Linkie *et al.* 2006; Guíllera-Arroita *et al.*, 2011) and Sumatra (Wibisono *et al.*, 2011), river otters *Lontra canadensis* in the United States (Aing *et al.*, 2011) and wolverines *Gulo gulo* in Canada (Magoun *et al.*, 2007). Graves *et al.*, (2011) used interviews with local communities to determine jaguar *P. onca* presence in Nicaragua, while hair traps and rub trees indicated the passage of grizzly bears in the US (Graves *et al.*, 2011). Motion-sensitive camera traps have been widely utilised for detecting presence, including for American martens *Martes americana* in the US (Baldwin & Bender, 2008), sun bears *Helarctos malayanus* in Sumatra (Wong *et al.*, 2012), brown hyaenas *Hyaena brunnea* (Burton *et al.*, 2011) in South Africa and complete carnivore guilds in Ghana's Mole NP (Burton *et al.*, 2011) and Kenya's Rift Valley (Schuette *et al.*, 2013b). In this chapter I use spoor surveys as my detection method in order to investigate the occupancy of lions in northern Kafue, a Type I Lion Conservation Unit (IUCN, 2006a) and one of Africa's largest PAs. Spoor surveys on roads have been successfully utilised to estimate large carnivore density in Africa and are considered a valid method of detecting lion presence (Funston *et al.*, 2010).

Distribution of dominant carnivore species is largely governed by the availability and biomass of suitable prey (Carbone & Gittleman, 2002; Spong, 2002; Karanth *et al.*, 2004), whilst subordinate species are affected by the presence of these dominant competitors (Loveridge *et al.*, 2007; Packer *et al.*, 2009). However, all large members of the taxa can be strongly influenced by anthropogenic persecution, such as trophy hunting (Loveridge *et al.*, 2007; Packer *et al.*, 2010) and snaring (Lindsey *et al.*, 2011), which typically manifest as edge effects within PAs (Woodroffe & Ginsberg, 1998). These human disturbances can have similar impacts on dispersion of ungulate (i.e. prey) biomass (Metzger *et al.*, 2010; Kiffner *et al.*, 2012), which may also be affected by availability of resources such as water (Valeix *et al.*, 2010). I thus predicted that lion occupancy in Kafue would be higher i) in areas with greater prey biomass and ii) with increasing distance from negative human disturbances. I considered potential natural drivers

(e.g. prey biomass, habitat type, proximity to water) of lion occupancy as well as proxies for negative (e.g. distance to boundary) and positive (e.g. anti-poaching patrol effort) human influences. Lion ranging behaviour varies seasonally in Kafue (Chapter 5), and my results should thus be interpreted as representing dry season occupancy only. I analysed the effects of all the identified factors by including them as covariates in a set of candidate univariate and multivariate occupancy models, used the top-ranked model to determine the primary drivers of lion distribution in the study area and finally produced a map of spatially explicit probability of lion occupancy for northern Kafue.

Methods

Study area

My study area for this chapter includes that area of Kafue that lies north of the M9 paved road (Figure 2.1), as well as those parts of southern Kafue and neighbouring GMAs encompassed by my occupancy survey grid (Figure 3.1) Using remotely sensed data (Online: <http://www.fao.org/geonetworks/srv/en/main/home>, accessed February 4 2013) and vegetation descriptions of Fanshawe (2010), I divided the study area into three major habitat classes, i) miombo and Kalahari woodland (MIO, 29% of study area) dominated by *Brachystegia spp.* and *Julbernardia spp.*, ii) munga and termitaria woodland (MUN, 32%) dominated by *Acacia spp.*, *Combretum spp.* and *Terminalia spp.*, and iii) munga scrub and grassland (SAG, 39%) comprising open scrubland up to 3m high and dambo, floodplain and riverine grasslands (Table 3.1).

Field data collection

I used a grid of square cells to define survey sites for the occupancy model. The objectives of my study were to estimate Probable Area Occupied (PAO) by lions and spatially explicit Probability of Lion Occupancy (PLO), rather than finer scale habitat selection. Mackenzie *et al.* (2006) recommend a balance between sites being large enough for a reasonable likelihood of the species being present, and small enough for occupancy measures to be meaningful, while for estimating PLO, cells greater than the largest home range of the species in the study area are suggested by Karanth *et al.* (2011). Home range estimates of nine Kafue lions (five male, four female) for the 2010 and 2011 (i.e. for survey planning prior to the occupancy survey) dry seasons ranged from 62.1 to 589.3 km² (Table 3.2). Due to this significant variation (\bar{x} =257.8 km², CV=80.6%), and the coarse resolution that would result from cells >590 km² (Karanth *et al.*, 2011), I calculated the median home range (188.7 km²) and accordingly selected a grid cell size of 200 km². Using software ARCGIS v10.1, I randomly overlaid my grid on the northern half

of Kafue. The grid comprised 73 cells covering 14,600 km², of which 11,480 km² was national park and the remainder a combination of GMAs (2839 km²) and a privately managed Open Area (OA; 281 km²).

Table 3.1. Reclassification of vegetation classes from Land Cover Classification System (LCCS) from most recent (2005) Globcover imagery (Online: <http://www.fao.org/geonetworks/srv/en/main/home>, accessed February 4 2013) into major habitat types relevant to lion ecology in Kafue.

LCCS regional map code	LCCS regional label	Proportion of survey grid	Reclassification
30	Mosaic vegetation (grassland/ shrubland/forest) (50-70%)	10.9%	Munga and Termitaria Woodland (MUN)
50	Closed (>40%) broadleaved deciduous forest (>5m)	0.3%	Miombo and Kalahari Woodland (MIO)
60	Open (15-40%) broadleaved deciduous forest/woodland (>5m)	23.1%	Miombo and Kalahari Woodland (MIO)
100	Closed to open (>15%) mixed broadleaved or needleleaved forest (>5m)	5.6%	Miombo and Kalahari Woodland (MIO)
110	Mosaic forest or shrubland (50-70%) /grassland (20-50%)	19.5%	Munga and Termitaria Woodland (MUN)
120	Mosaic grassland (50-70%)/ forest or shrubland (20-50%)	1.9%	Munga and Termitaria Woodland (MUN)
130	Closed to open (>15%) broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)	33.2%	Munga Scrub and Grassland (SAG)
140	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)	2.3%	Munga Scrub and Grassland (SAG)
143	Open grassland	2.9%	Munga Scrub and Grassland (SAG)
210	Water	0.3%	N/A

Using software GOOGLE EARTH, I identified grid cells ($n = 41$) that contained unpaved roads (for track detection), and selected sections of these roads for survey transects. Unlike work conducted in Asia on tigers (eg. Hines *et al.*, 2010), off-road animal trails were predominantly on hard clay soils unsuitable for track detection. I was thus constrained in my selection of transects to the limited network of roads with suitable substrate, a situation likely to be encountered in most large African PAs.

Table 3.2. Dry season (combined 2010 and 2011) home range (90% isopleth) data for 9 Kafue lions based on GPS collar downloads.

Lion	Home range (km ²)	Data collection period
F018	62.1	6 months
F021	100.8	6 months
F028	188.7	6 months
F039	593.1	2 months
M008	91.4	2 months
M016	348.8	6 months
M031	102.4	2 months
M037	250.3	2 months
M048	582.3	2 months
Mean	257.77	
CV	80.6%	
Median	188.70	

Valid inference from occupancy models usually requires detections to be independent of each other (Mackenzie *et al.*, 2002, 2006). However, Hines *et al.* (2010) developed a model which accounts for the spatial correlation of animal sign detections along sequential segments of a road or trail, thus allowing logistically feasible survey designs that follow the biologically likely reality of animals traveling along these routes (Karanth *et al.*, 2011). The model adds three parameters, θ_0 , denoting probability of detection on a segment given *absence* on the previous segment, θ_1 , denoting probability of detection on a segment given *presence* on the previous segment (Hines *et al.*, 2010) and $\theta_0\pi$, for the situation where a transect does not begin at a natural boundary (e.g. a major river that cannot be crossed by the species of interest), and thus the preceding segment could have a presence or an absence of sign (introduced in PRESENCE, Hines, 2013).

I identified 17 transects between 17 and 30 km in length, each traversing more than one grid cell, ensuring coverage of as many cells as possible (Figure 3.1). I was assisted in the field by a ZAWA scout, and both of us were competent at detecting and identifying tracks. We drove each transect 2-4 times between 1 July and 15 October 2012, with at least a week separating temporal replicates, and split transects into one-km segments (Hines *et al.*, 2010; Karanth *et al.*, 2011), resulting in a detection history comprising temporal and spatial replicates numbering 4-60 per surveyed cell. We started all surveys within 30 minutes either side of sunrise when tracks are most visible (Liebenberg, 1990) and drove at a speed of approximately 10 km h⁻¹ to maximise the likelihood of track detection. Both observers scanned the road for signs of lion, one person sitting on the front left corner of the vehicle and the other the front right driver's seat. We recorded substrate quality (ease of detecting tracks; scale of 1-5) and vehicle impact on substrate (impact of other vehicles on likelihood of detecting fresh tracks; scale of 0-2) for each segment (Table 3.3). We identified lion tracks based on their size and shape and recorded the detection (1) or non-detection (0) of lions on each one-km segment. If we were uncertain of the species responsible for a track we discounted it to ensure that we did not violate the model requirement of no false detections (Mackenzie *et al.*, 2002).

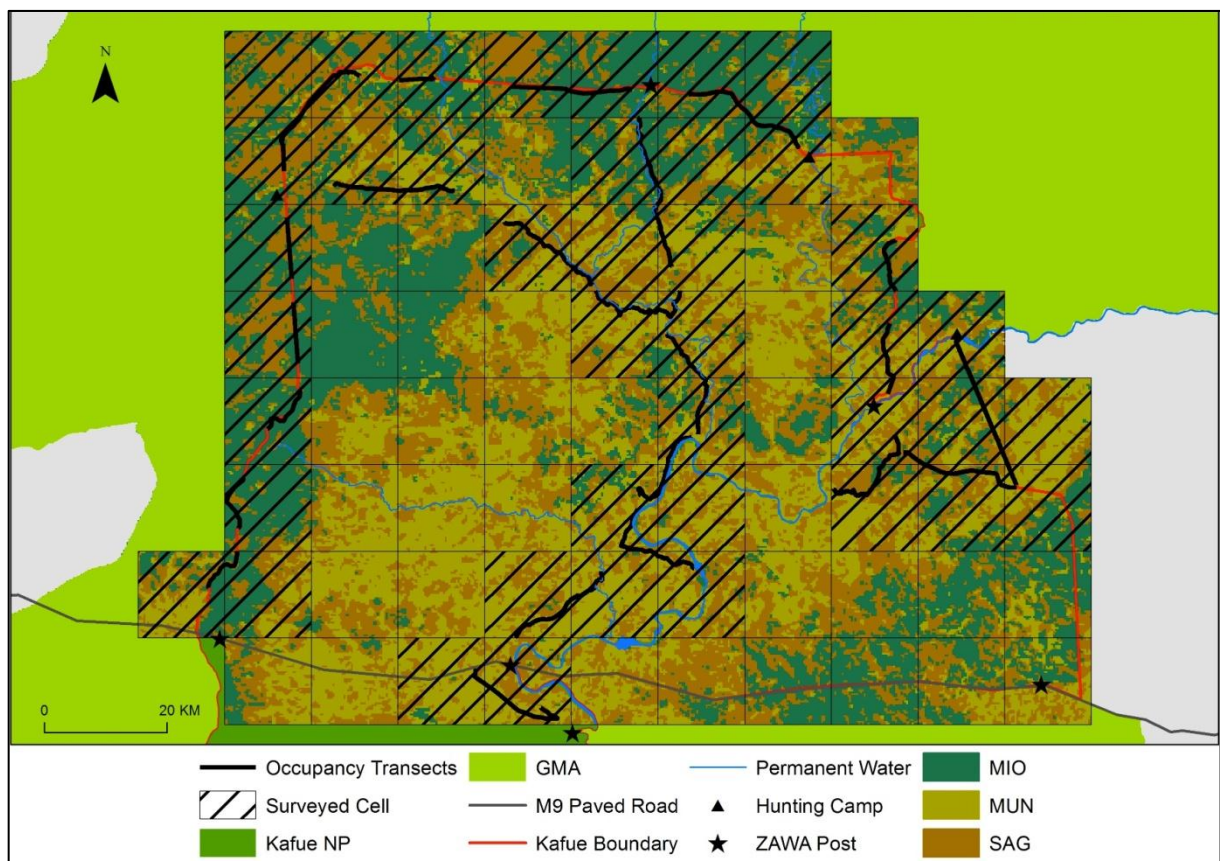


Figure 3.1. Occupancy survey design. NP: National Park; GMA: Game Management Area; ZAWA: Zambia Wildlife Authority; MIO: miombo and Kalahari woodland; MUN: munga and termitaria woodland; SAG: munga scrub and grassland.

Model building, model selection and data analysis

A further assumption of occupancy models is that the species of interest does not become extinct from, nor colonise, any sites during the survey period (Mackenzie *et al.*, 2002; Mackenzie, 2006). The short duration (3.5 months) of my study should ensure population closure, but wide-ranging species such as lions may have home ranges that overlap multiple sites, thus jeopardising the assumption of geographic closure. However, the random occupation of sites by lions during the survey period (i.e. on any given day an animal could be present in any of the sites within its home range) renders occupancy and detection parameters unbiased, although their interpretation changes (Mackenzie *et al.*, 2006; Kendall & White, 2009). I thus interpret ψ_i as the probability that a lion(s) used site i , and p_i as the probability that the lion(s) was detected given use of the site i during the survey. I thus calculate Proportion of Area Used (PAU) rather than PAO, and my spatial model predicts Probability of Lion Use (PLU) rather than PLO.

Occupancy models also assume that both detection and occupancy probabilities remain constant across survey sites (Mackenzie *et al.*, 2002). Spatial variation in abundance may induce heterogeneity in both parameters, but this violation can be overcome by modelling relevant covariates in the occupancy analysis (Royle & Nichols, 2003; Mackenzie, 2005b). I therefore used Software ARCGIS v10.1 to derive spatially explicit values, allocated to individual cells in my grid, for a suite of factors hypothesised to potentially influence lion occupancy in Kafue. Site specific factors considered are prey biomass (PB), habitat class (MUN, MIO, SAG), fire (FI) and law-enforcement effort (LE), and proximity (measured from the centre of the cell) to: water (PW), park boundary (PE), external human activities (PP), photographic tourism camps (PT), safari hunting camps (PH) and permanently manned ZAWA posts (PZ; Table 3.3). Although in all cases I used the best available data sets to derive layers for these factors (Table 3.3), I caution that some of these may have inferential limitations. Additionally, I considered the effect of the number of replicates (NR) per cell on occupancy to determine whether my sampling regime affected the model outcome. I did not consider elevation, slope or aspect due to the relatively homogeneous elevation of northern Kafue. I also modelled vehicle impact on roads (VI) and substrate quality (SU) as survey-specific factors (i.e. affecting p_i), giving an initial total of 15 covariates.

I used software PRESENCE (Hines, 2013) for occupancy analyses, and AIC_c values (Akaike Information Criterion adjusted for small sample sizes) to rank candidate models (Burnham & Anderson, 2002). I compared the top-ranked model with others in the set using evidence ratios (ER; Mazerolle, 2006), based on the formula $ER = w_j/w_i$ where w_j is the AIC_c weight of the top-ranked model and w_i the AIC_c weight of the model being compared. The lowest AIC_c ranking

indicated the top-ranked model, and I considered resulting models with $\Delta AIC_c < 2$ to be competing with the top model, while models with ΔAIC_c from 2-7 had some support (Burnham & Anderson 2002: 70). I analysed β (i.e. regression coefficient) of individual covariates within the top ranking models for significance of effect (i.e. 95% confidence intervals (CI) exclude zero; Zeller *et al.*, 2011) and calculated ERs comparing the top model with all models with $\Delta AIC_c < 7$ (Mazerolle, 2006).

Processing my detection history in PRESENCE with no covariates, I obtained AIC_c scores of 794.22 and 683.48 for the “Custom” ($\Psi(.)p(.)$) and “Custom with Spatial Correlation” ($\Psi(.)p(.)\theta_0(.)\theta_1(.)\theta_0\pi(.)$) models respectively. I therefore used the latter for all subsequent analyses in PRESENCE. I allowed the software to estimate θ_0 , θ_1 and $\theta_0\pi$ for all candidate models, and denote the inclusion of these parameters as $sc(.)$ in my model building process.

To build candidate models, I first considered covariates affecting p_i (i.e. survey-specific) through univariate analysis of each factor, as well as multivariate combinations thereof, in PRESENCE, holding $\Psi(.)$ constant (Karanth *et al.*, 2011). I carried the model with the lowest resulting AIC_c score forward for the selection of site-specific covariates, and used it to conduct univariate analyses in PRESENCE. Thereafter I used a Spearman’s correlation matrix in program STATISTICA to test for pair-wise correlation between these covariates (Graham, 2003; Table 3.4). For each pair with a strong correlation ($r \geq 0.80$) I eliminated the covariate with the lower AIC_c score from subsequent analyses. Following Zeller *et al.* (2011), I also eliminated covariates that had a non-significant effect (95% CI included zero) in univariate form from the final model set. Next I compared AIC_c scores for covariates in the same category (e.g. habitat class) and retained only the highest ranked factor in each category. Using my *a priori* hypotheses and predictions based on lion biology and the Kafue system, I created a final set of candidate models and entered these in PRESENCE. I used PRESENCE to apply the resulting predictive model to both surveyed and unsurveyed sites and software ARCGIS v10.1 to derive a map of spatially explicit PLU for the study area. Finally, I calculated the coefficient of variation of PLU for each cell as a measure of the variability in my data (*sensu* Sunarto *et al.*, 2012).

Table 3.3. Derivation of covariate layers used in occupancy model. All analyses performed in software ARCGIS v10.1 unless otherwise indicated.

Covariate	Data source	Data type	GIS analysis
Proximity to water (PW)	ZAWA GIS department	GIS shapefiles of major rivers, minor permanent rivers and drainage lines	I used the NEAR tool to measure distance between grid cell centres and nearest water including seasonal drainage lines, and divided the result by 100 for analysis in PRESENCE.
Proximity to boundaries (PE)	ZAWA GIS department	GIS shapefiles of Kafue National Park boundary	I used the NEAR tool to measure distance between grid cell centres and nearest national park boundary, and divided the result by 100 for analysis in PRESENCE.
Proximity to hunting camps (PH)	Personal visits; GOOGLE EARTH	GPS coordinates of camp locations	I used the NEAR tool to measure distance between grid cell centres and nearest safari hunting camp, and divided the result by 100 for analysis in PRESENCE.
Proximity to tourist camps (PT)	Personal visits; GOOGLE EARTH	GPS coordinates of camp locations	I used the NEAR tool to measure distance between grid cell centres and nearest photographic tourism camp, and divided the result by 100 for analysis in PRESENCE.
Proximity to ZAWA posts (PZ)	Personal visits	GPS coordinates of permanently manned ZAWA posts	I used the NEAR tool to measure distance between grid cell centres and nearest permanently manned ZAWA post, and divided the result by 100 for analysis in PRESENCE.
Proximity to human settlements/ activities (PP)	Aerial survey data (Frederick 2011)	GPS coordinates of transect subunits where human activities were noted, namely habitation (huts), cultivation (crops) and livestock (domestic animals)	I used the NEAR tool to measure distance between grid cell centres and nearest sign of human habitation detected during aerial survey work conducted in the 2011 dry season, and divided the result by 100 for analysis in PRESENCE.

Table 3.3. Derivation of covariate layers used in occupancy model. All analyses performed in software ARCGIS v10.1 unless otherwise indicated.

Covariate	Data source	Data type	GIS analysis
Proportion of cell burnt (FI)	MODIS (2013)	GeoTIFF files based on satellite imagery representing areas burnt during a calendar month	As the MODIS (2013) GeoTIFF tile arrangement cuts the Kafue system in half, I joined the north and south MODIS images for the study area using the EXPORT DATA function. I aggregated daily burn data into monthly summaries using the RECLASS tool, and subsequently combined these into annual burnt areas for the years 2010-2012 using the RASTER CALCULATOR. Lastly, I used the TABULATE AREA tool to calculate proportion of each grid cell burnt per year, and entered the mean annual proportion burnt in PRESENCE.
Law enforcement patrol effort (LE)	ZAWA Ecologist	Monthly GPS coordinates recorded by ZAWA law enforcement patrol teams. Teams record waypoints on deployment and withdrawal routes, and every two hours between 07:00 and 17:00 during patrols	I combined monthly waypoint shapefiles from individual patrol teams using the MERGE tool. I used the SPATIAL JOIN tool to count waypoints per grid cell per month. I used the cumulative data for the period January 2009 to October 2012 for analysis, and performed a z-transformation on these data to enter them in PRESENCE.
Habitat class	http://www.fao.org/geonetworks/srv/en/main/home	GIS shapefiles derived from Globcover satellite imagery, representing land cover types per the Land Cover Classification System (LCCS) of	I accumulated seven LCCS classifications into three relevant habitat classes, MUN, MIO and SAG (Refer Table 3.1 for details.). I used the TABULATE AREA tool to calculate the proportion within each grid cell covered by each vegetation class, and entered these proportions in PRESENCE.

Table 3.3. Derivation of covariate layers used in occupancy model. All analyses performed in software ARCGIS v10.1 unless otherwise indicated.

Covariate	Data source	Data type	GIS analysis
		the UN FAO	
Prey biomass (PB)	Aerial survey data (Frederick 2011)	Prey biomass layer as per Chapter 2.	<p>I used the ZONAL STATISTICS tool to spatially allocate prey biomass estimates to individual 200 km² grid cells.</p> <p>I exported the results to EXCEL and calculated prey biomass per grid cell using the formula</p> $CB_i = \frac{(a_i \times b) + (c_i \times d) + (e_i \times f)}{200}$ <p>where <i>CB</i> is grid cell biomass (kg), <i>i</i> is the cell number, <i>a</i>, <i>c</i> and <i>e</i> are the sums of biomass km⁻² for each raster cell size within cell <i>i</i>, <i>b</i>=6.25, <i>d</i>=12.5 and <i>f</i>=25 and 200 is the size of the grid cell in km². I divided the result by 1,000 prior to entering these data into PRESENCE.</p>
Substrate grade (SU)	Personal observations	Subjective grading of substrate quality for detecting tracks.	1: very poor; 2: poor; 3: moderate; 4: good; 5: very good
Vehicle impact (VI)	Personal observations	Subjective grading of impact of vehicle traffic on track detection. Grading applied to the impact on fresh tracks only. i.e. Another vehicle had driven the road on the same morning as our survey.	0: no impact; 1: light impact; 2: heavy impact

Table 3.4. Spearman’s correlation matrix of site-specific covariates (r-values). PW: Proximity to Water; PZ: Proximity to permanent ZAWA post; PE: Proximity to park boundary; PT: Proximity to tourist lodge; PH: Proximity to safari hunting camp; PP: Proximity to human activity/settlement in GMA; LE: Law enforcement effort; FI: Proportion of cell burnt; PB: Prey Biomass; MIO: proportion of miombo and Kalahari woodland; MUN: Proportion of munga and termitaria woodland; SAG: Proportion of munga scrub and grassland. A negative sign linked to a “Proximity to” variable indicates that the value of the other variable decreases with increasing proximity). Bold type indicates statistically significant correlation ($p < 0.05$).

	PW	PZ	PE	PT	PH	PP	LE	FI	PB	MIO	MUN	SAG
PW	1.00											
PZ	0.22	1.00										
PE	0.06	0.29	1.00									
PT	0.04	0.01	-0.25	1.00								
PH	-0.04	-0.29	0.21	0.04	1.00							
PP	0.09	0.25	0.67	-0.51	-0.17	1.00						
LE	-0.14	-0.10	-0.08	-0.36	0.55	-0.30	1.00					
FI	-0.01	0.26	0.73	-0.17	0.30	0.54	0.05	1.00				
PB	-0.11	-0.09	0.13	-0.42	0.04	0.23	0.10	0.25	1.00			
MIO	0.07	0.16	-0.49	0.37	-0.43	-0.43	-0.09	-0.69	-0.30	1.00		
MUN	-0.08	-0.17	0.54	-0.39	0.35	0.48	0.01	0.73	0.40	-0.91	1.00	
SAG	0.14	0.20	0.02	-0.23	-0.08	0.19	-0.03	-0.02	0.17	-0.21	-0.01	1.00

Results

I drove six transects four times and 11 transects twice for a total of 46 individual surveys and 1010 one-km segments. I graded substrate quality on 6.6% of segments as very good, 27.9% good, 49.9% moderate, 14.6% poor and 1.0% very poor. There was no vehicle impact on 94.3% of segments, light impact on 5.3% and heavy impact on 0.4%. I detected lion tracks on 147 segments (14.6%), and in 24 of 41 surveyed cells, producing a naïve occupancy estimate of 0.585. The null model $\Psi(.)p(.)sc(.)$ estimated PAU, after adjusting for detection probability, as 0.721 (95% CI: 0.529-0.913).

The null model $\Psi(.)p(.)sc(.)$ had the highest AIC_c ranking in analysis of survey-specific factors affecting p_i . Based on ERs, this model provided a fit that was 2.6 times better than the closest competing model, $\Psi(.)p(SU)sc(.)$ (SU = substrate quality; Table 3.5). Both SU and vehicle impact (VI) had 95% CIs for β that included zero, indicating non-significant effects (Zeller *et al.*, 2011). I therefore held the $p(.)$ term constant with no covariates for subsequent analyses.

Table 3.5. Role of survey-specific covariates in determining probability of detecting lion sign on 1 km long segments using the model of Hines *et al.* (2010). Number of sites = 41. Covariates are substrate quality (SU) and vehicle impact on substrate (VI).

Model	AIC_c	ΔAIC_c	AIC_c weight	Evidence ratio	Number of parameters
$\Psi(.)p(.)sc(.)$	683.48	0.00	0.5806	1.0	5
$\Psi(.)p(SU)sc(.)$	685.43	1.95	0.2194	2.6	6
$\Psi(.)p(VI)sc(.)$	686.24	2.76	0.1463	4.0	6
$\Psi(.)p(SU + VI)sc(.)$	688.24	4.76	0.0537	10.8	7

Only four site-specific covariates had significant effects on PLU in the univariate analysis, namely habitat MUN (positive), habitat MIO (negative), mean proportion of cell burnt (FI; positive) and proximity to water (PW; positive). These were thus the only covariates considered for the final model set in univariate form, although I nevertheless retained those covariates required to build my hypothesised multivariate models. Univariate analysis ranked $\Psi(MUN)p(.)sc(.)$ as the top model, with an AIC_c weight of 0.69 (Table 3.6). The next best fitting model was $\Psi(MIO)p(.)sc(.)$ with AIC_c weight of 0.23, but this model had $\Delta AIC_c=2.24$ and was 3.1 times less likely than the top-ranked model. In addition, correlation testing detected a very strong negative correlation ($r= -0.91$) between MUN and MIO. I therefore eliminated MIO from subsequent analyses. Although there was a weak negative correlation between habitats MUN

and SAG ($r = -0.21$), the model $\Psi(\text{SAG})p(\cdot)sc(\cdot)$ was 761.3 times less likely than $\Psi(\text{MUN})p(\cdot)sc(\cdot)$. I therefore eliminated habitat SAG from multivariate combinations and MUN was the only habitat class considered in further analyses.

Table 3.6. Top five univariate models for multivariate model-building purposes using the model of Hines *et al.* (2010). * Denotes significant univariate effect (95% confidence intervals exclude zero). β is the regression coefficient of the covariate. Negative β indicates a negative relationship between PLU and the covariate. Number of sites = 41. Covariates listed are proportion of cell comprising munga and termitaria woodland (MUN), proportion of cell comprising miombo and Kalahari woodland (MIO), mean proportion of cell burnt 2009-2012 (FI), proximity to water (PW) and proximity to tourist camp (PT).

Model	AIC _c	Δ AIC _c	AIC _c weight	Evidence ratio	Number of parameters	β
$\Psi(\text{MUN})p(\cdot)sc(\cdot)$	672.85	0.00	0.6916	1.0	6	2.28*
$\Psi(\text{MIO})p(\cdot)sc(\cdot)$	675.09	2.24	0.2257	3.1	6	-2.09*
$\Psi(\text{FI})p(\cdot)sc(\cdot)$	678.22	5.37	0.0472	14.7	6	1.57*
$\Psi(\text{PW})p(\cdot)sc(\cdot)$	679.42	6.57	0.0259	26.7	6	13.54*
$\Psi(\text{PT})p(\cdot)sc(\cdot)$	683.28	10.43	0.0038	184.0	6	2.00

Due to the relative strength of the model $\Psi(\text{MUN})p(\cdot)sc(\cdot)$, it was unlikely that a multivariate combination excluding habitat MUN would generate a competitive AIC_c score, and most of my high-ranking candidate model combinations therefore include this factor. I nevertheless excluded it from some models in order to test my original hypotheses. My final set of candidate models tested in PRESENCE comprised the null model $\Psi(\cdot)p(\cdot)sc(\cdot)$, 3 univariate and 25 multivariate models. I present the top ten results in Table 3.7 ranked by AIC_c, which selected $\Psi(\text{MUN} + \text{PW})p(\cdot)sc(\cdot)$ (PW = proximity to water) as the top model, ahead of $\Psi(\text{MUN})p(\cdot)sc(\cdot)$ and $\Psi(\text{MUN} + \text{PW} - \text{PH})p(\cdot)sc(\cdot)$ (PH = proximity to safari hunting camp), although the latter had a Δ AIC_c > 2 and is thus not a competing model. A further 18 models had Δ AIC_c < 7 and thus received some support, but were at least 3.5 times less likely than the best model. The highest ranked model excluding MUN, $\Psi(\text{FI} + \text{PW})p(\cdot)sc(\cdot)$ was ranked 10th with AIC_c = 3.14. However, FI was correlated with MUN ($r = 0.73$), below my cut-off of 0.80 and I suspect this is the reason for the positive relationship between PLU and area burnt, as other studies have found that lions do not preferentially use burnt areas (e.g. Eby *et al.*, 2013). AIC_c scores of high-ranking models did not improve with the addition of number of replicates (NR) as a covariate.

Due to the low ER between them (1.3) and Δ AIC_c of 0.57 for the second model, I considered the top two models as having equivalent support. However, in the top ranked model, the influence of PW was not significant ($\beta = -10.3$, 95% CI: -21.6 to 1.0; *sensu* Zeller *et al.*, 2011). Due to the

lack of competing models, and the equivocal utility of the method (Richards, *et al.*, 2011), I did not conduct model-averaging and instead followed the principle of parsimony *sensu* Wibisono *et al.* (2011). I thus selected $\psi(MUN)p(.).sc(.)$ as my final occupancy model, indicating a significant positive relationship between proportion of cell comprising habitat class MUN ($\beta = 2.3$, 95% CI: 1.1 - 3.5) and probability of lion use (PLU). Site-specific PLU's for the survey area based on the final model ranged from 0.760 to 0.952. Of the 73 grid cells, PLU was below 0.800 for 19 cells (26.0%), 29 cells (39.7%) were between 0.800 and 0.899 and 25 (34.3%) were greater than 0.900. I applied these values to my survey grid in ARCGIS v10.1 to produce a map of spatially explicit PLU for northern Kafue (Figure 3.2).

Table 3.7. Top ten multivariate models in determining probability of use of cells by lions in Kafue using the model of Hines *et al.* (2010). Number of sites = 41. Covariates considered are munga and termitaria woodland (MUN), proximity to water (PW), proximity to safari hunting camp (PH), mean proportion of cell burnt 2009-2012 (FI), prey biomass (PB), law enforcement patrol effort (LE) and proximity to tourist camp (PT).

Model	AIC _c	ΔAIC _c	AIC _c weight	Evidence ratio	Number of parameters
$\psi(MUN+PW)p(.).sc(.)$	672.28	0.00	0.1967	1.0	7
$\psi(MUN)p(.).sc(.)$	672.85	0.57	0.1482	1.3	6
$\psi(MUN+PW-PH)p(.).sc(.)$	674.66	2.38	0.0600	3.3	8
$\psi(MUN+PW+FI)p(.).sc(.)$	674.79	2.51	0.0562	3.5	8
$\psi(MUN+PW+PB)p(.).sc(.)$	674.82	2.54	0.0553	3.6	8
$\psi(MUN+PH)p(.).sc(.)$	675.03	2.75	0.0497	4.0	7
$\psi(MUN+PW+LE)p(.).sc(.)$	675.22	2.94	0.0453	4.3	8
$\psi(MUN+FI)p(.).sc(.)$	675.36	3.08	0.0422	4.7	7
$\psi(MUN+PW+PT)p(.).sc(.)$	675.38	3.10	0.0418	4.7	8
$\psi(FI+PW)p(.).sc(.)$	675.42	3.14	0.0409	4.8	7

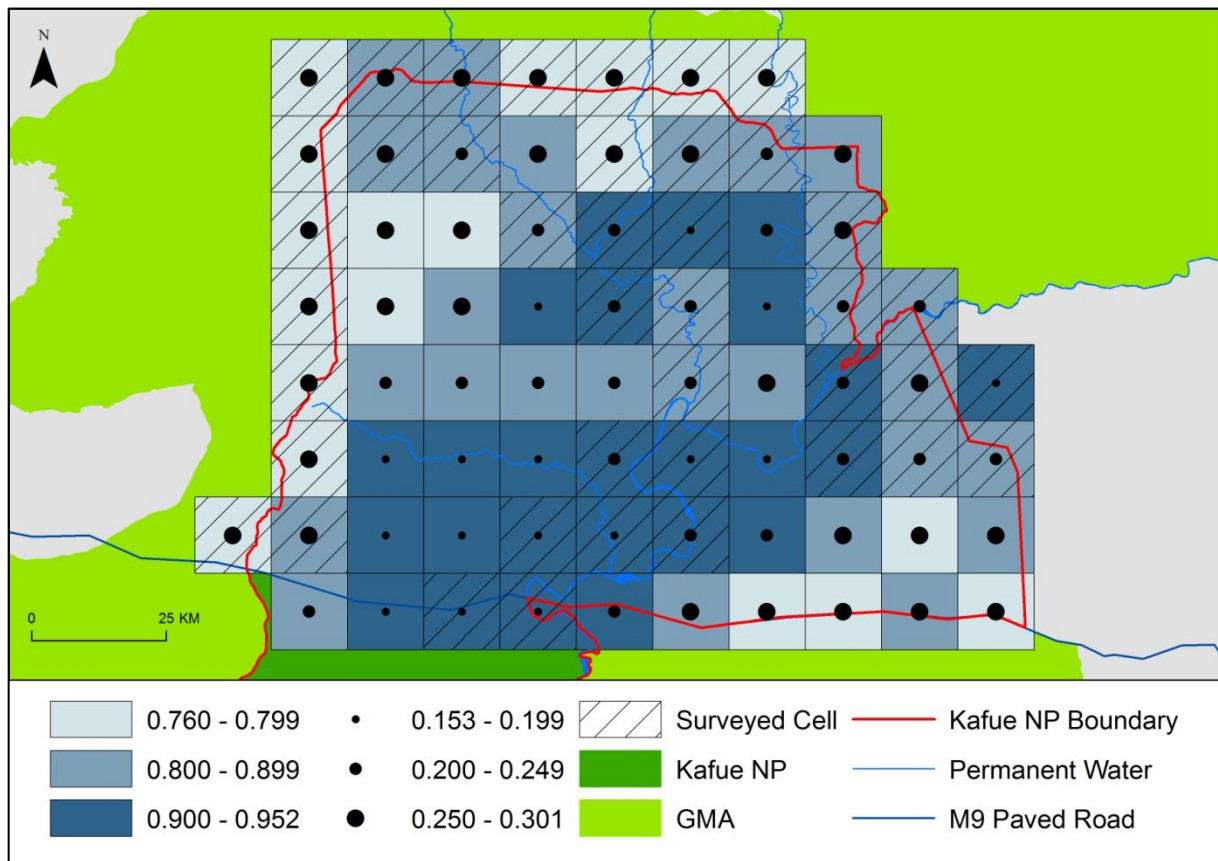


Figure 3.2. Occupancy survey results. Probability of lion use (PLU) of individual grid cells, represented by colour of cells, resulting from the final selected occupancy model $\Psi(MUN)p(.)sc(.)$. Black dots represent cell-specific coefficient of variation of the estimate (following Sunarto *et al.*, 2012). NP: National Park; GMA: Game Management Area.

Discussion

My study is the first to survey lions using track-based occupancy techniques, and allowed effective analysis of data sampled from a very large area with limited access and resources. Ignoring the issue of false absences, my survey would have predicted that lions used approximately 8541 km² of my study grid (i.e. the naïve estimate). This estimate grew to 10,527 km² (95% CI: 7,723-13,330 km²) - an increase of 23.3% - when I accounted for imperfect detection probability through the use of occupancy modeling, and clearly demonstrates the benefit of this approach.

By incorporating individual covariates in my models, I refined this estimate into a unique probability of lion use (PLU) for each grid cell, whether surveyed or not (Figure 3.2). My first prediction was that cells with the greatest prey biomass would have the highest PLU, but this model had little support and ranked 13th out of 14 candidates in the univariate set. I note some caution around this result, due to the timing of the aerial survey discussed under the Prey Biomass calculation described in Chapter 2. I used a kernel density estimator (Table 3.3) to smooth the aerial survey data spatially, thus allowing for some intra- and inter-seasonal

movements of ungulates. I thus believe that my prey biomass distribution layer is reasonable, but note the possibility that this factor may have ranked more highly in my model set if it had been measured concurrently with my occupancy survey.

Loveridge *et al.* (2007) demonstrated the effects of sport hunting outside Hwange NP in Zimbabwe on lion populations inside the PA, while in the Save Valley Conservancy, snaring, more prevalent near the boundaries, accounted for seven known lion mortalities (Lindsey *et al.*, 2011). Accordingly, presence of three lion-hunting concessions adjacent to northern Kafue (where at least one of my study animals, collared within the park, was shot by safari hunters), and observations of seven and six snared lions in my 2011 and 2012 field seasons respectively (N. Midlane, unpublished data), led to my prediction of anthropogenic edge effects (Woodroffe & Ginsberg, 1998) influencing lion distribution in Kafue. However, none of the models including covariates used as proxies for these edge effects (i.e. distance to nearest park boundary, human settlement or safari hunting camp) provided a good fit for my detection history and all were ranked lower than the null model. My expectation that PLU would increase as a result of the deterrent effect on illegal hunters of increasing ZAWA patrol effort or proximity to ZAWA scout posts and photographic tourist camps also received little support among my set of candidate models.

My *a priori* predictions were thus poorly supported by the occupancy model framework. Instead, habitat class MUN (munga and termitaria woodland) emerged as the best supported of the univariate models and the second-ranking model in the final set. The top-ranking model in the set (Table 3.7) was the additive combination of MUN habitat and proximity to water. However, as in the lion occupancy findings of Schuette *et al.* (2013b) in Kenya, proximity to water was a non-significant factor. I thus selected the second-ranked MUN model as the basis for my spatially explicit prediction of PLU (Figure 3.2). Habitat type emerged as an important occupancy driver for tigers (Harihar & Pandav 2012; Karanth *et al.* 2011; Sunarto *et al.* 2012; Wibisono *et al.* 2011) and jaguars (Zeller *et al.* 2011), and my results suggest it is also the most significant factor driving lion spatial use in northern Kafue. I postulate that increased PLU in munga and termitaria woodland is due to the patchy, heterogeneous nature of this habitat being more suited to the stalk-and-pounce hunting technique of lions (Hopcraft, *et al.*, 2005) than heavily wooded miombo woodland (MIO) or the sparse cover of munga scrub and grassland (SAG).

My final model produced PLU for individual grid cells ranging from 0.760 to 0.952, meaning that lions were 25% more likely to use the most suitable cell than the least. Although the underlying driver of PLU differed from my primary hypothesis, the resulting spatial distribution of cells in my three classes (PLU <0.800, from 0.800 to 0.899 and >0.900; Figure 3.2) was a reasonable

match to my *a priori* expectations of lion distribution in Kafue, engendering confidence in the model.

I was surprised that anthropogenic disturbance was not an important factor in predicting probability of lion use (Woodroffe & Ginsberg, 1998; Kiffner *et al.*, 2009) or dispersion of prey biomass (Laurance, 2008), which was only weakly correlated with increasing distance from boundaries ($r = 0.13$) and human settlements ($r = 0.23$). This does not, however, preclude the possibility that these factors may influence lion abundance in Kafue. Snaring is often more extensive closer to human settlements (Muchaal & Ngandjui 1999, Wato *et al.* 2006) and Van der Westhuizen (2007) found a greater frequency of illegal activities in GMAs and near the boundary of the North Luangwa NP than deeper within the PA. Illegal hunting of wildlife is highly prevalent in some Zambian wildlife areas. For example, in their study area straddling South Luangwa NP and adjacent GMAs, Becker *et al.* (2013) found that 12% of lions over one year old and 20% of adult males (>4 years) were snared. However, in Kenya's Maasai Mara National Reserve (MMNR), Ogutu *et al.* (2011) found that despite major decreases (driven primarily by illegal human activities) in wildlife populations over a 30-year period, declines at the edges of the reserve were no more dramatic than those in the interior. Similarly, Katavi NP in Tanzania faced significant pressure from illegal hunting, but proximity to the park edge or human villages had no significant effect on herbivore distribution, leading Kiffner *et al.* (2012) to hypothesise that the problem was simply too widespread to manifest as an edge effect.

I believe that a similar situation exists in Kafue. Tourism operators at camps at least 30 km from the nearest park boundary reported multiple incidents of illegal hunting (gunshots fired) within earshot of their camps during the dry season in 2011 and 2012 (G. Dickson, pers. comm.), and butchered hippo *Hippopotamus amphibius* carcasses have been found in this vicinity (N. Midlane, unpublished data). Lindsey *et al.* (In press), using biomass estimation methods of Coe *et al.* (1976), found that Kafue's ungulate biomass was significantly below carrying capacity, and more than six times lower than that of Mushingashi Limited, a privately managed Open Area contiguous with northern Kafue. Katavi NP is located in the same central Zambezi miombo ecoregion as Kafue with comparable rainfall (Celesia *et al.*, 2009), but, despite also suffering significant illegal hunting pressure (Kiffner *et al.*, 2012), its estimated biomass of medium to large ungulates (2307 kg km^{-2} ; Kiffner *et al.* 2009) is an order of magnitude greater than our estimate for Kafue. I thus believe that the ubiquity of illegal hunting across northern Kafue renders the impact on lions and their prey too diffuse to manifest as an edge effect in occupancy analysis. The centre of a larger park should be more robust to external human influence than a smaller one (Laurance, 2008), and northern Kafue is 2.5 and 7.1 times larger than MMNR and Katavi respectively. My results imply that the interiors of even the largest of

Africa's PAs are not immune to this threat, and highlight the urgent need for more effective law enforcement in Kafue.

As the first application of the Hines *et al.* (2010) spatial correlation occupancy model in the context of an African felid, my study demonstrates the utility of the method in obtaining an understanding of the distribution of lions in a vast, previously unsurveyed African PA. Primary limiting factors for managers to consider prior to employing track surveys as a detection method are road networks with suitable substrate for tracking and staff with requisite tracking skills. I caution that the approach may not be as effective in multiple use landscapes outside of PAs, as carnivores in these areas are more wary of humans and less likely to use roads to move through their ranges (e.g. in fragmented landscapes in India, tiger occupancy was negatively associated with proximity to public roads; Linkie *et al.* 2006). In these landscapes, alternative means of detection such as audio lures (Ferreira & Funston, 2010) or camera traps (Schuette *et al.*, 2013b) may be more appropriate.

I chose to analyse my data in a single-season single-species framework, but further options are available to practitioners, including multi-species (Burton *et al.*, 2012; Schuette *et al.*, 2013b) and multi-season models (Mackenzie *et al.*, 2006). The former enable analysis of intra-guild effects on occupancy, while the latter can provide a valuable proxy for population trends in areas where data on species abundance are not readily available. The explicit inclusion of relevant covariates in occupancy analysis can present management with further insight into the key threats faced by species in their reserves and thus assist in the effective deployment of scarce human and financial resources. My study delivers this initial insight for northern Kafue, and provides a basis for further research, better understanding and more effective management of one of Africa's key lion populations.

CHAPTER 4

To call or to track: how to count Kafue's lions

Summary

Protected area managers require population data on threatened species to guide conservation decisions and enable effective and efficient allocation of scarce resources. However, the wide-ranging behaviour of large carnivores and low densities at which they occur make direct population surveys of these species expensive and time consuming, and indirect methods are therefore widely used. In this chapter, I compared the accuracy, precision and cost of two methods commonly used to survey African lions, namely call-up surveys and track-count surveys. I carried out surveys using both methods in the 11,000 km² northern sector of Zambia's Kafue National Park, an area for which no previous empirical lion population data are available. I used the results of the occupancy survey in Chapter 3 to stratify the study area, and tested whether this improved the resulting estimates. I used GPS collars and regular observations of lions to establish a reference population in an Intensive Study Site for comparison with survey results. Both survey methods produced accurate results, though precision was higher for call-up surveys, despite lower costs. However, call-up estimates are sensitive to variations in lion response distances and probabilities, which are difficult to quantify. Stratification of the study area did not improve the survey estimates. I thus recommend track-count surveys as the most appropriate method for surveying lions in large protected areas, provided that competent trackers are available and road substrate is suitable for detecting tracks. I estimate lion abundance of 200 individuals over one year of age in the northern Kafue, at a density of 1.83 lions 100 km⁻².

Introduction

Global biodiversity is declining at an accelerating rate (Ceballos *et al.*, 2005; O'Brien *et al.*, 2010) with 21-36% of 5282 extant terrestrial mammal species threatened with extinction (Schipper *et al.*, 2008). Large carnivores, such as the African lion, are among the most severely affected (Inskip & Zimmermann, 2009; Karanth & Chellam, 2009). Lions have lost more than 75% of their historical distribution and experienced a dramatic population decline over the last 30 years (Riggio *et al.*, 2013), primarily as a result of anthropogenic impacts (Loveridge *et al.*, 2010). Reliable, cost effective measures of local abundance and density of extant wild lion populations are thus urgently required to monitor current and future threats, and the effectiveness of existing and planned management interventions that are essential for the continued persistence of this species (Funston *et al.*, 2010; Pollock *et al.*, 2012).

However, limited human and financial resources necessitate a trade-off between the effectiveness (accuracy and precision of population estimates) and efficiency (minimising time and monetary cost) of methods used to obtain such data (Field *et al.*, 2007; Sims *et al.*, 2008; Reynolds *et al.*, 2011). Direct counts have been used to estimate abundance in some long-term studies (e.g., lions, Schaller 1972; Packer *et al.* 2005a; cheetah, Durant *et al.* 2007), but they are usually too expensive and time-consuming to be applied across large areas for low density carnivore populations (Stander, 1998; Gese, 2001).

Carnivore population trends can be tracked using relative abundance indices (RAIs) from indirect counts, which are cheaper, faster, repeatable and include a measurement of precision (Ogutu & Dublin 1998; Stander 1998; Mills *et al.* 2001; Funston *et al.* 2010). However, converting RAIs to abundance estimates presents challenges, as it relies on assumptions of constant detection between habitats, observers, environmental conditions and geographic areas (Gibbs *et al.* 1998; Anderson 2001; Stephens *et al.* 2006). Nonetheless, Bart *et al.* (2004) argue that a constant detection rate is not required, so long as the "detection ratio (index result/parameter of interest)" remains stable. Eberhardt and Simmons (1987) recommend that the detection ratio be calculated by double sampling (i.e. the index is calibrated against a direct estimate of absolute abundance), but Conroy (1996) cautions that this relationship may not remain constant, particularly at high or low population densities. Nevertheless, if the average number of signs per animal can be calculated reliably and shown to be stable, the resulting ratio can be used as a correction factor to convert the RAI to an abundance estimate (Schwarz & Seber, 1999; Pollock *et al.*, 2002). Furthermore, some authors argue that analysis of longitudinal variation in RAIs is as useful to managers as similar comparisons of absolute abundance estimates, negating the need for inference of abundance (Funston *et al.*, 2010).

Various indirect methods have been applied to estimate demography and density of terrestrial carnivores. Camera trap surveys are effective for animals which are uniquely identifiable through coat markings such as tigers (Karanth & Nichols 1998; Karanth *et al.* 2003; Linkie *et al.* 2006; Jhala *et al.* 2010), jaguars (Soisalo & Cavalcanti 2006) and leopards (Balme *et al.* 2009a; Chapman and Balme 2010). Call-up surveys using audio lures have been used to count spotted hyaena (*Crocuta crocuta*; Ogutu & Dublin 1998; Mills *et al.* 2001) and African wild dogs (Robbins & McCreery 2003) while track (spoor) counts have been employed to estimate numbers of puma (*Puma concolor*; Van Dyke *et al.* 1986; Smallwood & Fitzhugh 1995), leopard (Stander 1998; Gusset & Burgener 2005; Balme *et al.* 2009a), cheetah (Houser *et al.* 2009), caracal (*Caracal caracal*; Melville & Bothma 2006) and tigers (Hayward *et al.* 2002; Barlow *et al.* 2009; Jhala *et al.* 2010). Recently, mark-recapture analyses have been applied to DNA samples collected non-invasively from hairs of grizzly bears (Boulanger *et al.* 2008) and tiger scats (Mondol *et al.*, 2009) to derive density estimates for these species.

As with other carnivores, multiple methods, with varying degrees of limitation, have been used to survey lion populations. Total counts were conducted in the Serengeti by Schaller (1972) and Packer *et al.* (2005), and in the Maasai Mara by Ogutu & Dublin (2002), but this method is expensive and time-consuming. Capture, mark and recapture techniques were utilised in Kruger NP (Smuts, 1978) and the Kalahari (Funston *et al.* 2001; Castley *et al.* 2002) but costs are similarly high. Tende *et al.* (2008) used DNA analysis from scat samples in Nigeria's Yankari NP, but were only able to generate a minimum count. Distance sampling was employed by Durant *et al.* (2011), though they caution that the method is only applicable to systems where the habitat is open enough to allow regular observation. Similarly, capture-recapture analysis was applied to lion observations in Kenya's Mara Game Reserve, but low encounter rates preclude the use of this technique in areas of lower lion density (Ogutu *et al.*, 2006). To date, due to their cost-effectiveness over large areas, the two most widely used methods for lion surveys are track counts (Stander 1998; Funston *et al.* 2001; Lichtenfield 2005; Funston *et al.* 2010; Henschel *et al.* 2010; Burton *et al.* 2011; Croes *et al.* 2011; Davidson *et al.* 2012) and call-up surveys (Ogutu & Dublin, 1998; Maddox, 2003; Whitman, 2006; Kiffner *et al.*, 2007; Ferreira & Funston, 2010; Burton *et al.*, 2011; Brink *et al.*, 2012).

In this chapter I explored both track count and call-up surveys as potential methods for estimating lion density and abundance in the northern sector of Kafue. I also tested the importance of stratifying the study area for survey purposes. I used GPS collars and individual identification (Pennycuick & Rudnai, 1970) to estimate home range sizes and density of known lions as a reference population in a core "intensive study site" (ISS). I subsequently compared the results of the two survey methods in terms of accuracy, precision and cost. Kafue is a vast area with extremely limited access and thus provides a good representation of the challenges

faced in surveying and monitoring wild lion populations in Zambia and elsewhere. My study will therefore provide ZAWA with guidance on the most appropriate method for surveying lions in the country. I also generate baseline lion population data for the northern sector of Kafue, an area that comprises a significant proportion of Zambia's remaining lion range.

Methods

Study area

My study area for this chapter is that part of Kafue that lies to the north of the M9 paved road (Figure 2.1). Within this larger study area I delineated the ISS, the area within which my reference population occurred (Figure 4.1).

Reference population

In order to locate, identify and count lions, as well as calculate home ranges, I fitted select individuals (one female per pride, one male per coalition) in my study area with VHF/GPS collars. I deployed collars in 2010, 2011 and 2012, set to record locations daily at 18h00, 24h00 and 06h00. I used photographs of vibrissae patterns and other unique markings (Pennycuick & Rudnai 1970) to identify all lions in the prides and coalitions associated with the collared animals, and located and monitored these groups on a regular basis.

I used daily midnight GPS locations for each collared lion in the HOME RANGES extension of software ARCGIS v9.2 (ESRI, Redlands, California) to calculate dry season home ranges using 90% fixed kernels (Loveridge *et al.*, 2009). I combined the home ranges of four collared females (representing four prides) whose home ranges included survey points and transects, and used this as my ISS to calculate estimated density of known lions (Figure 4.1). The combined home range of four collared male lions (four coalitions) in the system was significantly larger than the ISS, and some of these males thus spent only a portion of their time within this area (Figure 4.1). Using the method of Stander (1998), I therefore calculated the proportion of GPS locations for each collared male that fell within the ISS and multiplied it by the number of males in that coalition to obtain an adjusted male count for the ISS. I added the sum of all adult females and subadults (>1 yr) in prides associated with collared females to the adjusted male count for 2011 and 2012, and divided this by the area of the ISS to obtain a density estimate for my reference lion population. No lions from non-collared groups responded to call-ups in the ISS and, based on my knowledge of collared group size, composition and movements, I was confident that all the tracks detected in the ISS in the 2012 survey could be attributed to known

lions. I occasionally observed lions from non-collared female groups within the periphery of the ISS, and there was some overlap of home range between two neighbouring collared female groups (12.8% and 5.5% of their respective home ranges). However, I argue that the addition of the groups of non-collared lions to the count would be accompanied by an expansion of the ISS to accommodate their home ranges, and thus should not materially affect the estimated density of known lions. I am thus confident that the density of the reference lion population can be reasonably compared to the estimates derived from the two surveys in the ISS.

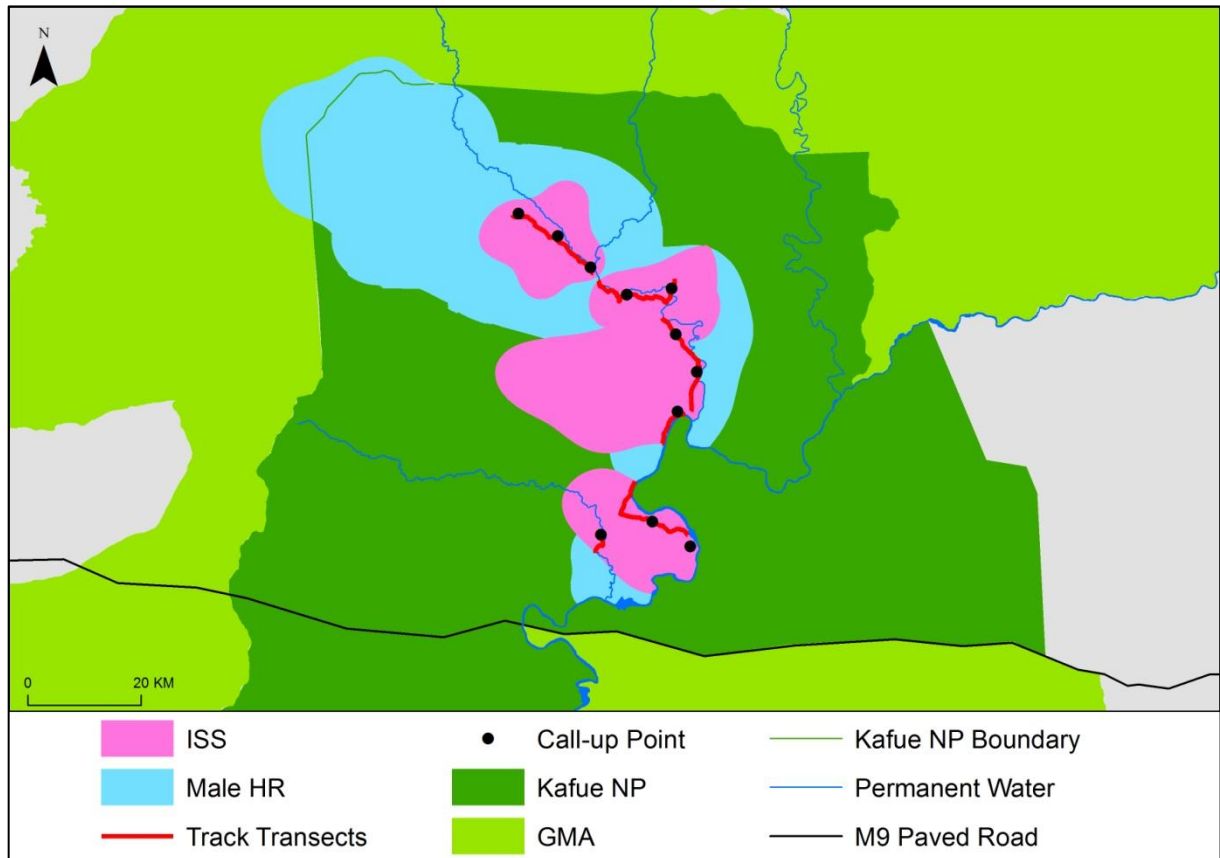


Figure 4.1. A map showing the location of the intensive study site (ISS), derived from combined home ranges of four collared females, within the northern sector of Kafue National Park (NP). Male home ranges (HR) were derived from the combined home ranges of five male coalitions whose home ranges had some overlap of the ISS.

Call-up surveys

I conducted annual call-up surveys from June to September in 2010 and 2011. A pilot study showed off-road surveys to be unfeasible due to logistical and safety constraints; all survey points were therefore located on roads. Using software GOOGLE EARTH, I selected a random point on a road, and thereafter spaced survey points 8 km apart (straight-line distance; Figure 4.2) in order to avoid the double-counting that may arise from attracting the same animals to adjacent sample points (Mills *et al.*, 2001). If vegetation rendered visibility at a point unsuitable, I

relocated it a maximum of 500m in either direction. In order to avoid habituation of lions, no point was surveyed more than once in a 12-month period.

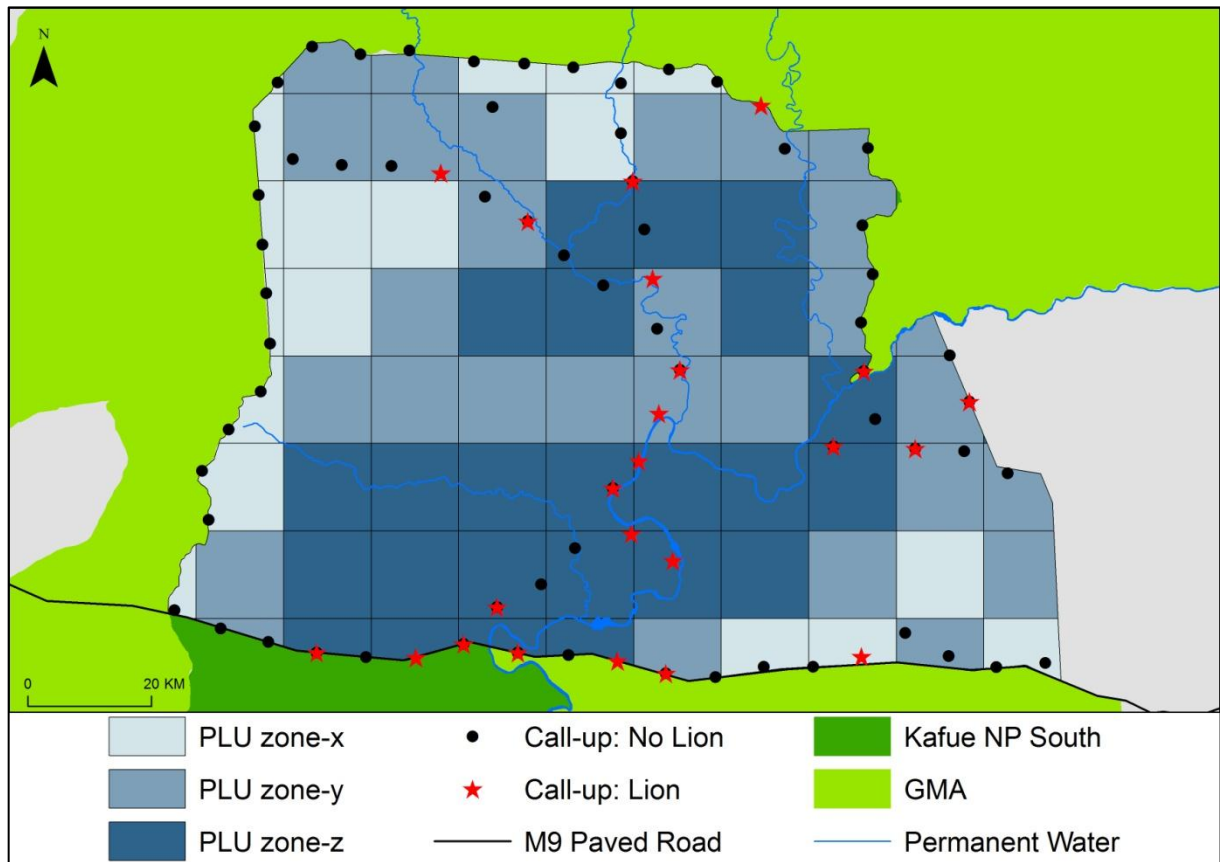


Figure 4.2. Call-up survey design in northern Kafue NP showing combined lion responses from 2010 and 2011 surveys. PLU: Probability of Lion Use from occupancy model (Chapter 3); NP: National Park; GMA: Game Management Area.

With the assistance of a ZAWA scout, I completed surveys at three to five points per night, when lions are most active (Schaller, 1972; Stander, 1992), beginning 45 minutes after sunset, and ending by 02h00. Limiting my surveys to winter nights eliminated potential effects of seasonal and diurnal changes in lion activity (Ferreira & Funston, 2010), and cold nights ensured maximum sound travel (Garstang *et al.*, 1995). I conducted playbacks from the roof of a vehicle, approximately 2.5m above ground level. At each survey point I recorded start time, end time, luminosity (on a scale of 1-3) and wind speed (on a scale of 0-3). I spent one hour at each point playing a looped 7.5-min distress call of a buffalo *Syncerus caffer* calf at maximum volume through two Foxpro Snow-Crow Pro SP-108SC horn speakers, using a Foxpro Snow-Crow Pro predator caller (Foxpro Inc., Lewistown, Pennsylvania). I used a playback schedule of 20 minutes on, 10 minutes off, 10 minutes on, 10 minutes off and 10 minutes on. I faced speakers 180° from each other and rotated them by 90° every 10 minutes. I continued the playback in the presence of responding animals in order to avoid bias against other responders that had not yet arrived. I made regular sweeps of the surrounding area using a Lightforce Lance 140mm Sporting Light (Lightforce Australia Pty. Ltd., Hindmarsh, Australia). Upon

sighting an animal, I applied a red filter to the light, and used 10 x 42 binoculars (Swarovski Optik, Absam, Austria) to determine the species, number of animals and age and sex class where possible, and recorded these data for all large carnivores. I also recorded survey days, observer hours and distance driven to complete the 2011 survey.

Spatial variation in species abundance can influence population estimates and appropriate stratification of the sampling area may be required (Stander, 1998; Stephens *et al.*, 2006). Accordingly, I divided my study site into three zones (Figures 4.2, 4.3) based on an occupancy analysis, which demonstrated that habitat type was the best predictor of Probability of Lion Use (PLU) in northern Kafue (Chapter 3). I designated these zone-x (PLU = 0.70-0.79), zone-y (0.80-0.89) and zone-z (0.90-1.00), assigned each call-up station to a zone, and calculated zone-specific lion density and abundance estimates for each survey. I summed these to obtain an abundance estimate for my entire study site and divided this by the total area of northern Kafue to estimate local lion density. I excluded lions <1 year old from all analyses due to the high mortality suffered by this age class (see Chapter 6).

To estimate lion abundance from my survey data, I selected the calibration performed by Ferreira and Funston (2010) in Kruger National Park, South Africa (Kruger). I selected this calibration due to i) the large sample size (170 lions in 37 groups), ii) the largely wooded vegetation of Kruger, which would likely share similar acoustic properties with the wooded vegetation of the majority of my study site, iii) the survey being done in winter, iv) the use of a buffalo calf distress call audio track and v) non-baited call-up stations.

I therefore calculated lion abundance (N_j) for each PLU zone j as

$$N_j = \frac{A_T \sum_{s=1} f_{nc,s}}{n\bar{A}P_{nc,p}P_{nc,i}(1-P_{nc,r})} + \frac{A_T \sum_{s=1} f_{c,s}}{n\bar{A}P_{c,p}P_{c,i}(1-P_{c,r})} \text{ (Ferreira \& Funston 2010),}$$

where A_T is the total area of the PLU zone, $\sum f_{nc,s}$ and $\sum f_{c,s}$ are the total responding adult and subadult lions without (nc) and with (c) cubs in the PLU zone respectively, n is the number of call-up stations in the PLU zone and \bar{A} is the effective area sampled by an individual call-up station (57.8 km² per the calibration of Ferreira & Funston 2010). $P_{nc,p}$ is the probability of a group with no cubs responding (0.734), $P_{nc,i}$ the probability of an individual within a group with no cubs responding (0.902) and $P_{nc,r}$ the probability of an individual in a group with no cubs responding more than once (0.0). Parameters $P_{c,p}$, $P_{c,i}$, and $P_{c,r}$ represent the same probabilities for groups with cubs (0.286, 0.957 and 0.0 respectively; see Ferreira & Funston (2010) for full derivation). I calculated 2010 and 2011 estimates independently as some lions were observed in both surveys.

Track count surveys

With the assistance of a ZAWA scout, I conducted track count surveys during the 2012 dry season. We were both experienced at detecting tracks from a moving vehicle. Transect start points were placed randomly on the unpaved road network (Figure 4.3), and each transect was repeated between two and seven times. We started all surveys within 30 minutes either side of sunrise when tracks are most visible (Liebenberg, 1990) and drove at a speed of approximately 10 km h⁻¹ to maximise the likelihood of track detection. We scanned the road for signs of lion, one person sitting on the front left corner of the vehicle and the other in the drivers seat (right hand side). When tracks were detected, we got out of the vehicle and used a ruler and track ID sheets to ensure correct species identification. We identified lion tracks based on their size and shape, and recorded the number of individuals, age and sex classes (where possible), substrate type, substrate quality, vehicle impact, latitude, longitude, distance from the start of the transect, and distance walked on the road (where possible) by the animal(s) for each set of tracks. If we were unable to identify the species with certainty, we ignored the track set. To prevent double counting, we only counted tracks adjudged to have been made in the last 24 hours, and avoided surveying the same transect on consecutive days. This is a distinction from the occupancy survey of Chapter 3, where all signs of lions were recorded regardless of the age thereof. We discounted multiple tracks of the same species located within 500m unless it was obvious they were not from the same individual. We recorded substrate quality (ease of detecting tracks; scale of 1-5) and vehicle impact on substrate (impact of other vehicles on likelihood of detecting tracks; scale of 0-2) for 1 km intervals. In addition, we recorded survey days, observer hours and distance driven to complete the survey.

Where transects covered multiple PLU zones, I split them into appropriate segments where they crossed zone-boundaries and used track count data to calculate track density (number of track sets detected 100 km⁻¹ driven) for each segment/transect (Stander, 1998; Balme *et al.*, 2009a; Funston *et al.*, 2010) and mean track densities (with 95% CIs) for all segments/transects in each PLU zone. Due to the nature of the substrate of Kafue's roads, I used Funston *et al.*'s (2010) regression for "all carnivores on sandy soil" ($t_i = 3.15 \chi_i + 0.40$; where t_i is track density and χ_i is lions 100 km⁻²) to convert track density to lion density.

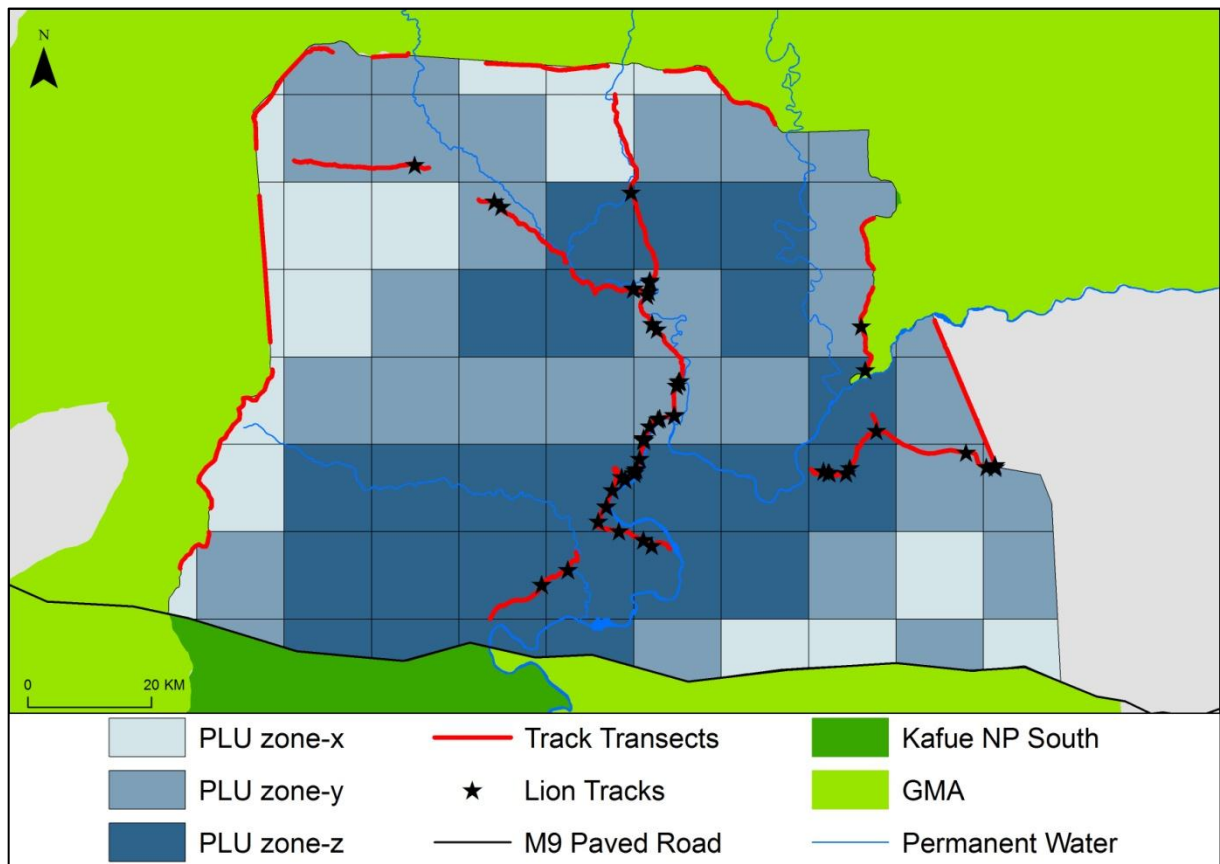


Figure 4.3. Track-count survey design in northern Kafue NP showing combined lion track detections from 2011 and 2012 surveys. PLU: Probability of Lion Use from occupancy model (Chapter 3); NP: National Park; GMA: Game Management Area.

Comparison of survey methods

I compared track counts with call-up surveys in terms of effectiveness (accuracy and precision) and efficiency (cost). To compare accuracy, I calculated the percentage by which the estimate from each survey differed from my reference density of known lions in the ISS. For precision, following Ferreira & Funston (2010), I calculated percentage confidence limits (PCLs) using the formula

$$PCL_j = \frac{UCL_j - \bar{x}_j}{\bar{x}_j}$$

(where UCL is the upper 95% confidence limit and \bar{x} is the mean for survey j) for the 2011 call-up and the 2012 track count surveys for the entire study area. To compare cost of the two methods, I used data from fieldwork logbooks and calculated total survey days, observer hours and kilometres driven to complete each survey. I also calculated the cost of any equipment that was not common to both surveys.

Results

Reference population

The ISS, derived by combining the home ranges of four female groups, was 1483 km² (Figure 4.1). It contained 27.9 known lions in 2011 (23 females and sub-adults; 4.9 “corrected” males) and 26.9 in 2012 (22 females and sub-adults; 4.9 “corrected” males), resulting in density estimates of 1.88 and 1.82 lions 100 km⁻² respectively.

Call-up surveys

I conducted 76 call-ups in 2010 and 73 in 2011, covering an estimated sample area of 4390 km² (40% coverage) and 4217 km² (38% coverage) respectively. Twenty nine per cent of call-ups were in zone x (18% of study area), 41% in zone y (43% of study area) and 30% in zone z (39% of study area). Sample effort was 6.9 stations 1000 km⁻² in 2010 and 6.7 stations 1000 km⁻² in 2011. I attracted 44 lions without cubs (15 groups) in 2010 and 31 (10 groups) in 2011, as well as four lions with one cub (one group) and 11 lions with seven cubs (three groups) in 2010 and 2011 respectively. Number of lion responses did not differ significantly with the time of night of the call-up ($\chi^2 = 2.77$, $p = 0.60$, $df = 4$), luminosity ($\chi^2 = 0.66$, $p = 0.72$, $df = 2$) or wind speed ($\chi^2 = 10.17$, $p = 0.17$, $df = 3$). Applying the calibration of Ferreira and Funston (2010) produced abundance estimates for northern Kafue of 228 lions (95% CI: 179-277) in 2010 and 264 (95% CI: 204-325) in 2011. Estimated population density was 2.08 lions 100 km⁻² in 2010 (95% CI: 1.63 – 2.53) and 2.41 100 km⁻² (95% CI: 1.86 – 2.96) in 2011 (Table 4.1).

Track counts

I completed 46 transects, covering a total of 967 km, of which 22% was in zone-x (18% of study area), 43% in zone-y (43% of study area) and 35% in zone-z (39% of study area). Mean transect length was 21.8 km, while mean segment length (i.e. transects split between PLU zones) was 11.2 km. Penetration index (Stander, 1998) was 11.3 km² per km driven. I located 64 sets of lion tracks, none of which were in zone-x, while zone-y and zone-z produced 31 and 33 sets respectively. Neither vehicle impact on substrate ($\chi^2 = 1.18$, $p = 0.55$, $df = 2$) nor substrate quality ($\chi^2 = 4.45$, $p = 0.35$, $df = 4$) had a significant effect on observed versus expected numbers of lion tracks detected. Lions walked an average of 0.98 km on the road ($n=61$), and in 8 instances crossed the road without walking along it. Using the Funston *et al.* (2010) regression, I estimated population density for 2012 at 2.21 lions 100 km⁻² (95% CI: 0.86

– 3.17), which translated into an abundance estimate for northern Kafue of 243 lions (95% CI: 37 – 448; Table 4.1).

Table 4.1. Summary of results of call-up and track count surveys for the overall study area.

	Call-ups		Track counts
	2010	2011	2012
Total transect distance (km)	-	-	967
Number of track sets	-	-	64
Number of call-up stations	76	73	-
Number of lion responses (>1 year old)	48	42	-
Study area stratified:			
Density (lions 100 km ⁻²)	2.08	2.41	2.21
Density 95% CI	1.63 – 2.53	1.86 – 2.96	0.34 – 4.09
Abundance (no. of lions)	228	264	243
Abundance 95% CI	179 – 277	204 – 325	37 – 448
Study area not stratified:			
Density (lions 100 km ⁻²)	1.85	2.06	1.83
Density 95% CI	1.63 – 2.07	1.80 – 2.33	0.86 – 2.80
Abundance (no. of lions)	202	226	200
Abundance 95% CI	178 – 227	197 – 256	94 – 307

Comparison of survey methods

I conducted 11 call-ups within the ISS in 2011 (7.4 stations 1000 km²), surveying an estimated 635 km² (43% of the ISS) and attracted nine lions without cubs in two groups. Applying the calibration of Ferreira and Funston (2010), I estimated abundance for the ISS of 31.7 lions (95% CI: 20.5 – 42.9) and density as 2.14 lions 100 km⁻² (95% CI: 1.38 – 2.89), 13.6% greater than the reference lion density.

In 2012, I completed 20 track counts in the ISS, surveying a total of 319 km, a penetration index (Stander, 1998) of 4.6 km² per km driven. I located 28 sets of lion tracks and mean track density was 6.76 tracks 100 km⁻¹ (95% CI: 1.97 – 11.16). Using the Funston *et al.* (2010) regression, I estimated lion density in the ISS as 1.74 lions 100 km⁻² (95% CI: 0.23 – 3.14) and abundance as 25.9 lions (95% CI: 3.3 – 46.6), underestimating the reference density estimate by 3.9%.

The 2011 call-up survey of the entire study area produced a percentage confidence limit (PCL) of 22.8%, compared to 84.5% for the 2012 track count survey. Time constraints led to me stratifying the study site after I had conducted my track count survey, which necessitated the splitting of track transects into segments where they straddled multiple PLU zones. The coefficient of variation (CV) for segment length was 54.6% compared to 13.3% for transect length and hence splitting track transects negatively influenced the PCL for track counts. Recalculating this metric using complete transects produced a PCL of 42.5% for the same period.

The cost of equipment required for the call-up survey that was not required for the track count was USD1145, while the track count survey had no special equipment requirements. The 2011 call-up survey was completed in less time and with lower distance driven than the 2012 track-count survey (Table 4.2).

Table 4.2. Comparison of accuracy, precision and efficiency of 2011 call-up survey and 2012 track count survey. # PCL: Percentage Confidence Limits. * PCL calculated under the assumption that transects were not split into segments to accommodate post hoc study site stratification.

	2011 Call-up survey	2012 Track count survey
Intensive Study Site (ISS)		
Reference population estimate (lions 100km ⁻²)	1.88	1.82
Survey density estimate (lions 100km ⁻²)	2.14	1.74
Overestimate	13.6%	-
Underestimate	-	-3.9%
Entire Study Area		
PCL [#]	22.8%	84.5%
Unstratified PCL [*]	-	42.5%
Survey days	19	46
Survey hours	133	173
Km driven	1724	2802

Discussion

In my ISS, track counts produced a more accurate result than call-ups, but the call-up estimate was more precise. Across the entire study area, the call-up percentage confidence limit was 3.7

times more precise than the track count. A survey designed after stratification of the study site (to eliminate segmentation of transects) would have reduced this value to 1.9, but the call-up result is still more precise, despite this method requiring less than half the number of survey days, 23% fewer survey hours and 38% less kilometres driven. Although additional equipment was required for the call-up survey, such equipment can be used for multiple spatial and temporal replicates. The per-survey cost of this equipment thus decreases with each additional replicate, and over time will more than offset the additional fuel and maintenance costs of the track count survey.

My call-up survey effort was approximately double the 20% minimum area coverage recommended by Ogutu and Dublin (1998), but below Ferreira and Funston's (2010) recommendation of >8 stations 1000 km². The risk of double-counting precluded the inclusion of more stations in my study site, but the accuracy of the result in the ISS suggests that my sampling effort was sufficient.

For track counts, Funston *et al.*, (2010) suggest that 30 track incidences will usually ensure a CV for track frequency of <20%. However, my CV after 64 incidences (assuming an unstratified study area for comparability) was 220%. According to Zar (1999), CV is the standard deviation (*s*) divided by the mean, but (Stander, 1998) defines CV as the Standard Error (SE) divided by the mean, a definition for which I found no reference in the statistical literature. In this case, as $SE = s/\sqrt{n}$, its use as the numerator in Stander's (1998) equation means that even with constant precision, CV will, by definition, decrease as *n* increases. This equation was used to calculate CV by Funston *et al.* (2001), Balme *et al.* (2009a) and Kent and Hill (2013), and, though not explicitly defined, the similarity of the graphical representation of CV decreasing with increasing sample size in Funston *et al.*, (2010: p61) suggests that Stander's (1998) definition was applied here too. Using my data, the Stander (1998) CV follows a similar trend to these papers, as well as to $1/\sqrt{n}$, while the Zar (1999) CV does not necessarily decrease with increasing *n*, but does tend to stabilise (Figure 4.4; K. Mauff, pers.comm.). This suggests that although track count surveys produce accurate results, there is more variability in the data than previously thought.

In addition to efficiency and effectiveness, both survey methods tested have practical limitations that require consideration. Stander (1998) suggests that highly skilled trackers are required for track counts, but Funston *et al.* (2001) argue that moderate skills are sufficient to identify species. Suitable substrate for track detection is a further requirement of the method (Stander, 1998). Balme *et al.* (2009a) found that variable substrate and higher carnivore densities reduced accuracy of density estimates, but Funston *et al.* (2010) demonstrate a consistent relationship between track density and carnivore density across geographically dispersed sites

with varying quality of substrate. Substrate quality did not affect the likelihood of detecting lion tracks in my study site, possibly due to my slow driving speed (10 km h⁻¹ cf. 20 km h⁻¹ of Stander (1998)) and the fact that, on average, lions walked on the road for almost one kilometer, providing reasonable opportunity to detect tracks. However, track counts may be less useful in areas where carnivores are heavily persecuted by humans, as these animals are less likely to travel on roads (Linkie *et al.*, 2006; Ngoprasert *et al.*, 2007).

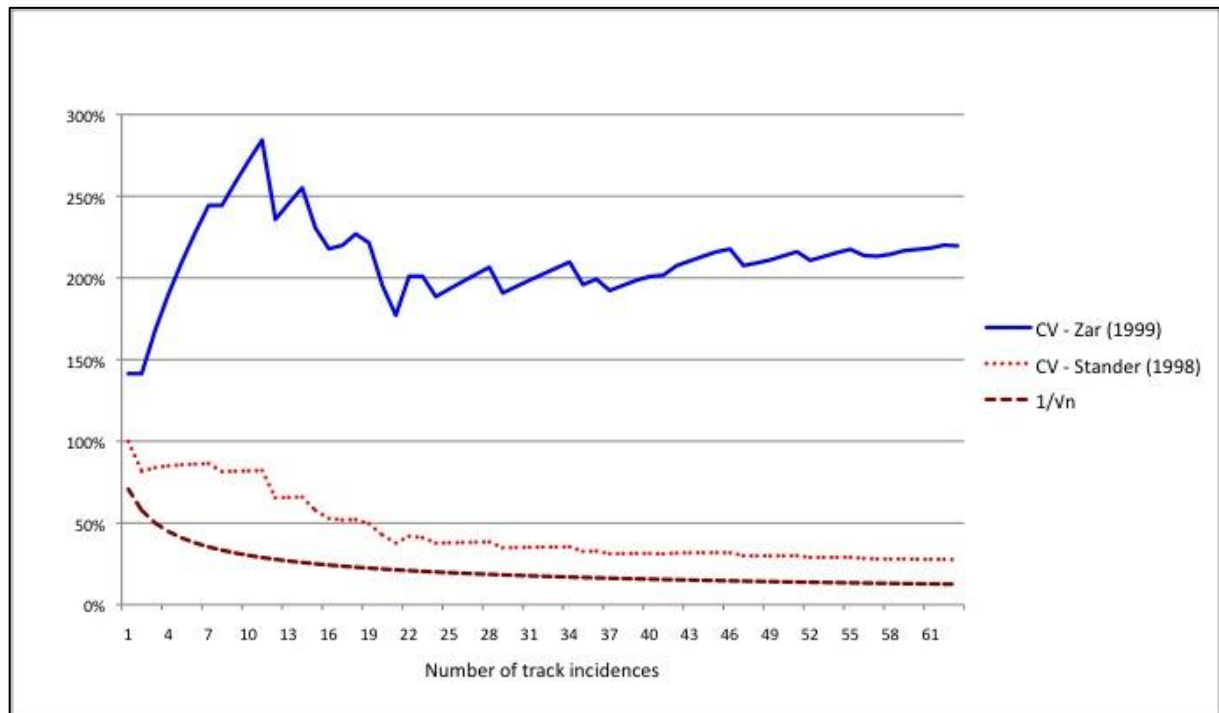


Figure 4.4. Comparison of change in coefficient of variation (CV) for track frequency of my 2012 survey data, calculated per Zar (1999) and Stander (1998), with increasing sample size. Inclusion of $1/\sqrt{n}$ as an indicator of the effect of the standard error (SE) on the CV as used by Stander (1998).

Call-up surveys rely on the assumptions that all responders are detected and no animals are double-counted (Mills *et al.*, 2001). Kiffner *et al.* (2007) recorded 15 of 17 lion groups approaching within 40m of the survey vehicle, while 10 of 13 groups in my 2011 survey behaved similarly. This proximity, and general boldness of approach, suggest that non-detection of responding lions was unlikely (Kiffner *et al.*, 2007). Double-counting can be avoided by sufficient spatial separation of call-up stations, and I had no lions respond at more than one station in a survey. However, at least two groups did respond in both years, suggesting that my surveys were sufficiently temporally separated to avoid non-response associated with habituation (Ogutu & Dublin, 1998; Ferreira & Funston, 2010).

A major limitation of call-up surveys involves calculating the distance at which lions respond from the calling station, and the proportion that respond, in order to convert responses to lion density. Various studies have shown likelihood of response to be affected by i) location of the

call-up within the lion home range, ii) age and sex of lions, iii) presence or absence of cubs, iv) season, v) duration of calling and vi) whether lions are feeding or not (Ogutu & Dublin, 1998; Whitman, 2006; Kiffner *et al.*, 2007). Maximum response distance also varies from 1.5 km (Maddox, 2003) to 6.1 km (Ferreira & Funston, 2010), though the call-ups in the former were only conducted during the day when lions are less active (Schaller, 1972). Conversely, response rates were not affected by time of night or moon phase in Katavi NP (Kiffner *et al.*, 2007), and these factors were not significant in my study either.

Further complication arises from the variety of audio tracks used as lures in different studies, including spotted hyaenas on a kill (Whitman, 2006), spotted hyaenas mobbing lions (Ogutu & Dublin, 1998) combinations of carnivores feeding and ungulate distress calls (Ogutu & Dublin, 1998; Burton *et al.*, 2011), and buffalo calf distress calls (Kiffner *et al.*, 2007; Ferreira & Funston, 2010; Brink *et al.*, 2012). Both male and female lions exhibit varying responses to the calls of conspecifics depending on the threat level posed by group size, presence/absence of cubs and location within a home range (McComb *et al.*, 1993; Grinnell & McComb, 2001), and I postulate that similar cost-benefit considerations are likely to affect probability of lion response to different audio playbacks.

These multiple sources of variation in response to audio lures underlie recommendations to calibrate call-up surveys in each new site (Eberhardt & Simmons, 1987; Ogutu & Dublin, 1998; Mills *et al.*, 2001). However, in PAs such as Kafue, low lion density and limited access mean that attempts at calibration would be costly and time-consuming, produce small sample sizes and risk negative habituation of lions. This led me to select the calibration of Ferreira & Funston (2010), which produced reasonably accurate results in the ISS for 2011. I note, however, sensitivity to variation in the estimated distance, as well as probability, of lion responses (Table 4.3). The proportion of lion groups with cubs in a population also affects the result, as the probability of a group without cubs responding is 2.4 times higher than for a group with cubs (Ferreira & Funston, 2010). In my study, the greater number of lions with cubs responding in 2011 resulted in a higher abundance estimate than in 2010, despite lower total lion responses (0.58 lions per station in 2011 cf. 0.63 in 2010).

From a management perspective, track counts are advantageous as they can produce density estimates for other carnivore species, including spotted hyaena, and possibly leopard and cheetah (Funston *et al.* 2010, but see Balme *et al.* 2009a). For these uniquely identifiable species, density estimates can be calibrated with camera traps if required (Balme *et al.*, 2009a). Although call-ups have also been used to estimate spotted hyaena densities (Mills *et al.*, 2001), Kiffner *et al.* (2007) found a decrease in spotted hyaena responses (albeit non-significant) when lion responses were high, and, although leopards did respond during my survey (2010: n = 11;

2011: n=8), I postulate that the presence of the two larger competitors may affect the likelihood of such responses. In addition, the wary nature of leopards increases the risk of non-detection, and call-ups are therefore likely of little use for this species.

Table 4.3. Sensitivity of stratified 2011 Kafue lion population estimates to adjustments of parameters in call-up calibration formula of Ferreira and Funston (2010).

Increase in 2011 population estimate	
Decrease in response distance	
10% (430m)	23.6%
20% (860m)	56.4%
50% (2150m)	300.4 %
Decrease in response probability	
10%	11.4%
20%	25.0%
50%	100.4%

My density estimates for the stratified study area over three years (2010 – 2012) ranged from 2.08 to 2.41 lions 100 km⁻² (Table 4.1), >10% higher than the ISS densities of 1.82 – 1.88 (Table 4.2), despite the fact that the ISS only comprised areas of PLU-y and PLU-z, where I expected higher densities. Reanalysing my data without stratifying the study area, estimates decreased to 1.83 to 2.06 lions 100 km⁻² (Table 4.1), which more closely approximate the ISS figures, suggesting that stratification in this case may have led to overestimating density.

My overall estimate exceeded that of Becker *et al.* (2012), who used 107 known lions from 2003 to 2005 to estimate density of 1.8 lions 100 km⁻² for a 4,720 km² (arbitrarily defined) section of northern Kafue, but my ISS estimate was similar. However, Becker *et al.* (2012) excluded lions <2 years old (21% of their known population, whereas I included all lions >1 year old. Kafue’s lion population is thus at the lower end of density ranges for southern and east African PAs (Bauer & Van Der Merwe, 2004), falling between the arid Kgalagadi Transfrontier Park (0.77 – 1.63; Funston 2011) and Hwange NP (2.7 lions 100 km⁻²; Loveridge *et al.* 2007).

Regardless of the metrics applied, selecting the best survey method inevitably includes an element of subjectivity due to the “virtually infinite number of ways of defining estimator performance” (Walther *et al.* 2005: p 820). Nonetheless, based on the findings in this chapter, I recommend track counts over call-up surveys for surveying lions in Kafue and similar PAs due to the more accurate result, utility for multiple species and the uncertainties underlying call-up responses and calibration. My results suggest that stratification does not necessarily improve the output, and I thus do not recommend this additional step for future surveys in Kafue. I

caution, however, that the large CI of my results (95% CI: 0.86 – 2.80 lions 100km²) is cause for concern as it suggests some limitation in the utility of the result as a tool to assist managers detect changes in lion density that may require management intervention.

As with previous studies (Stander, 1998; Balme *et al.*, 2009a; Funston *et al.*, 2010), my surveys confirmed a positive linear relationship between track density and lion density. From a management perspective, I thus recommend monitoring track density (rather than lion density) over time as a proxy for population trend, thus eliminating the complications of stratification and conversion. For this purpose, I recommend standardising survey effort and transect lengths, repeating standardised surveys on the same transects on a regular basis (as defined by management objectives) and assessing and improving tracking skills to allow comparisons between areas and over time. I also recommend periodic double-sampling (Eberhardt & Simmons, 1987) to corroborate track count indices. However, where substrate quality is poor or tracking skills inadequate (Stander, 1998), I recommend call-ups instead, and similarly suggest that the longitudinal trend in lion response rates is a more valuable measure than estimates of lion density. To ensure comparability and reduce behavioural variation in call-up surveys I recommend the use of the buffalo calf distress call and standardised equipment, survey design and calling protocol. Judicious application of these survey methods will provide managers with sufficient data to establish baseline population indices, monitor population trends, identify areas of concern, implement interventions where necessary and, finally, assess the results of those interventions over time.

CHAPTER 5

Spatial ecology of lions in the seasonally inundated landscape of Kafue National Park

Summary

Understanding the ranging behaviour and habitat selection of wild fauna provides information on what resources they require for their survival, thus enabling managers to identify threats to these resources and design interventions for the mitigation thereof. In this chapter, I use location data from 15 radio-collared lions to investigate their spatial ecology in northern Kafue, an area characterised by significant seasonal rainfall and associated flooding. Females used smaller home ranges and travelled shorter daily distances than males. Female dry season home range size was correlated positively with distance to park boundary and pride size, and negatively with mean prey biomass, but these relationships were non-significant when controlled for the remaining variables. Male dry season home ranges showed no correlation with any of these variables. Females used larger home ranges and covered greater distances in the wet season than in the dry, but no inter-seasonal variation was evident for males. Dry and wet season home ranges of all lions were significantly more inundated in the wet season than the dry season, but there was no correlation between proportion inundated and increase in home range for the wet season. Both males and females exhibited intra-sex spatial overlap, but I found evidence of temporal overlap for males only. Site fidelity from one dry or wet season to the next ranged from 74 to 90%, and did not differ between sexes. Both sexes changed their habitat preference between seasons. Patches favourable to lions in the dry season are flooded in the wet, which may limit reproductive success, exacerbate the effects of anthropogenic mortalities and affect the rate at which Kafue's lion population is able to recover from external perturbation.

Introduction

The persistence of wild populations of fauna is dependent upon access to natural habitat that yields sufficient quantity and quality of essential resources (Cumming, 2004). Understanding how animals select and use home ranges (*sensu* Burt, 1943) can thus be used to identify critical resource requirements (McLoughlin *et al.*, 2010), and ultimately minimum viable areas to support wild populations facing pressure from the rapidly increasing human population (Woodroffe, 2000). However, significant intraspecific differences in home range selection and size precludes species-specific generalisations (e.g. Hoffman & O’Riain, 2012), and in some species these differences are largely driven by variation between individual animals or habitat types (Börger *et al.*, 2006). Understanding the spatial ecology of a species at the local scale is thus necessary to guide allocation of scarce conservation resources within geographically distinct locations.

Spatial ecology of the African lion has been widely documented (eg. Davidson *et al.*, 2012; Hopcraft *et al.*, 2005; Loveridge *et al.*, 2009; Schaller, 1972; Spong, 2002), but few data exist for lions living in areas where widespread seasonal inundation occurs (but see Tumenta *et al.*, In press). In this chapter I investigate the spatial ecology of lions in Kafue, a PA strongly influenced by seasonal flooding.

Lions are social carnivores with, typically, 2-18 closely related adult females and their dependent offspring comprising a pride, which is a fission-fusion social unit often accompanied by 1-9 unrelated adult males (Schaller, 1972). The establishment and defence of territories and protection of offspring against unrelated females and infanticidal males are considered the major drivers of sociality in lions (Packer *et al.*, 1990, 2005a), and larger prides are more likely to hold, maintain and expand the best territories through their ability to dominate disputes with neighbours (Mosser & Packer, 2009). Female home ranges are thus primarily configured around resources such as food and denning sites, while males establish ranges based on the need to access and defend female prides (Schaller, 1972). Intra-population variation in home range size has been linked to lean season prey biomass (Van Orsdol *et al.*, 1985), pride size (Loveridge *et al.*, 2009) and lion density (Davidson *et al.*, 2011).

In many systems, however, availability of resources such as food or water varies spatially on a seasonal basis (Boyce & McDonald, 1999), and animal ranging behaviour may shift accordingly. For example, Thomson’s gazelles *Gazella thomsonii* and wildebeest *Connochaetes taurinus* migrate to different regions of the Serengeti-Mara system based on rainfall patterns and resultant availability of grazing (Durant *et al.*, 1988; Holdo *et al.*, 2009) while flooding in the Amazon drives range shifts for an assemblage of ungulates (Bodmer, 1990). This movement of

ungulate species can in turn influence seasonal carnivore home ranges; for example, Durant *et al.* (1988) found that female and non-resident male cheetahs followed the movements of migratory Thomson's gazelles in the Serengeti. Similar inter-seasonal shifts have been observed in pumas (Dickson & Beier, 2002) and grey wolves (Nelson *et al.*, 2012), while seasonal flooding in the Brazilian Pantanal caused jaguars to shrink their home ranges for foraging and, possibly, for reproductive purposes (Cavalcanti & Gese, 2009).

Despite their inherent territoriality (Schaller, 1972), lions may also display seasonal home range shifts in accordance with prey distribution and movement patterns. Thus some lions in the Makgadikgadi Pans and Serengeti follow migratory prey species (Valeix *et al.*, 2012; Hopcraft *et al.*, 2005), while those in the Kalahari increased their home ranges in the dry season due to the wider distribution of their prey (Owens & Owens, 1985). Seasonal flooding may also influence home range shifts in lions. They may travel further to forage for more widely dispersed prey (*sensu* Davidson *et al.*, 2013) and may also move or extend their home ranges to higher ground to limit the energy costs incurred by walking through water (*sensu* Hall *et al.*, 1998).

In this chapter, I used GPS collars to monitor the daily movements of a sample of lions in northern Kafue, all of which had a permanent river as a key feature of their dry season home ranges. I first calculated home range sizes for all collared lions for each season. Thereafter I investigated potential drivers of dry season lion home range size, such as prey biomass, pride size and distance to park boundary to determine if these were similar to other populations. Finally, I considered the effects of Kafue's seasonal flooding, and predicted that i) lion home range size will increase in the wet season due to a more widely distributed prey base (*sensu* Davidson *et al.*, 2013) and swollen rivers flooding dry season home ranges; ii) larger home ranges in the wet season will result in greater spatial and temporal overlap between neighbouring prides; iii) annual shifts in home ranges between wet and dry seasons will reduce fidelity from one year to the next as lions are forced to constantly re-establish their home ranges; and iv) habitat utilisation within home ranges will vary between seasons as prey shifts and some habitats become less accessible.

Methods

Study site

In this chapter, my study area is a 4395 km² section of northern Kafue, defined by the combined home ranges of 15 collared lions (13 groups) sampled over a combined 31-month period. In the north-west of this area is a region called the Busanga Plains (Busanga), a floodplain that experiences more dramatic seasonal fluctuations in water levels than elsewhere in the park. I

defined the Busanga as that part of the study area north of the confluence of the Lufupa River and Ntemwa Stream that had an elevation of less than 1100m above sea level. I selected this elevation as the resultant polygon best represented wet season flood levels around a large well-known island in the area. The resulting extent of the Busanga was 589.6 km² (13.4% of study area).

Use of satellite imagery and the Normalised Difference Water Index (NDWI; McFeeters, 1996), generated a map showing approximately 7.25 km² (0.2%) of the study area was under water in the 2012 dry season, compared with 503.14 km² (11.5%) in the 2012-2013 wet season, the two seasons for which I had the most collared lions (Figure 5.1; Refer Annexure B for methods used to derive these layers in software ARCGIS v10.1). In the Busanga, 5.8 km² (1.0%) was covered by water in the dry season, which increased to 439.8 km² (74.6%) in the wet season. In the rest of the study area 1.5 km² (0.04%) and 63.3 km² (1.7%) were under water in the dry and wet seasons respectively.

The underlying map for the Land Cover Classification System used to classify vegetation in Chapter 3 is a raster layer, and vegetation types are thus classified in a grid structure. At the scale of my occupancy analysis this was acceptable, but for fine-scale habitat selection the results would be misleading. Using the same classifications as in Chapter 3, I therefore used software GOOGLE EARTH to adjust the layer and manually create polygons representing each vegetation type within the study area. I divided it into four habitat classes, i) miombo and Kalahari woodland (MIO, 40%) dominated by *Brachystegia spp.* and *Julbernardia spp.*, ii) munga and termitaria woodland (MUN, 29%) dominated by *Acacia spp.*, *Combretum spp.* and *Terminalia spp.*, iii) munga scrub and grassland (SAG, 30%) comprising open scrubland up to 3m high and dambo, floodplain and riverine grasslands and iv), wetland (WET, 1%) comprising a mosaic of *Cyperus papyrus*, marshes and tree islands (Figure 5.1). The latter did not feature at the scale of the occupancy analysis, but formed a significant portion of the dry season home range of certain lion groups and is found only in the Busanga region of the study area. I used ARCGIS v10.1 to convert the resulting polygons into shapefiles for analysis.

Data on lion prey density, obtained from an aerial survey carried out in the dry season of 2011 (Frederick, 2011), included ungulate species in the weight range from bushbuck to buffalo, and I calculated prey biomass per the method described in Chapter 2. I used the ZONAL STATISTICS tool in ARGIS v10.0 to spatially allocate prey biomass estimates to individual lion home ranges. I present normally distributed data as means \pm standard errors (SE), and other data as medians with quartile range (QR).

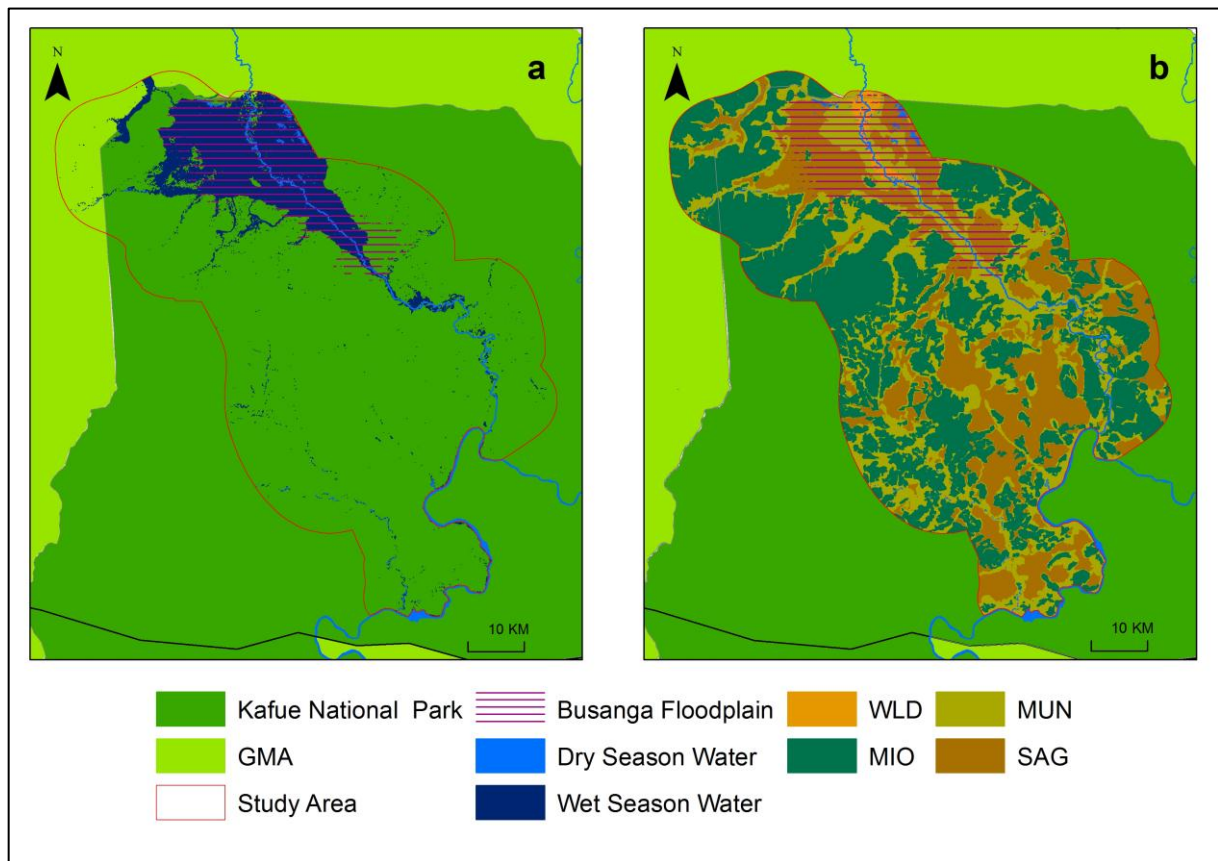


Figure 5.1. Seasonal flooding extent (a) and habitat types (b) within the study area in northern Kafue National Park. GMA: Game Management Area; WLD: Wetland; MIO: miombo and Kalahari woodland; MUN: munga and termitaria woodland; SAG: munga scrub and grassland.

Lion spatial and demographic data

I deployed 20 GPS collars on 15 lions (seven adult females from six prides; eight adult males from seven coalitions) between September 2010 and October 2012 (see Chapter 2). Collars were programmed to record GPS fixes at 00h00, 06h00 and 18h00 each day. I retrieved these data via handheld UHF receiver or the Iridium satellite network, from date of deployment to 31 May 2013 (Table 2.2). I collected lion demographic data through regular observation of groups in which collared lions resided during this period.

Home range size

I calculated home range (HR; 90% isopleth) and core area (CA; 50% isopleth) for each lion group (Spong, 2002) per the methods described in Chapter 2. I used Mann-Whitney U-tests (MWU) to compare male and female ranges, and Wilcoxon Matched-Pairs (WMP) tests to investigate inter-seasonal variation in range size.

I considered i) group size (number of lions >1yr old), ii) distance to park boundary (from centroid of dry season home range) and iii) mean dry season prey biomass (mean kg km⁻² of aerial survey subunits) within the HR as potential drivers of dry season HR size (Table 5.1). I did not analyse effects of proximity to water as all collared lion groups had permanent river access within their HRs, nor did I consider the effect of number of female prides on male HR size (Loveridge *et al.*, 2009) as I could not establish how many unknown prides occupied the remote, inaccessible areas of some male HRs. I did not conduct wet season analysis as I had no data on wet season prey distribution. My small sample size in relation to number of covariates precluded me from using mixed linear models to analyse the effects of these covariates on HR size. I therefore performed univariate Spearman's correlation tests to assess the correlation between HR size and each potential driver thereof. I also ran partial Spearman's correlations using the package *ppcor* (Seongho, 2012) in software *R* (R Core Team, 2013), to test for a correlation between home range size and a given covariate, while controlling for the other two.

Table 5.1. Data used to evaluate potential drivers of dry season home range size of lion groups in Kafue National Park, Zambia.

Lion	Year	Home range size (km ²)	Distance to boundary (km)	Mean prey biomass (kg km ⁻²)	Group size
F18	2012	65.0	14.7	1250	3
F21	2012	80.9	6.8	1427	4
F28	2012	340.0	24.7	409	5
F53	2012	665.8	32.2	164	7
F72	2012	304.6	18.1	362	4
F77	2012	274.4	30.5	253	7
M06	2012	1530.0	28.0	443	2
M16	2012	240.7	12.8	1299	2
M37	2012	826.7	32.4	258	3
M43	2012	379.5	31.9	223	3
M48	2012	1283.9	9.8	538	2
M73	2012	250.1	9.1	343	1
F18	2011	63.1	14.4	1496	4
F21	2011	130.4	7.5	1323	4
F28	2011	293.7	25.8	345	5
M16	2011	460.8	15.0	963	2

I used Student's *t*-test to compare inter-seasonal (dry season 2012 with wet season 2012-2013 as this was my largest sample) Mean Minimum Daily Distance Moved (MMDDM; linear distance

between 00h00 GPS positions on consecutive days) for each sex, and, within seasons, for males versus females.

The greater fluctuation in seasonal inundation of the Busanga (1.0% dry season to 74.6% wet season) compared with the rest of the study area (0.04% dry season to 1.7% wet season), suggested that its effects on ranging behaviour of lions in the two areas may differ. I thus split collared individuals into two groups, namely “plains” lions (2012 dry season HR overlapped with WET habitat, found only in Busanga) and “woodland” lions (no such overlap). I compared the proportion of dry season home range inundated in the dry season versus the proportion of dry season home range inundated in the wet season (i.e. if the lion had not shifted its range in the wet season) using a WMP-test for all lions and for both groups (plains versus woodlands). I used the same test to compare extent of standing water in dry season home range with that in wet season home range. I also compared inundation levels between plains lions and woodland lions using a MWU-test. For all lions, plains lions and woodland lions, I used a Spearman’s Rank Order Correlation test to determine whether proportional increase in HR size from the dry season (2012) to the wet season (2012-2013) was correlated with the proportion of dry season HR flooded in the wet season.

Site exclusivity and fidelity

To measure overlap between neighbouring male-male and female-female groups, I calculated intra-season two-dimensional (2D) overlap indices (Kernohan *et al.*, 2001) for both wet and dry seasons. I calculated the proportion of a group’s HR covered by the HR of a neighbouring group using the formula

$$HR_{i,j} = \frac{A_{i,j}}{A_i}$$

where $HR_{i,j}$ is the proportion of animal i ’s HR that is overlapped by animal j ’s HR, A_i is the area of animal i ’s HR and $A_{i,j}$ is the overlap area between the two HRs (Kernohan *et al.*, 2001). I used MWU-tests to compare male-male with female-female, and wet with dry season overlaps. Simultaneous locations of neighbouring lions from my collar data allowed more direct analysis of temporal overlap than alternatives such as the Utilisation Distribution Overlap Index (Fieberg & Kochanny, 2005). For those groups with spatial overlap, I therefore compared distances between collared individuals for all simultaneous (<5 min apart) GPS locations to determine whether spatial overlap implied temporal overlap. I assumed a proximity of <200m constituted an interaction between individuals (*sensu* Cavalcanti & Gese, 2009). I further used simultaneous locations to determine whether neighbouring lions of the same sex showed patterns of temporal avoidance: if the mean distance between actual simultaneous locations

was significantly greater (Student's *t*-test) than between randomly paired locations, I concluded that the two individuals were actively avoiding each other.

To analyse inter-annual site fidelity of individual lions from one dry season to the next, and one wet season to the next, I adapted the formula of Kernohan *et al.* (2001) to calculate site fidelity as

$$SFB_{t,t-1} = \frac{B_{t,t-1}}{B_{t-1}}$$

where $SFB_{t,t-1}$ is the proportion of the home range of animal B in year t that overlaps its home range in year $t-1$, $B_{t,t-1}$ is the area of overlap between the home range of animal B in years t and $t-1$ and B_{t-1} is the area of animal B's home range in year $t-1$. Finally, I measured the distance between the centroid of each lion's HR in year t and year $t-1$, and compared the variation between sexes and seasons. I further measured the distance between HR centroids of each lion to determine whether regions of higher activity shifted from one year to the next.

Habitat utilisation

Following Revilla *et al.* (2000), I evaluated third order habitat selection (Johnson, 1980) using Jacobs' selection index (Jacobs, 1974):

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

where r is the proportion of daily GPS locations for an individual lion in a given habitat class and p is the proportional availability of that habitat class in the lion's HR (calculated for the duration of collaring for each lion). Values for D range from -1 (strong avoidance) to $+1$ (strong preference). I analysed selection of plains and woodland lions by sex and season to determine whether these factors affected preferential selection and/or avoidance of habitat classes.

To measure the effects of permanent rivers on lion dispersion, I created a set of random locations (n = matched to actual number of locations) within each lion's 2012 dry season HR, and measured the distance to the nearest river. I used Student's *t*-test to compare these distances with those between actual locations and nearest river to determine whether lions were located closer to permanent water than expected in a random dispersion. Finally, I used Student's *t*-test to compare distance to nearest river in the 2012 dry season with the 2012-2013 wet season distances to the same dry season river courses for each lion to determine whether there was any seasonal shift in dispersion.

Results

Home range size

Median female HRs (MWU $Z = -2.46$, $p = 0.01$) and CAs (MWU $Z = -2.01$, $p = 0.04$) were significantly smaller, and mean female MMDDM ($t = -16.53$, $d.f. = 2914$, $p < 0.01$) was significantly less, across both seasons than those of males.

I found significant positive correlations between female HR size and distance to the park boundary ($r = 0.76$, $p < 0.05$) and number of lions ($r = 0.72$, $p < 0.05$), and a significant negative correlation with mean prey biomass ($r = -0.77$, $p < 0.05$). The positive correlation between HR size and distance to boundary persisted, though it was not significant, when controlling for prey biomass ($r = 0.42$, $p = 0.42$), number of lions ($r = 0.45$, $p = 0.39$) or both these factors ($r = 0.29$, $p = 0.67$). Similarly, a non-significant positive correlation was found between HR size and number of lions, controlling for prey biomass ($r = 0.33$, $p = 0.55$), but not when controlling for distance to boundary ($r = 0.08$, $p = 0.88$) or both these factors ($r = 0.07$, $p = 0.92$). HR size showed a non-significant negative correlation with prey biomass when controlling for number of lions ($r = -0.36$, $p = 0.51$), but no correlation when controlling for distance to boundary ($r = 0.06$, $p = 0.91$) or both these factors ($r = 0.04$, $p = 0.95$). Finally, female pride size was positively correlated with distance to boundary when controlling for HR size and prey biomass, though this relationship was also non-significant ($r = 0.61$, $p = 0.28$). Male HR size was not significantly correlated with any of the factors investigated.

Median HRs (WMP $Z = 2.39$, $p = 0.02$, $n = 17$) and CAs (WMP $Z = 2.01$, $p = 0.04$, $n = 17$) for combined sexes were significantly larger in the wet season than the dry season. Female HR was significantly larger in the wet season (WMP $Z = 2.40$, $p = 0.02$, $n = 10$) while the difference in inter-seasonal female CA was not significant (WMP $Z = 1.68$, $p = 0.09$, $n = 10$). I found no evidence of significant inter-seasonal size differences between male HRs (WMP $Z = 1.35$, $p = 0.18$, $n = 7$) or CAs (WMP $Z = 1.18$, $p = 0.24$, $n = 7$). MMDDM of female lions was significantly greater in the wet season ($t = -3.73$, $d.f. = 1456$, $p < 0.01$), but there was no significant inter-seasonal difference for males ($t = 0.75$, $d.f. = 1456$, $p = 0.45$; Table 5.2). Locations of all lions ($n=12$) were significantly ($p < 0.01$) closer to rivers in the 2012 dry season than expected in a random dispersion, while locations of 83.3% ($n = 12$) of lions were significantly further from dry season rivers in the wet season than in the dry season (Annexure A Table A2).

Dry season HRs of all lions (WMP $Z = 3.18$, $p < 0.01$, $n = 13$), plains lions (WMP $Z = 2.20$, $p = 0.03$, $n = 6$) and woodland lions (WMP $Z = 2.37$, $p = 0.02$, $n = 7$) were significantly more

inundated in the wet season than in the dry season (i.e. if lions had not shifted their ranges for the wet season). Wet season HRs were significantly more inundated in the wet season than dry season HRs in the dry season for all lions (WMP $Z = 3.06$, $p < 0.01$, $n = 13$), plains lions (WMP $Z = 2.20$, $p = 0.03$, $n = 6$) and woodland lions (WMP $Z = 2.20$, $p = 0.03$, $n = 7$). I found no significant differences between flooded proportions of dry season HRs compared to wet season HRs using wet season inundation levels for any groups. Plains lions' HRs were significantly more inundated in the wet season than woodland lions (MWU $Z = 2.93$, $p < 0.01$), while there was no significant difference in the dry season (MWU $Z = 0.21$, $p = 0.83$). I found no significant correlation between proportional increase in HR size in the wet season and proportion of dry season HR flooded for all lions ($r = 0.24$, $p > 0.05$), plains lions ($r = 0.03$, $p > 0.05$) or woodland lions ($r = 0.14$, $p > 0.05$; Table 5.3).

Table 5.2. Descriptive statistics detailing ranging behaviour of lions in Kafue National Park, Zambia. M: Male; F: Female; HR: Home Range (90% isopleth); CA: Core Area (50% isopleth); LQ: Lower Quartile; UQ: Upper Quartile; CI: Confidence Interval. HR and CA data of individual lions are presented in Annexure A Table A1).

Sex	Season	Measure	n	Median (km ²)	LQ - UQ (km ²)	Mean (km)	95% CI (km)
M&F	Both	HR	34	309.2	150.4 – 618.6	-	-
F	Both	HR	20	275.0	126.6 – 332.4	-	-
M	Both	HR	14	575.0	250.1 – 826.7	-	-
M&F	Both	CA	34	67.1	30.9 – 133.5	-	-
F	Both	CA	20	43.6	25.2 – 107.0	-	-
M	Both	CA	14	97.4	64.6 – 168.3	-	-
F	Both	MMDDM	1458	-	-	2.92	2.80 – 3.04
M	Both	MMDDM	1458	-	-	5.19	4.95 – 5.43
F	Wet	MMDDM	729	-	-	2.69	2.53 – 2.86
F	Dry	MMDDM	729	-	-	3.16	2.98 – 3.33
M	Wet	MMDDM	729	-	-	5.29	4.95 – 5.62
M	Dry	MMDDM	729	-	-	5.10	4.76 – 5.44
M&F	Dry	HR	17	293.7	200.4 – 460.8	-	-
M&F	Wet	HR	17	324.8	150.4 – 708.5	-	-
M&F	Dry	CA	17	64.6	32.4 – 98.3	-	-
M&F	Wet	CA	17	69.6	30.9 – 166.2	-	-
M	Dry	HR	7	460.8	250.1 – 826.7	-	-
M	Wet	HR	7	708.5	150.4 – 993.8	-	-
M	Dry	CA	7	96.4	64.6 – 168.3	-	-
M	Wet	CA	7	104.7	30.9 – 179.9	-	-
F	Dry	HR	10	237.4	65 – 304.6	-	-
F	Wet	HR	10	294.7	148.0 – 470.6	-	-
F	Dry	CA	10	39.2	18.0 – 87.2	-	-
F	Wet	CA	10	60.6	25.7 – 126.8	-	-

Table 5.3. Percentages of lion home ranges (HR) covered by water in the ¹dry season with dry season water levels, ²dry season with wet season water levels (i.e. if lions did not shift ranges) and ³wet season with wet season water levels. ⁴ Wet season HR size divided by dry season HR size. LQ: Lower Quartile; UQ: Upper Quartile. Refer Annexure A Table A3 for underlying data.

Group	n	HR Season	Flood Season	HR inundated		Wet HR size/Dry HR size ⁴	
				Median (%)	LQ – UQ (%)	Median	LQ – UQ
Plains Lions ¹	6	Dry	Dry	1.8	0.3 – 1.7		
Plains Lions ²	6	Dry	Wet	47.1	18.7 – 80.6		
Plains Lions ³	6	Wet	Wet	65.1	14.7 – 88.4	1.77	0.62 – 1.86
Woodland Lions ¹	7	Dry	Dry	0.6	0.5 – 0.9		
Woodland Lions ²	7	Dry	Wet	1.2	0.9 – 3.3		
Woodland Lions ³	7	Wet	Wet	1.4	0.5 – 2.3	1.20	0.92 – 1.65
All Lions ¹	13	Dry	Dry	0.6	0.5 – 0.9		
All Lions ²	13	Dry	Wet	4.2	1.2 – 25.2		
All Lions ³	13	Wet	Wet	3.6	1.4 – 43.0	1.55	0.93 – 1.83

Site exclusivity and fidelity

There was no significant intra-sex difference in overlap between seasons for females (MWU $Z = -0.14$, $p = 0.89$) or males (MWU $Z = -0.50$, $p = 0.62$). Overlap between females in the dry season was significantly less than for males (MWU $Z = -2.01$, $p = 0.04$), but this relationship was not significant in the wet season (MWU $Z = -1.86$, $p = 0.06$; Table 5.4). Distances between simultaneous positions of neighbouring lions were not significantly greater than between randomly paired locations for the same lions (Table 5.5). Mean distance between related females F39 and F53 ($t = -28.4$, d.f. = 3546, $p < 0.01$) and males M37 and M43 ($t = -11.1$, d.f. = 1688, $p < 0.01$) was significantly less than between randomly paired locations for the same lions (Table 5.5). I found wet season overlaps of CAs of two females (F18 and F21) and two male

pairs (M16 with M06 and M48 respectively; Annexure A Table A4), while there were no intra-sex CA overlaps in the dry season. There were no simultaneous locations <200m apart for any two unrelated females (n = 855 - 2533 paired locations), while M16 was within 200m of M06 and M48 once (of 334 paired locations) and twice (of 925 locations) respectively.

Table 5.4. Median intra-sex overlap between neighbouring lions, and inter-annual site fidelity of lions from dry season in year *t-1* to dry season in year *t*, and wet season in year *t-1* to wet season in year *t* in Kafue National Park. Refer methods for details of overlap and site fidelity calculation. F: female; M: male; n: number of pairs of neighbouring lions (overlap) or individual lions (fidelity); LQ: Lower Quartile; UQ: Upper Quartile. Details of overlaps in Annexure A Table A4.

Sex	Season	Measure	n	Median (%)	LQ - UQ (%)
F	Dry	Overlap – HR	10	11.0	8.8 – 15.4
F	Wet	Overlap – HR	18	12.9	7.7 – 15.7
M	Dry	Overlap – HR	12	16.8	13.2 – 65.9
M	Wet	Overlap – HR	8	38.8	16.2 – 47.2
F	Dry	Fidelity – HR	5	90.2	85.7 – 91.4
M	Dry	Fidelity – HR	2	64.3	50.4 – 78.2
F	Wet	Fidelity – HR	7	83.2	73.6 – 96.6
M	Wet	Fidelity – HR	3	74.1	26.7 – 94.3
F	Dry	Fidelity – CA	5	93.6	87.0 – 94.4
M	Dry	Fidelity – CA	2	42.4	33.0 – 51.8
F	Wet	Fidelity – CA	7	49.9	32.5 – 96.3
M	Wet	Fidelity – CA	3	42.5	32.6 – 59.2
M&F	Both	Fidelity – HR	17	83.2	73.6 – 91.4
M&F	Both	Fidelity – CA	17	59.2	42.5 – 93.6
F	Both	Fidelity – HR	12	86.1	75.4 – 94.0
F	Both	Fidelity – CA	12	76.6	46.5 – 95.4
M	Both	Fidelity – HR	5	74.1	50.4 – 78.2
M	Both	Fidelity – CA	5	42.5	33.0 – 51.8

Females showed more fidelity to HRs and CAs from one season to the next than males (Table 5.4), but the difference approached significance for dry season CAs only (MWU Z: 1.74, p = 0.08). Inter-seasonal fidelity to HRs was significantly greater than CAs for combined males and

females (WMP $Z = 2.12$, $p = 0.03$), but in unisex analysis, this difference approached significance for males only (WMP $Z = 1.75$, $p = 0.08$; Table 5.4). Centroids of HRs showed intra-seasonal shift from one year to the next (median = 5.14 km, QR: 1.76 – 9.74). I found no significant differences in centroid shifts between sexes or seasons.

Table 5.5. Distances between lions of the same sex with overlapping home ranges, 2010 - 2013. Bold indicates actual distances significantly less than random distances.

Lion pair	Mean distance (km)		<i>n</i>	<i>t</i>	<i>P</i>
	Actual	Random			
F39/F53	4.4	11.8	1774	-28.393	<0.01
F21/F18	8.7	8.8	2138	-0.647	0.52
F28/F18	22.3	22.1	2532	0.949	0.34
F39/F28	31.2	31.2	1800	0.119	0.91
F39/F77	16.4	16.5	856	-0.287	0.78
F53/F77	17.7	17.9	855	-0.477	0.63
M37/M43	9.1	14.1	845	-11.099	<0.01
M16/M06	25.5	25.6	334	-0.049	0.96
M16/M48	18.0	17.9	925	0.126	0.90
M37/M06	33.0	33.4	675	-0.532	0.60

Habitat utilisation

In the dry season, plains females preferred wetland (WET) habitat, used munga and termitaria (MUN) and miombo and Kalahari (MIO) at expected frequencies, and munga scrub and grassland (SAG) less than expected. In the wet season, these females' preference for WET was not as strong, the avoidance of SAG was reduced, and both MUN and MIO were used more than expected. Plains males preferred habitat types WET and MUN in the dry season, while avoiding MIO and SAG. In the wet season, these males preferentially selected MUN, while all other habitats were used less than expected (Figure 5.2).

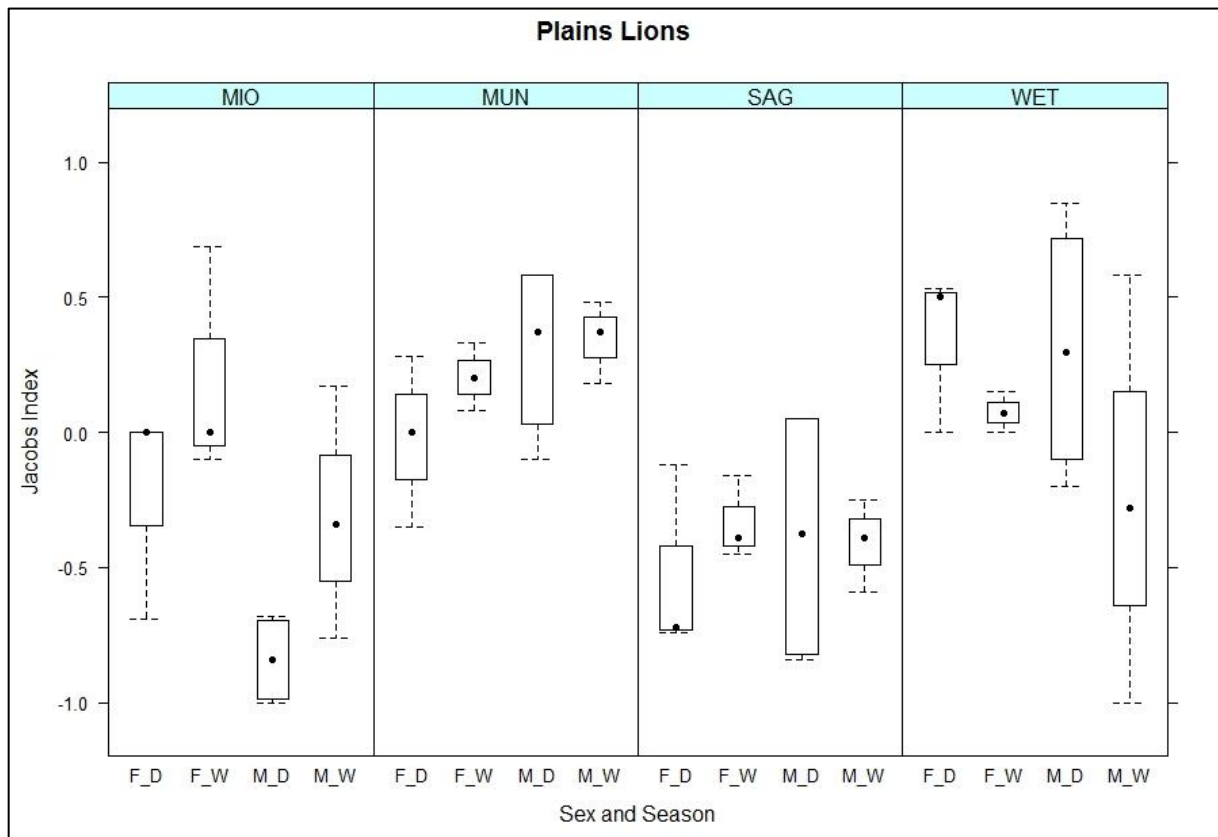


Figure 5.2. Jacobs selection (Jacobs, 1974) index analysis of habitat selection by plains lions in northern Kafue National Park. Index value of 1.0 indicates very strong selection, -1.0 very strong avoidance and 0.0 no preference shown. Dots indicate medians, boxes quartile ranges and whiskers ranges. F: Female; M: Male; D: Dry Season; W: Wet Season; MIO: miombo and Kalahari woodland; MUN: munga and termitaria woodland; SAG munga scrub and grassland; WET: wetland.

Male and female woodland lions preferentially selected MUN and used SAG less than expected in both seasons. These lions avoided MIO in the dry season and used it more than expected in the wet (Figure 5.3).

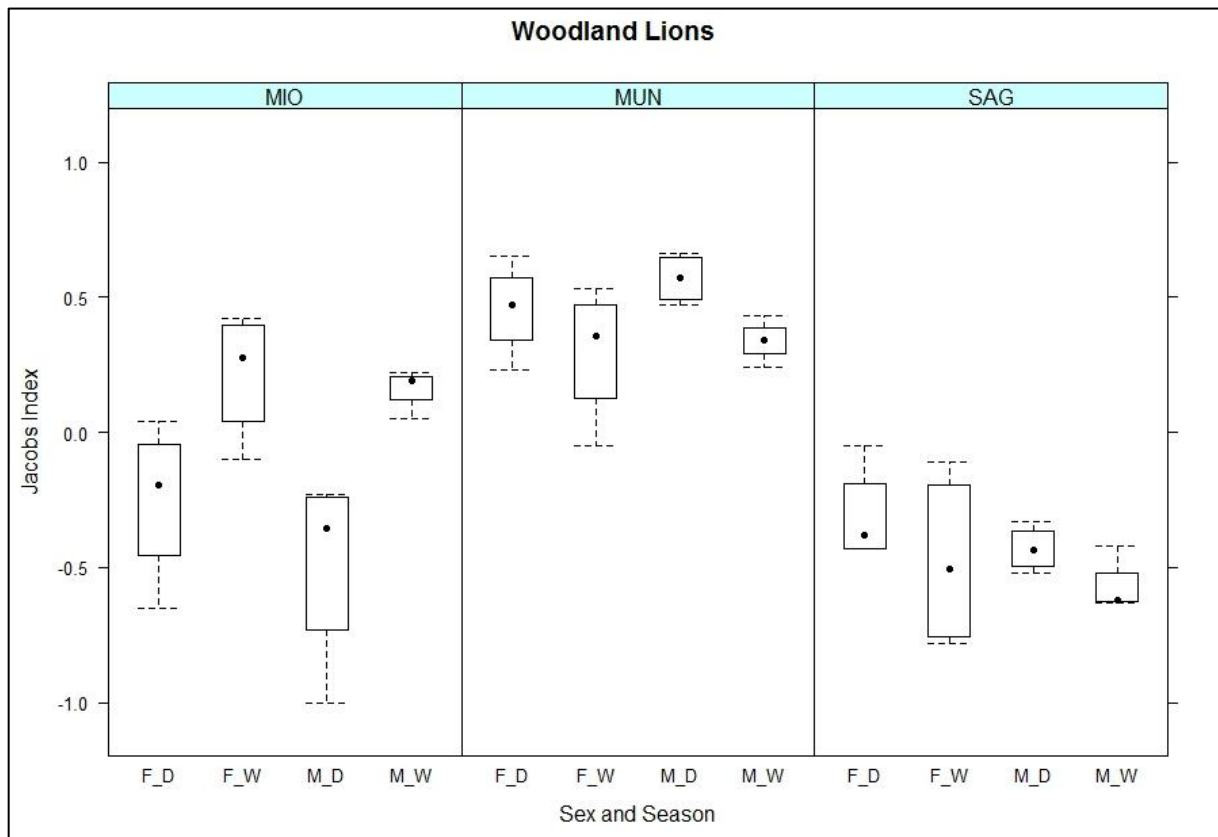


Figure 5.3. Jacobs selection (Jacobs, 1974) index analysis of habitat selection by woodland lions in northern Kafue National Park. Index value of 1.0 indicates very strong selection, -1.0 very strong avoidance and 0.0 no preference shown. Dots indicate medians, boxes quartile ranges and whiskers ranges. F: Female; M: Male; D: Dry Season; W: Wet Season; MIO: miombo and Kalahari woodland; MUN: munga and termitaria woodland; SAG munga scrub and grassland.

Discussion

Lion home range size in northern Kafue is similar to that of lions in Hwange NP (Loveridge *et al.*, 2009), an order of magnitude smaller than those in the dune savanna of the arid Kgalagadi Transfrontier Park (Funston, 2011) and larger than lion HRs in East African PAs such as Selous Game Reserve or the Ngorongoro Conservation area (Spong 2002, Hanby *et al.*, 1995). Celesia *et al.* (2009) found that rainfall, temperature and landscape features (e.g. elevation, slope direction) together explained 94% of variation in lion demography between 27 different sites. Although influential in univariate analyses, herbivore biomass had little independent effect in their analyses due to its relationship with rainfall and temperature. However, within the limited geographic range of my study area, climate and landscape (except the Busanga in the wet season) are largely homogeneous. At this scale, prey biomass, pride biomass and the interactions between the two are thus more likely to affect the size of individual HRs.

My analysis of drivers of dry season home range size produced similar results to those of Loveridge *et al.* (2009) in Hwange, namely that female HR size increased with increasing pride

size, but decreased with increasing prey biomass after controlling for pride size (although the latter relationship in my case was not significant). In Kafue, pride size also increased with increasing distance from the park boundary. Prey availability was not the limiting factor for size of prides closer to the edge, as dry season prey biomass available per lion in the HRs of these groups was nearly double that of study prides further inside the park. This greater biomass is a result of the attractive effect of the Busanga wetlands, particularly on buffalo, red lechwe *Kobus leche* and puku *Kobus vardonii*, all of which formed a significant portion of dry season prey biomass in this area. Loveridge *et al.*, (2007) found that trophy hunting outside Hwange NP affected lion populations in the park, while in South Luangwa NP, snaring was more prevalent near the boundary than deeper inside the park (Watson *et al.*, 2013). I suspect that these anthropogenic perturbations may thus have a limiting effect on the sizes of prides closer to the boundary in Kafue, as demonstrated in Katavi NP, Tanzania (Kiffner *et al.* 2009). During my study, three of four collared male lions whose HRs overlapped the boundary disappeared. One was confirmed shot by a trophy hunter, and rumours from villagers suggest that another was killed in a snare (I. Mulenga, pers. comm.). Additionally, two females in the pride whose HR overlapped the boundary were found (and subsequently treated) with life-threatening snares, one of which lost a litter of three cubs shortly after treatment.

The temporal concentration of rainfall in Kafue causes extensive flooding in the wet season, which likely affects the ranging behaviour of many resident fauna. The HRs of all collared lions in my study included at least one permanent river, while the HRs of three female and three male groups (plains lions) also included areas of the seasonally inundated Busanga floodplain. The seasonal increase in water levels in these water bodies thus led to the proportion of individual lion home ranges covered by standing water being significantly greater in the wet season than the dry season, with as much as 94.2% of a female's dry season HR being flooded. Walking through water is energetically more costly than dry land (Hall *et al.*, 1998), and the significant increase in female HR sizes, and shift away from dry season river courses in the wet season, suggest that these seasonal range expansions may have been an attempt to reduce such exertions by moving away from inundated terrain.

However, increasing HR size in the wet season did not significantly reduce the inundated proportion of HR, and thus the shift may have been to shallower water rather than dry land, particularly for plains lions that experienced a greater degree of flooding. Simultaneously, the increased HR size may also have been influenced by prey species being more homogeneously dispersed in the wet season due to widespread availability of water (*sensu* Davidson *et al.*, 2013). This assertion is supported by the fact that female lions' minimum daily movement was significantly greater in the wet season than the dry, suggesting that they had to travel further to find prey. Tumenta *et al.* (In press) found similar shifts in lion ranging behaviour in Cameroon's

Waza NP, whilst lions in the Central Kalahari Game Reserve have larger HRs in the dry season as their prey disperses more widely in search of scarce water (Owens & Owens, 1985). Jaguars in Brazil showed dry season HR increases, with both the cats and their prey being confined to smaller islands during the wet season, which is characterised by largescale inundation (Cavalcanti & Gese, 2009). Conversely, in Hwange NP, a system with similar seasonality of rainfall to Kafue, Loveridge *et al.* (2009) found no significant inter-seasonal variability in lion HR sizes. In Hwange, mean annual rainfall is lower (~ 50% of Kafue's mean), and the topography is less prone to extensive flooding and thus lion HR is seldom impacted by abiotic variables such as flooding.

Despite seasonal fluctuations in HR size and habitat use, median inter-annual (i.e. dry to subsequent dry, wet to subsequent wet) site fidelity was over 80%, suggesting that individuals largely re-establish similar seasonal HRs between years despite regular upheaval. Nonetheless, areas of higher activity within these home ranges did change, as evidenced by a median shift of more than 5 km in inter-annual HR centroids. Within seasons, I found intra-sex spatial overlap of HRs and CAs for male and female groups, which is not unusual for the species, and was found by Spong (2002) to have no correlation with levels of relatedness amongst individuals between groups. These overlaps did not vary seasonally, and did not translate into likely physical encounters (<200 m apart) for any females (except F39 and F53, who were members of the same pride), despite no evidence of active temporal avoidance by neighbouring lions. I did, however, record likely encounters between males, which were possibly territorial conflicts between the incumbent coalition on the Busanga floodplain (M15 and M16) and rival two-male coalitions represented by M48 and M06 respectively.

I also recorded likely encounters between each of these male coalitions and collared females from two or more of the three plains prides during the 2012 calendar year. It is not uncommon for prides to associate with more than one male coalition, and genetic analysis in Etosha NP confirmed extra-group paternity in 45% (n = 22) of litters (Lyke *et al.*, 2013). Schaller (1972) suggested that females may mate with extra-group males to confuse paternity and thus reduce the likelihood of losing cubs to infanticide, a strategy that would likely be beneficial in Kafue, where most female HRs overlap with more than one male coalition.

The preferential use of wetland habitat (WET) by lions in the dry season may reflect the higher water availability in this area, and its attractant effect on ungulates, as demonstrated by Valeix *et al.*, (2010) in Hwange NP. However, the majority of this habitat in Kafue is inundated in the wet season, forcing these groups to move away from these areas. Lions without WET habitat preferred munga and termitaria woodland (MUN), likely due to its patchy nature which suits their stalk and pounce hunting strategy (Hopcraft *et al.* 2005). These results support my findings in

Chapter 3, where the proportion of MUN habitat was the best predictor of local lion occupancy in the dry season. Lions without *WET* also used the more uniform, but higher elevated and drier, MIO areas in the wet season.

It is possible that plains prides are thus adversely affected by both higher levels of anthropogenic influence (closer to the park edge) and greater flooding during the wet season which together may adversely affect pride size relative to woodland lions. During my study, only three of 16 observed cubs born to plains prides survived to one year of age, and all three were born in late wet or early dry seasons. Local tourist guides confirm that historically cubs of females born near the end of the dry season seldom survive the subsequent wet season (I. Mulenga pers. comm.). In East Africa, proximity to rivers and drainage lines was the best predictor of reproductive success (Kissui *et al.*, 2009; Mosser *et al.*, 2009), yet in my study area, where all prides had river access, only 5 of 34 known cubs (14.7%) survived past one year, less than half of Serengeti and 25% of Ngorongoro Crater cub survival rates (Packer *et al.*, 1988). Dry season prey biomass distribution suggests that the Busanga floodplain should be a prime territory for lions in Kafue, but the extreme seasonal fluctuations in the system, along with the potential anthropogenic pressures close to the boundary, mean that dry season habitat selection may not translate into increased fitness.

The best quality landscape patches for lions are those that furnish sheltered den sites, access to water, sufficient prey, habitat that allows successful hunting and minimum anthropogenic disruption (Spong, 2002; Hopcraft *et al.*, 2005; Mosser *et al.*, 2009). However, in Kafue, such patches are only available to lions for a portion of the year, and the upheaval that this causes likely has a detrimental effect on population productivity and persistence. Seasonal rainfall and flooding are a natural part of this system, yet the intensity and duration of floods may be affected by anthropogenic influences such as damming of rivers for traditional fishing. Furthermore, changes in rainfall patterns as a result of climate change are likely to affect distribution of surface water in Zambia, though the nature of the resulting fluctuations are unpredictable (De Wit & Stankiewicz, 2006). Lion (Smuts *et al.*, 1978; Davidson *et al.*, 2011) and leopard (Balme *et al.*, 2009b) populations suppressed by anthropogenic pressure have the ability to recover rapidly once that pressure is lifted. However, the effects of the seasonal inundation of Kafue on lion ranging behaviour and, potentially, their reproductive success, may limit the rate at which this population can recover from over-harvesting through legal and illegal hunting. Understanding these effects will help management authorities to better protect the species in Kafue and other areas of lion range with similar environmental challenges.

CHAPTER 6

Threats to Kafue's lions and recommended management interventions

Summary

Protected areas are critical to the future of lions and other large carnivores, yet living in these sanctuaries does not guarantee their safety from anthropogenic persecution. In this chapter I use my earlier findings to investigate the threat posed to Kafue's lions by illegal hunting, poorly managed trophy hunting and uncontrolled bush fires. My results suggest that the park's lion population is limited by available prey biomass, which is suppressed below carrying capacity by illegal hunting. Illegal hunting is also a direct cause of lion mortality. Trophy hunting of lions is currently banned in Zambia, but previous quotas were too high and, in concert with other hunting regulations, threatened the sustainability of lions in the system. Regular anthropogenic bush fires may alter habitat favoured by lions and result in juvenile mortality. I recommend the implementation of new open-source monitoring software to improve the efficiency with which limited law enforcement resources are deployed, and reduce levels of illegal hunting and the frequency of illegal fires. The paucity of adult male lions in my study area suggests that the current ban on lion hunting should be retained for at least three years. Minimum age limits, robust monitoring systems and an adaptive management framework are required prior to any consideration of lifting the ban. I recommend an initial annual quota cap of 5.25 male lions, over six years of age, across Kafue's hunting concessions. My results provide the wildlife authority with science-based recommendations as a basis for a management plan for lions in Kafue and other protected areas in Zambia.

Introduction

Wildlife management authorities must manage threats to biodiversity under their stewardship, but information concerning species or systems at risk is often lacking or conflicting (Pullin & Knight, 2001). Consequently, management interventions are often based on intuition and past experience, not scientific evidence (Sutherland *et al.*, 2004). The African lion has lost more than 75% of its historical range, yet few data exist on the scale, scope and impacts of the risks faced by many extant populations (Riggio *et al.*, 2013). In 2009, the ZAWA published *Zambia's Conservation Strategy and Action Plan for the African Lion* (Chansa *et al.*, 2009), which mandated the development of action plans for individual lion management units/clusters (of which Kafue is one) within three years. However, due largely to a shortage of resources, no such plan exists for Kafue. In this chapter I attempt to identify the major anthropogenic threats to the persistence of lions in this system, and, as the basis for the required action plan, suggest steps to be taken by management to mitigate against these risks.

Focusing management activities on a single species in the context of a large PA with limited conservation funding is controversial, as it may come at the cost of other vulnerable species within the system (Caro & O'Doherty, 1999). Nonetheless, the use of surrogates in the form of umbrella or flagship species to prioritise areas for protection is widespread and can be effective (Walpole & Leader-Williams, 2002). Noss (1990), defines an umbrella species as one "with large area requirements, which if given sufficient protected habitat, will bring many other species under protection" and a flagship as a "popular, charismatic species that serves as a symbol and rallying point for major conservation initiatives." Lions satisfy both definitions, and, as apex predators requiring large quantities of prey, they play a critical role in maintaining ecosystem functionality through top-down limiting effects on mesopredator (Crooks & Soule, 1999) and herbivore (Creel & Christianson, 2008) populations.

Lions also fulfil key economic roles in PAs, attracting both photographic tourists (Okello *et al.*, 2008) and trophy hunters (Lindsey *et al.*, 2012b). In northern Kafue, the most recent annual financial contribution of just two photographic tourism operators to ZAWA is approximately USD490,000. One of these operators paid an additional wage bill of USD645,000 in the period, much of which is paid to staff from communities adjacent to Kafue. Both these companies would cease their operations if the park lost its lion population (C. Roche, C. McBride pers. comm.), depriving ZAWA of critical revenue and communities of benefits associated with wildlife tourism. Similarly, the GMAs surrounding the park generate considerable income for ZAWA and resident communities (who should retain 50% of trophy fees and 20% of concession fees) through trophy hunting, although communities do not receive all revenue due to them (Lindsey *et al.*,

2013b). Having lion on quota contributes significantly to the financial viability of these hunting operations (Lindsey *et al.*, 2012b).

The future economic and ecological viability of Kafue is thus inextricably linked to the fate of its lions. However, the species faces a number of anthropogenic threats in the park, and appropriate management strategies are required to mitigate the effects thereof. Firstly, illegal hunting, primarily targeting ungulates for meat, is a major threat to lions and other large carnivores, as the practice reduces available prey biomass, and predators are often caught as by-catch in wire snares (Lindsey *et al.*, 2013a). Although surveys suggest that Kafue's ungulate numbers remained fairly stable from 2008 to 2011 (Frederick, 2011), biomass in the park is suppressed and well below carrying capacity (Lindsey *et al.*, In press). More recently, a demand for wild lion bones for use in Traditional Asian Medicine (TAM) has arisen, and this may result in illegal hunters intentionally targeting the species (Lindsey *et al.*, 2012a). In their study area in South Luangwa NP and an adjacent GMA, Becker *et al.* (2013) found 12% of adult and subadult lions, and 20% of adult males were snared.

Secondly, although trophy hunting has financial benefits (Lindsey *et al.*, 2012b), if poorly managed, it can have detrimental effects on lion populations (Loveridge *et al.*, 2007; Packer *et al.*, 2010). As a result of perceived declining numbers, the Zambian government banned lion (and leopard) hunting in January 2013 (<http://www.bbc.co.uk/news/world-africa-20969868>, accessed March 15 2013). The government has indicated that it will consider a future lifting of the ban, but only if scientific estimates of lion populations and sustainable quota levels have been established, and appropriate monitoring frameworks implemented. Zambia's lion (and other species) hunting quotas have historically been based on coarse estimates of ungulate abundance, which were used to classify individual GMAs as prime, secondary, under-stocked or depleted (Lindsey *et al.*, In press). These classifications were supplemented by recommendations from hunting operators, ostensibly based on knowledge of their concessions (Lindsey *et al.*, 2013b). Despite this potential conflict of interest, two-thirds of Zambian operators interviewed in 2011 felt that quotas in their concessions were too high (Lindsey *et al.*, 2013b) and fulfilling them would impact adversely on the sustainability of hunting in GMAs.

A third potential anthropogenic threat is the bush fires that burn much of Kafue each year (Figure 6.1). Although fire is a critical driver of many biomes on a global scale, its effects on savanna ecosystems are both varied and complex (Roques *et al.*, 2001; Van Langevelde *et al.*, 2003). When fires are too frequent and extensive in such systems, they may affect herbivore assemblages and thus available prey biomass (Bond & Keeley, 2005), as well as reduce vegetative cover used by lions for hunting (Eby *et al.*, 2013). However, the illegal hunting of bulk grazers such as zebra *Equus quagga* and buffalo, which naturally control the above-ground

biomass of grasses (Harrington *et al.*, 1999), perpetuates the need for fires as a management tool to compensate for reduced grazing pressure (Archibald *et al.*, 2005). ZAWA's policy requires management to ignite fires in the early dry season (before vegetation becomes too dry) to reduce the fuel load and prevent hotter, potentially more damaging fires later in the season. However, ad hoc fires ignited by other parties (e.g., illegal hunters, tour guides) challenge the implementation of a systematic fire regime (Van Wilgen *et al.*, 2004). This, together with ZAWA's limited capacity to control fires, results in extensive areas of the Kafue system being burnt on an annual basis.



Figure 6.1. An uncontrolled bush fire ignited illegally on the Busanga Plains, Kafue National Park, July 2013. Photo: P. Lindsey.

In this chapter I consider the threats to lions in Kafue posed by i) illegal snaring of ungulates and lions, ii) trophy hunting and iii) uncontrolled bush fires. I suggest management steps to reduce the impact of these threats. Prominent threats to lions elsewhere such as habitat conversion and conflict-related killing are less relevant in Kafue due to its status as a National Park (Lindsey *et al.*, In press) and the general low levels of livestock in neighbouring GMAs. Habitat conversion in areas surrounding the park is, however, escalating (Lindsey *et al.*, In press) and I account for this when establishing sustainable trophy hunting quotas for lions. Finally, I recommend a protocol for monitoring Kafue's lions that will enable effective adaptive management of the species.

Methods

Study area

In this chapter, my study area comprises the entire Kafue NP, as well as the adjacent 43,692km² of GMAs, which are split into nine hunting concessions (Figure 6.2).

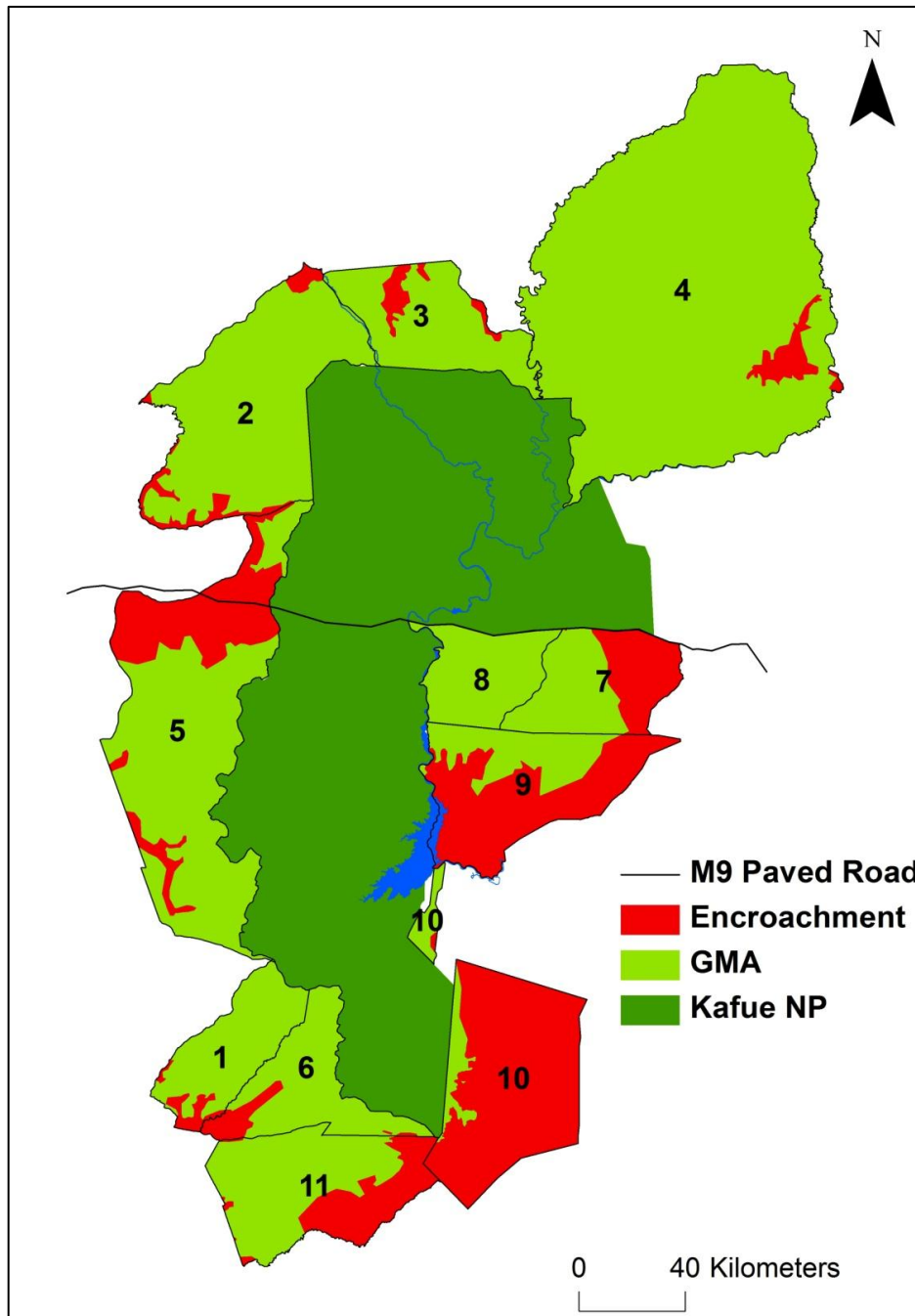


Figure 6.2. Kafue National Park (NP) and adjacent Game Management Areas (GMAs) divided into hunting concessions. Encroachment is areas within GMAs converted to agricultural use. Key to GMAs: 1: Bilibili; 2 Kasonso-Busanga; 3: Lunga-Busanga; 4: Lunga-Luswishi; 5: Mufunta; 6: Mulobezi; 7: Mumbwa-East; 8: Mumbwa West; 9: Namwala; 10: Nkala; 11: Sichifulo.

Illegal hunting and snaring of lions

In the absence of human pressure, the abundance of dominant large carnivores is primarily determined by prey availability (Spong, 2002). In this context, Carbone and Gittleman (2002) demonstrated that 10,000 kg of prey biomass supports approximately 90 kg of a given carnivore species. I used this relationship to test whether illegal hunting, through its suppressive effect on Kafue's ungulate populations (Lindsey *et al.*, In press), is limiting lion abundance in the park. Using the methods described in Chapter 2 and Table 3.3, I first calculated estimated prey biomass (all ungulates in the size range from bushbuck *Tragelaphus scriptus* to buffalo) for northern Kafue. I then calculated lion carrying capacity (C) using the formula

$$C = \frac{A}{10000} \times \frac{90}{B}$$

where *A* is prey biomass for northern Kafue, and *B* is mean lion weight. As I did not have weight estimates for Kafue lions, I used the mean lion weight (142 kg) calculated by Carbone and Gittleman (2002) from a sample of 21 lion populations. Finally, I compared this carrying capacity with an independent estimate of northern Kafue's lion population determined in a track count survey undertaken in 2012 (Chapter 4). The track count estimate included only lions >1yr old, whilst Carbone and Gittleman (2002) include all age classes. However, only 5.9% of lion tracks observed in the track count survey were from lions <1r old (Chapter 4) and, as they are young animals with lower mass and food requirements, their effect on the overall estimate is likely negligible.

Trophy hunting of lions

I determine four potential lion quota caps for the Kafue GMAs, three using variations on hunting concession sizes and one using prey biomass, and compare these with the quotas in place immediately prior to the 2013 hunting ban. Based on historical off take data, Packer *et al.* (2010) suggest that lion quotas in Tanzania should be limited to 0.5 lions/1000 km² outside of Selous Game Reserve, and that other lion range states should conduct similar analyses to derive local quota caps. However, this is not possible in Zambia due to poor record keeping and unreliable off take data (Becker *et al.*, 2012). As such, I use the recommendation of Packer *et al.* (2010) to derive a quota cap for each hunting concession based on its gazetted size. Following the precautionary principle (Foster *et al.*, 2000), I round the resultant cap down to the nearest "quarter-lion" (Quota A). So, for example, a 1700 km² GMA with a quota of 0.85 based on area, will receive a quota of 0.75 lions per year, effectively allowing the harvest of three lions every four years.

However, using the gazetted area of GMAs is potentially misleading, as large proportions of some GMAs have been converted to commercial and/or subsistence agricultural use (Lindsey *et al.*, In press). Although land conversion did not emerge as a significant factor in Tanzanian lion harvest declines, this is likely a reflection of outdated agricultural data (Packer *et al.*, 2010). Additionally, human settlement is not permitted in Tanzanian Game Reserves, where much trophy hunting occurs, while it is permitted in Zambian GMAs. To correct for these discrepancies, I used GOOGLE EARTH imagery (dated between 2004 and 2013) to identify and delineate the extent of converted land. I created shape files from the resulting polygons in software ARCGIS v10.1 and added a 2 km buffer to each polygon to allow for further habitat conversion since imagery dates. Although this buffer size may overestimate conversion for recent imagery, it also likely underestimates conversion for older imagery, and I believe it produces a reasonable estimate of the current land conversion status. Accordingly, I reduced the estimated area of natural land within individual GMAs, recalculated quota caps based on this new “available” area for lions, and rounded down to the nearest quarter-lion to allocate quotas to concessions (Quota B).

For my third quota cap, I considered the results of an occupancy survey (Chapter 3), which found that the probability of Kafue lions using an area was positively related to presence of munga and termitaria woodland (MUN) and negatively correlated with miombo and Kalahari woodland (MIO). Munga scrub and grassland (SAG) had little effect on lion occupancy. I reduced the “available” area by the extent of avoided MIO habitat in each GMA, and calculated new quota caps. I rounded down to the nearest quarter-lion to allocate quotas to concessions (Quota C).

A common method of calculating quota caps for a given species is to apply a sustainable harvest rate based on its life history traits (Edwards *et al.*, 2013), but this generally requires an estimate of population size. Due to opposition from local hunting operators, I was not able to conduct track count or call-up surveys in GMAs. In order to estimate lion population size in southern Kafue and surrounding GMAs, I therefore exploited the relationship between prey biomass and carnivore abundance demonstrated by Carbone and Gittleman (2002). Accordingly, estimated lion abundance (LA) in area *i* was:

$$LA_i = D_i \div \frac{A}{E}$$

where D_i is prey biomass in area *i* (per methods in Chapter 2 and Table 3.3), and *A* and *E* are prey biomass and estimated lion abundance (Chapter 4) in northern Kafue respectively. Caro *et al.* (2009) suggest that an annual off take of 5.1% of a lion population is sustainable. I therefore

multiplied my population estimate in each GMA by 5.1%, and calculated a quota cap by rounding the results down to the nearest quarter-lion (Quota D). To assess whether prey biomass is a reasonable gauge of lion abundance in Kafue, I compared the estimated prey biomass per lion in northern Kafue with that derived from Carbone and Gittleman's (2002) estimate.

Uncontrolled bush fires

I used software ARCGIS v10.1 and GeoTIFF imagery from MODIS (2013) to create layers representing areas burned in Kafue and surrounding GMAs. I aggregated daily burn data into monthly summaries using the RECLASS tool, and subsequently combined these into annual burnt areas for 2010, 2011 and 2012. I then combined these annual totals to provide a three-year aggregate, using the RASTER CALCULATOR. Lastly, I used the TABULATE AREA tool to calculate the proportion of Kafue and the GMAs burnt each year, and for the three-year aggregate. I compared median annual proportion of area burned between the park and the GMAs using a Mann-Whitney U-Test. Finally, I calculated the proportion of 2012 dry season home range for each lion (Chapter 5) that burnt in the 2012 dry season.

Results

Illegal hunting and snaring

Estimated prey biomass in northern Kafue is 3,090,674 kg, which translates to a carrying capacity of 196 lions (Carbone & Gittleman, 2002). This is similar to my estimate ($n = 200$) derived from a track count survey in 2012 (Chapter 4).

Trophy hunting of lions

Total gazetted area of GMAs is 43,493 km², which translates to a quota cap of 21.85 lions (Table 6.1). Rounding down to nearest quarter-lion in each concession resulted in a total quota of 20.25 lions (Quota A) and a harvest rate of 15.6% (quota divided by estimated GMA population of 130 lions). After removing land within GMAs that has been converted to agriculture (Figure 6.2), I arrived at a total "available" GMA area of 33,452 km², and a reduced quota cap of 16.73 lions. Rounding down in concessions produced a total quota of 15.75 lions (Quota B) at a harvest rate of 12.1%. Removing MIO habitat reduced the "available" area to 18,037 km², and the quota cap to 9.02 lions. Rounding down in concessions limited quotas to a total of 7.50 lions (Quota C) at a harvest rate of 5.8%.

Estimated lion abundance in southern Kafue and the GMAs based on prey biomass is 152 and 130 lions (>1yr old) respectively (Table 6.2). This equates to a sustainable harvest for the GMA population of 6.55 lions per annum. The quota cap using the abundance estimate is 6.67 lions per annum (the difference is a result of rounding of lion abundance estimates in individual concessions). Rounding down in each concession, the total quota is 5.25 lions per annum (Quota D; Table 6.2). Estimated prey biomass per lion in northern Kafue based on my track count population estimate is 15,453kg (Table 6.2), and using the Carbone and Gittleman (2002) equation 15,778 kg.

Table 6.1. Suggested lion hunting quotas for Kafue GMAs based on recommendations of 0.5 lions 1000 km² (Packer *et al.*, 2010), considering three different “sizes” of GMAs. Size A: gazetted size of GMA. Size B: area of GMA “available” for lions after accounting for land converted to agriculture. Size C: area of GMA “non-avoided” by lions after removing miombo and Kalahari woodland habitat (MIO) based on occupancy model of lion distribution in Kafue (Chapter 3). Harvest limits are calculated on relevant GMA size. Quotas are calculated by rounding harvest limits down to the nearest “quarter-lion” to simplify quota setting.

GMA	Quota	Quota	Size A	Harvest		Size B	Harvest		Size C	Harvest	
	2007	2012	(km ²)	limit A	Quota A	(km ²)	limit B	Quota B	(km ²)	limit C	Quota C
Billi	2	2	1703	0.85	0.75	1565	0.78	0.75	1536	0.77	0.75
Kasonso - Busanga	4	3	4695	2.35	2.25	4380	2.19	2.00	1959	0.98	0.75
Lunga - Busanga	3	0	2165	1.08	1.00	1961	0.98	0.75	892	0.45	0.25
Lunga - Luswishi	3	3	13380	6.69	6.50	13076	6.54	6.50	4600	2.30	2.25
Mufunta	?	1	6376	3.19	3.00	4584	2.29	2.25	2561	1.28	1.25
Mulobezi	4	3	1881	0.94	0.75	1649	0.82	0.75	1640	0.82	0.75
Mumbwa - East	2	2	1957	0.98	0.75	1149	0.57	0.50	669	0.33	0.25
Mumbwa - West	4	3	1442	0.72	0.50	1442	0.72	0.50	969	0.48	0.25
Namwala	2	2	3168	1.58	1.50	1039	0.52	0.50	801	0.40	0.25
Nkala	4	2	3895	1.95	1.75	490	0.25	0.25	482	0.24	0.00
Sichifulo	3	1	3030	1.51	1.50	2117	1.06	1.00	1928	0.96	0.75
Total	31	22	43693	21.85	20.25	33452	16.73	15.75	18037	9.02	7.50

Table 6.2. Suggested lion hunting quotas (bold column) for Kafue GMAs based on recommended harvest limit of 5.1% of population (Caro *et al.* 2009). ¹ Prey biomass calculated from aerial survey data per method in Chapter 2; ² Lion carrying capacity based on 90kg of carnivore per 10,000kg of prey biomass (mean lion mass = 142kg; Carbone & Gittleman (2002)). ³ Lion abundance in KNP north per 2012 track count survey (Chapter 5); KNP South and GMAs: prey biomass divided by prey biomass per lion in KNP north. ⁴ Prey biomass in KNP north divided by estimated lion abundance. ⁵ Estimated lion abundance (not rounded) multiplied by 5.1% (Caro *et al.* 2009). ⁶ Harvest limit rounded down to nearest “quarter-lion” for quota setting.

Area/GMA	Prey biomass (kg)¹	Estimated lion carrying capacity²	Estimated lion abundance³	Prey biomass per lion (kg) in KNP north⁴	Harvest limit⁵	Quota D⁶
KNP North	3,090,647	196	200	15,453	-	-
KNP South	2,328,398	148	152		-	-
Bilibili	177,069	11	11		0.56	0.50
Kasonso						
Busanga	150,031	10	10		0.51	0.50
Lunga Busanga	88,793	6	6		0.31	0.25
Lunga Luswishi	517,176	33	33		1.68	1.50
Mufunta	297,457	19	19		0.97	0.75
Mulobezi	177,998	11	12		0.61	0.50
Mumbwa East	98,515	6	6		0.31	0.25
Mumbwa West	340,000	22	22		1.12	1.00
Namwala	67,676	4	4		0.20	0.00
Nkala	36,721	2	2		0.10	0.00
Sichifulo	70,878	4	5		0.23	0.00
Total	7,441,359	472	482		6.67	5.25

Uncontrolled bush fires

Median proportion of area burnt per annum in Kafue from 2010 to 2012 is 57.1% (range 57.1 - 61.8%) while median proportion of GMAs burnt is 19.7% (range 17.5 – 22.0%). Proportionally more of the park burned than the GMAs each year, but this difference was not significant ($Z = -1.75$, $p = 0.08$). Eighty-three percent of Kafue, and 36.9% of GMA surface area burnt at least once during this period (Figure 6.3). The median proportion of dry season home range burnt for 13 radio-collared lions was 56.3%, with as much as 80.6% of an individual's range being burnt in the 2012 dry season, the year for which I had the most collared lions (Table 6.3).

Table 6.3. Percentage of home range burnt for individual lions in Kafue National Park in the 2012 dry season.

Lion	HR burnt in 2012(%)
F018	31.2
F021	40.0
F028	34.4
F039	75.8
F053	80.6
F072	64.4
F077	64.3
M006	56.9
M016	42.5
M037	67.9
M043	61.7
M048	55.8
M072	56.6

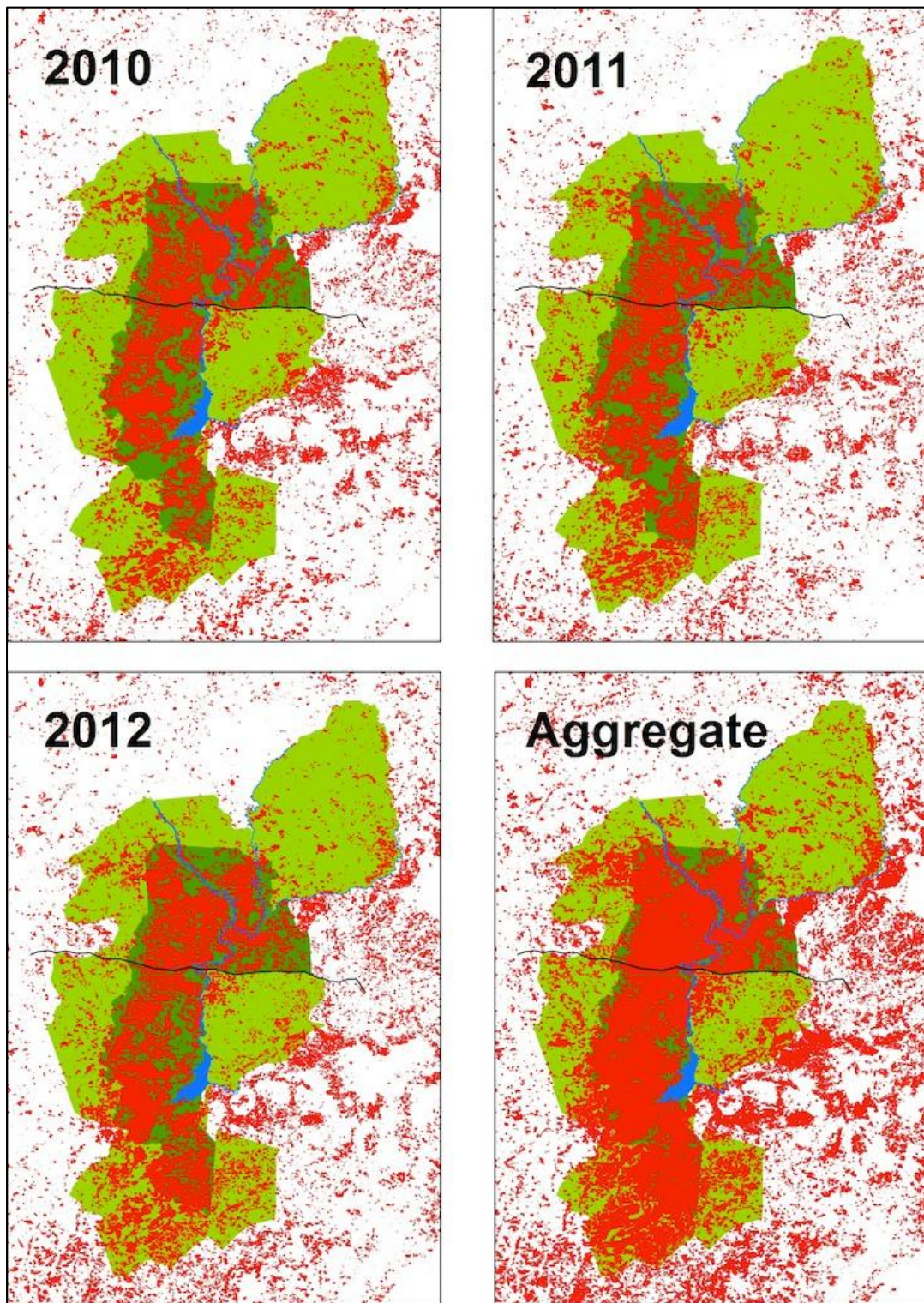


Figure 6.3. Burned land in northern Kafue and surrounding areas. Red areas represent land that burned during 2010, 2011 and 2012, as well as an aggregate of the three years in Kafue National Park (dark green), surrounding GMAs (light green) and adjacent non-protected areas (white).

Discussion

Illegal hunting and snaring

The similarity between the lion carrying capacity in northern Kafue based on Carbone and Gittleman's (2002) estimated prey biomass requirements and the population estimate derived from a track count survey (Chapter 4) suggests that prey availability is the primary limiting factor for the species in Kafue. Prey biomass in the park is considered to be well below capacity largely as a result of illegal bushmeat harvesting (Lindsey *et al.*, In press), which in turn severely limits the growth of Kafue's lion population. I estimate an overall lion population of 482 animals (>1yr old), with 352 in the park and 130 in the GMAs (Table 6.2). This slightly exceeds the predicted carrying capacity, but prey biomass may have been underestimated due to limitations of the aerial survey method (Ferreira & Van Aarde, 2009), as well as my exclusion of hippo from biomass calculations. I occasionally observed lions feeding on hippo but could not ascertain whether they had killed them or were scavenging. My estimate of lion abundance in GMAs may, however, be an overestimate as they have been subjected to both legal and elevated levels of illegal hunting in these areas (Becker *et al.*, 2012; Watson *et al.*, 2013).

In addition to their indirect effects on prey, snares are also likely to be a significant cause of local lion mortality (Becker *et al.*, 2013). Between August 2010 and July 2013, at least 14 adult lions (7% of estimated population) were observed with snares in northern Kafue (N. Midlane, unpublished data). Although historically these individuals would have been regarded as by-catch, reports from tourist guides of lions caught in baited snares (I. Mulenga, pers. comm.) suggest that illegal hunters may intentionally be targeting lions as a result of growing TAM demand for lion bone (Lindsey *et al.*, 2012a).

In the short- to medium term, effective law enforcement is the primary means of overcoming illegal hunting in a PA, while longer term mitigation relies on more complex solutions, such as increasing employment opportunities for communities living adjacent to PAs (Lindsey *et al.*, 2013a). Kafue currently has less than 100 wildlife police officers (WPOs) available for active patrol duty in an area of over 22,000 km², and is unlikely to significantly increase the budget allocated to anti-poaching activities in the foreseeable future (J. Milanzi, pers. comm.). However, the efficiency and effectiveness of deployment of WPOs could likely be improved through more rigorous and systematic collection of data on patrols, including records of where and when illegal activities are detected and the distribution of different species. A partnership of wildlife NGOs recently developed an open-source software package known as the Spatial Monitoring and Reporting Tool (SMART), designed to "increase efficiency, and promote credible

and transparent monitoring of the effectiveness of anti-poaching efforts” (<http://www.smartconservationsoftware.org>, accessed September 13 2013). Such a tool may assist ZAWA to enhance the planning and assessment of its law enforcement activities. Ensuring that areas identified as most important to lions in Kafue (Chapter 3) receive due attention, will likely benefit other species and the park in general given the umbrella effect of lions (*sensu* Noss, 1990).

Trophy hunting of lions

Poorly managed legal trophy hunting of lions can limit populations through over-harvesting (Packer *et al.*, 2010). My highest estimated quota cap (Quota A) determined using total area of hunting concessions approximates the 2012 quota for Kafue GMAs, but is 29% less than the quotas in place from 2007–2011 (Table 6.1). Using “available” area, the quota caps (Quota B) result in a reduction of 46 and 24% on 2007 and 2012 quotas respectively, whilst reducing the area further by including only non-avoided lion habitat (Quota C) reduced the cap even further, by 71 and 59% respectively. Finally, quota caps using a proposed sustainable harvest rate (Quota D; Caro *et al.* (2009)) were 78 and 70% lower than the actual quotas of 2007 and 2012 respectively.

My findings suggest that lion quotas for Kafue concessions were too high prior to the ban in 2013. This, along with the requirement to pay 60% of trophy fees upfront, regardless of whether a hunt was successful (Lindsey *et al.*, 2013b), likely resulted in overharvesting and poor trophy selection (Packer *et al.*, 2009), a combination likely to induce population declines. Consequently, the current moratorium on lion hunting appears justified to allow their recovery (e.g. Davidson *et al.*, 2011). However, given the importance of lions to the financial viability of Kafue’s hunting concessions (Lindsey *et al.*, 2012b), the long-term status of the ban requires careful evaluation.

Should the moratorium be lifted, my data suggest overall quota caps ranging from 5.25 to 20.25 lions per year across all Kafue concessions (Table 6.1 and Table 6.2). My caps based on area (Quotas A, B and C) use recommendations for Tanzanian lion populations (Packer *et al.*, 2010), which do not account for Zambian conditions and all three exceed the proposed sustainable harvest rate of 5.1% (Caro *et al.*, 2009). Quota D explicitly considers the limiting effect of suppressed prey populations on Kafue’s lions. I thus recommend a quota cap of 5.25 lions per annum across all Kafue hunting concessions (Table 6.2) as an initial limit if the Zambian government decides to lift the ban. Three concessions will thus no longer receive lion quotas, two will receive one lion every four years, three will have a lion every second year, one will have two lions every three years, one will hunt a lion every year and one will have three lions every

two years. However, I caution that even this conservative quota cap may be too high, as it does not account for the fact that human-induced lion mortality is likely higher in GMAs than in the National Park.

The number of lions on quota for a given GMA is important for both ZAWA and potential hunting operators when determining the financial value of a concession. However, quotas may not be as important for ensuring the sustainability of lion populations if other means of regulating harvest are implemented. Whitman *et al.* (2004) showed, using long-term data on Serengeti lions, that harvesting only male lions >6yrs old would have no detrimental effect on the population. This led to minimum trophy age thresholds being implemented in Tanzania and Niassa National Reserve (Niassa) in Mozambique (Lindsey *et al.*, 2013b). Strict enforcement of such regulations will reduce the biological significance of quotas, and thus lessen potential negative effects if quotas are erroneously set too high. In Niassa, a three-step “points system” has been implemented to drive adaptive management of quotas (Begg & Begg, 2008). Firstly, independent experts classify each lion trophy as either less than four years old, between four and six (difficult to age buffer class) or older than six. Secondly, points are allocated to each lion trophy depending on its age classification and the current quota in the concession. Finally, the quota for each concession for the following year is amended (increased, decreased or not changed) according to the points scored in the current year. Operators are thus incentivised to target older individuals and penalised for underage lions, while some leeway is allowed for trophies in the difficult-to-age intermediate category.

In Kafue, during my three-year study, I only observed eight male lions estimated to be over 6 yrs old in a 4395 km² study area (Chapter 5) within the national park (and no other mature males were reported by tourist guides despite daily game drives from six different camps distributed throughout the area). No more than six of the eight individuals were over 6 yrs old at any one time, and three of these males (two of which were collared) went missing and were presumed to have died during the study. As prey biomass suggests that lions are more abundant in Kafue than the surrounding GMAs, there are likely few males that currently qualify as suitable trophies, providing further justification for the recent moratorium.

I therefore recommend that the moratorium only be lifted if the following criteria are met: i) a minimum of three years have passed since the last legal lion hunt (i.e. until the start of the 2016 hunting season) to allow population recovery (e.g. Davidson, 2009); ii) quota caps are in place for each GMA based on a sustainable harvest rate (Caro *et al.*, 2009); iii) a robust, transparent trophy-monitoring framework is in place that allows independent verification of trophy age estimates; iv) a 6-year minimum age threshold, with an adaptive points system for scoring trophies and determining quotas (as used in Niassa), is firmly established; v) trophies classified

as underage are confiscated and precluded from export and vi) no upfront payments of trophy fees are required.

Uncontrolled bush fires

Igniting bush fires in Zambian PAs is illegal unless carried out by the management authority, but in Kafue fires are regularly ignited by illegal hunters, legal traditional fishermen and tourism guides (N. Midlane, pers. obs.). The combined effect is that almost 60% of the park burns every year, and more than 80% of it burned at least once in a three-year period. Proportionally, over three times more of the park was burnt than of the GMAs, despite large numbers of people inhabiting the latter. This suggests that either ZAWA's burning policy is driving most of the fire that occurs in the park, or the prevalence of illegally ignited fires is significantly higher in the park than in the GMAs.

The potential threat of fire to lions is primarily through its ability to drive habitat change and the subsequent effects on herbivore assemblages (Bond & Keeley, 2005). In Kafue, the heterogeneous, patchy habitat type MUN was the best predictor of lions occupying an area, but this habitat also burned regularly (Chapter 3); as much as 80% of a pride's home range burned each dry season. Regular fire can drive vegetation shifts from heterogeneous patches to either more uniformly wooded or grassland-dominated vegetation (Roques *et al.*, 2001; Van Langevelde *et al.*, 2003). Fire extent and MUN habitat were correlated in Kafue (Chapter 3), and burning may thus cause habitats less favourable for lions (e.g. MIO or SAG) to proliferate. Although it is difficult to quantify, fire can also pose a direct threat to carnivores, particularly denning juveniles (Laurenson, 1994). One lion den I observed was burnt a day after it had been vacated by a lioness with three six-week old cubs. It is unlikely that the lioness would have been able to move all three cubs to safety in time if they had been in the den when the fire arrived, and, given the extent of burning, I suspect that a proportion of lion (and other carnivore) juveniles are killed by fire in Kafue each year, although I caution that this notion is, by necessity, speculative.

Fire management strategies are not universally applicable across savanna systems, and many management authorities base their fire regime on outdated principles (Bond & Archibald, 2003). In order to understand and mitigate the potential negative effects on lions (and other biodiversity) associated with too regular burning, ZAWA should i) initiate research into the specific fire ecology of Kafue to inform better management thereof; ii) ensure legal traditional fishermen and tourism guides in the park are aware of the illegality of them igniting fires, and the potential problems caused by the practice; and iii) reduce the number of illegal fires by

improving law enforcement practices using tools such as the SMART system to locate and apprehend illegal hunters.

Other challenges to Kafue lions

The seasonal inundation of parts of Kafue, particularly in the northern region, poses a further challenge to the park's lions. Although access limitations meant I could not analyse this issue directly, I found 502.9 km² of my 4394.7 km² study area flooded during the wet season, compared to only 13.5 km² in the dry season (Chapter 5). As a result, lions travelled further each day in the wet season than the dry, thus requiring more energy at a time when prey is also likely to be more widely distributed. Although the seasonal inundation is a natural phenomenon, it is likely exacerbated by local anthropogenic activities. Traditional fishing rights exist on the Lufupa River in northern Kafue for communities displaced when the park was proclaimed in 1950 (Mwima, 2001). Regulations allow for 17 traditional fishing weirs, and a fishing season from 1 March to 30 June each year, after which the weirs are meant to be dismantled until the end of the dry season (Mwima, 2001). However, a number of particularly large, permanent weirs now exist, which appear to have a damming effect that slows the draining of the floodwaters (Figure 6.4). Furthermore, in excess of 30 weirs are currently in operation on the river (S. Wishikoti, pers. comm.), rather than the 17 allowed. Overharvesting of fish stocks can lead to declining catches over time, and communities may supplement this loss of protein with bushmeat (Brashares *et al.*, 2004), placing additional pressure on Kafue's ungulate and lion populations.

Seasonal flooding also likely contributes to the high levels of cub mortality observed in Kafue as females regularly lost cubs during the wet season (Chapter 5). The extended flooding period also affects the viability of photographic tourism camps on the Busanga Plains, the park's key tourism destination, by shortening the duration of the operating season and thus reducing revenues to operators and ZAWA (C. Roche, pers. comm.). I therefore recommend that ZAWA i) enforce existing regulations related to the number of permitted weirs, ii) initiate research into the viability of the local fishery and the effect of current fishing practices on fish stocks and flood levels and iii) investigate the feasibility of establishing fish farms in GMAs to relieve pressure on the park's fish stocks and potentially reduce demand for illegally acquired bushmeat.



Figure 6.4. Damming effect (right side of weir structure) of traditional fishing weir on Lufupa River, northern Kafue National park, July 2013. Photo: P. Lindsey.

Monitoring

An essential part of any conservation plan concerns the long term monitoring of population trends (Kiffner *et al.*, 2007). I suggest in Chapter 4 that track count surveys are the most effective and efficient method of monitoring lion numbers in Kafue, and I therefore recommend the implementation of annual track count surveys, in the northern and southern sectors in alternate years. However, due to its financial constraints, ZAWA will need to determine a threshold for longitudinal changes (and statistical power) in track frequency that it deems appropriate for management purposes and adjust survey effort accordingly. During my track count surveys (Chapter 4), no lion tracks were detected on the western, northern or north-eastern boundaries of the park. To ensure more efficient use of limited resources, I thus recommend that transects in the northern sector are limited to the roads in the centre of the park and the eastern sector south of the confluence of the Lunga and Kafue Rivers. Similarly, I recommend that surveys in southern Kafue be limited to roads inside the park. Once track frequency increases to a pre-determined level, boundary transects may be considered to evaluate the extent of the population recovery.

The relationship between lion track frequency and lion density is well established (Funston *et al.*, 2010) and has been demonstrated to hold in Kafue (Chapter 4). However, as I am

recommending a reduced survey area, I suggest that lion population trends be monitored using changes in lion track frequency as a relative abundance index, rather than converting these to absolute abundance estimates. Survey teams can simultaneously collect data on track frequencies for leopards and spotted hyaenas and monitor these trends accordingly.

The link between the status of Kafue's lion population and available prey biomass necessitates simultaneous monitoring of the ungulate population in order to understand constraints on lion population growth. I recommend that aerial surveys be conducted as regularly (but ≤ 1 /year) as possible, using consistent methodology to ensure comparability between counts (e.g. Frederick, 2011). The data collected can be used to inform ungulate hunting quotas in hunting concessions and, along with trophy monitoring, can provide an indication of the status of lion populations in the GMAs. Distance sampling (Buckland *et al.*, 2004) of ungulate populations can be undertaken using the road network within the park to supplement the aerial survey data. These surveys can be conducted simultaneously with track count surveys by adding additional observers, thus maximising the efficiency of vehicle and fuel expenditure.

Kafue holds a nationally and regionally important population of lions and ensuring the persistence of the species in the system should be a priority for Zambia's government and wildlife authority. The conservation benefits to the species will be matched by the ecological and economic benefits to the park and its surrounding GMAs. My recommended interventions are based on the results of the first intensive study of lions in the system. I thus provide ZAWA with an opportunity to implement evidence-based management of Kafue's lion population and to monitor the outcomes of these management decisions. Finally, I suggest that these recommendations form the basis for a management plan for lions in Kafue as envisaged and required by Zambia's *Conservation and Strategy Plan for the African Lion*.

CHAPTER 7

CONCLUSION

Protected areas are a critical component of biodiversity conservation (Pimm *et al.*, 1995; Naughton-Treves *et al.*, 2005). However, evidence for the effectiveness of PAs in maintaining species populations remains inconclusive (Geldmann *et al.*, 2013), often as a result of understaffing, underfunding and a suite of external threats (Le Saout *et al.*, 2013). The most effective parks are those that have clearly demarcated boundaries and effective enforcement and provide benefits to neighbouring communities (Bruner *et al.*, 2001). By contrast, the most ineffective are “paper parks:” legally protected but lacking infrastructure, staff and law enforcement presence (Braatz *et al.*, 1992). These parks typically degrade over time to become “empty forests,” where habitat persists but large animals have been extirpated by illegal human hunting (Redford, 1992).

Internationally, a target of protecting 17% of terrestrial habitat has been established, and global terrestrial PA coverage is now approximately 13% (Bertzky *et al.*, 2012). In Zambia, where more than 30% of land has been legally set aside for protection, only 8.5% is classified as Category II (National Parks, NPs), while the remainder (primarily GMAs) is in the less-protected Category VI, where consumptive utilisation of wildlife is permitted. My study suggests that more than 23% of the area of GMAs adjacent to Kafue has been converted into agricultural land (Chapter 6), and this pattern is reflected in other regions of the country as well (Lindsey *et al.*, In press).

Measuring the physical extent (area) of PAs alone as a proxy for effective biodiversity conservation is clearly of limited utility. Investigating the conservation status of appropriately selected indicator species within these parks may provide a better assessment of whether management authorities and other stakeholders are meeting stated objectives (Chape *et al.*, 2005). Large carnivores are ideal indicator species due to their role as ecological umbrellas, economic flagships and miner’s canaries (Macdonald *et al.*, 2010). In addition, many species in the taxa face a multitude of anthropogenic threats that jeopardise their long-term persistence in the wild, and are thus themselves in need of conservation attention (Karanth & Chellam, 2009). In this thesis I investigated the conservation status of a largely unstudied population of lions in Kafue, the largest PA in Zambia’s network and Africa’s second-largest NP.

My findings suggest that Kafue’s lion population is largely limited by available prey biomass, which in turn is suppressed by illegal hunting, an activity that is widespread throughout the park and neighbouring GMAs (Lindsey *et al.*, In press). Direct mortality of lions caught in wire snares, poorly regulated trophy hunting (prior to the current ban) and uncontrolled bush fires all add to the anthropogenic pressure on lions in the Kafue system. Lion populations can recover quickly from declines (Smuts, 1978; Munson *et al.*, 2008), and management interventions should thus be aimed at mitigating the afore-mentioned threats. However, Kafue’s seasonal inundation may

hamper the reproductive success of its lions and thus retard the speed of such population recovery (Chapter 6).

Riggio *et al.* (2013) define a lion stronghold as an area that i) has at least 500 individuals, ii) is within a protected area or designated hunting area and iii) has a stable or increasing lion population per IUCN Cat Specialist Group assessments (IUCN, 2006a, 2006b). Subsequently, Riggio *et al.* (2013) classified Kafue as a “potential stronghold” as their population estimate for the park (derived from Becker *et al.*, 2012) was below the threshold and, they note, due to poaching pressure on lion prey, the IUCN classification of Kafue’s lion population as stable may be optimistic. My results support this assertion, but suggest that, with improved law enforcement and regular, appropriate monitoring (Chapter 6), Kafue has the potential to meet the definition of a lion stronghold. In addition, the park forms part of the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA), which will potentially link its lion population with that in the Okavango-Hwange stronghold (Riggio *et al.*, 2013). However, ongoing human encroachment in GMAs south of Kafue threatens this link (Lindsey *et al.*, In press). Furthermore, Macdonald *et al.* (2010) caution that prior to source populations being linked, they need to be secured, a precaution that appears particularly relevant to Kafue in light of my results.

My occupancy model (Chapter 3) indicates where lions are most likely to be found in the dry season in Kafue, and by locally testing the efficiency and effectiveness of lion survey methods I have provided the wildlife authority with the tools to monitor the population trend of the species in the park, and thus assess the success or otherwise of management interventions (Chapter 4, 6). Increased lion abundance will suggest an increase in the lions’ prey base and thus increasing ungulate populations. This will further benefit other large carnivores such as spotted hyaenas, leopards, cheetahs and African wild dogs, though these species may also experience higher levels of mortality from inter-specific competition if lion numbers increase (e.g. Creel & Creel, 1996). Monitoring lion populations in this manner will provide the authority with a more meaningful measure of Kafue’s effectiveness in conserving biodiversity than simply reporting its size. There are, however, many species whose abundance will not affect that of lions, and others that may be negatively impacted by greater lion abundance. Some of these species may be of conservation concern and require specific monitoring.

My study further highlights the importance of evidence-based conservation in making management decisions (Sutherland *et al.*, 2004), particularly in the context of the controversial lion hunting industry. The ban on hunting large felids in Zambia, instituted in January 2013 (<http://www.bbc.co.uk/news/world-africa-20969868>, accessed March 15 2013), arose as a result of the perception that the practice was having a detrimental effect on lion and leopard numbers in the country’s GMAs and NPs. My results suggest, however, that although trophy quotas were

too high, illegal hunting for bushmeat likely has a greater overall limiting effect on lion populations in Kafue than trophy hunting (Chapter 6).

If the wildlife authority is able to reduce levels of illegal hunting for bushmeat then the lion population is predicted to recover to the point where a small but financially lucrative trophy harvest of lions may once again be sustainable. This will provide both the authority and neighbouring communities with much-needed revenue. Until such time, however, trophy hunting would be an additive, rather than compensatory, cause of lion mortality, and the ban/moratorium appears justified (Chapter 6). The ban has also provided Zambia with an opportunity to measure the effects of such an intervention on lion populations, and compare these results with the findings of Davidson *et al.* (2011) in Hwange NP, who found evidence of a population recovery after a three-year moratorium. Trophy hunting advocates regularly cite the economic value of the industry to local communities as an incentive for them to protect wildlife, and its contribution to law enforcement as a deterrent to illegal hunters (Lindsey *et al.*, 2006b). Any increases in intensity or scale of illegal hunting subsequent to the ban will thus be useful in assessing the veracity of these claims, and before and after measures of such illegal activities would thus be of significant value in assessing the merits of the trophy hunting industry's claims.

At a broader scale in Africa, there is a paucity of empirical population data for a number of current lion strongholds, such as Ruaha-Rungwa and Tsavo-Mkomazi, which, based on questionnaire surveys, are collectively estimated to hold over 4,500 lions (Mesochina *et al.*, 2010). However, following similar methodology, Chardonnet (2002) estimated Kafue's population at over 1,000 individuals, significantly higher than our estimate (Chapter 6). This highlights the importance of field surveys to understand local lion population dynamics, and suggests that adapting the approach used in this study to other lion strongholds would improve our knowledge of the conservation status of the species. Although survey methodology will differ, the approach of using occupancy models, surveying populations, investigating spatial ecology and identifying threats is equally applicable to other carnivores as well as other taxa in remote, previously unstudied areas.

The reintroduction of grey wolves to Yellowstone NP in the mid-1990's, and resultant ecological change have confirmed the importance of apex predators to the functioning of ecosystems (e.g. Fortin *et al.*, 2005; Laundré *et al.*, 2001). Africa's ten lion strongholds span a combined area of over 1,100,000 km² (Riggio *et al.*, 2013). The loss of the species from these areas would therefore likely affect the ecosystem functionality of almost 4% of the continent's land area.

Managing Kafue's lion population to the point that it qualifies as the eleventh stronghold for the species, and securing its future should therefore be a primary objective of the Zambian Wildlife

Authority. The results of this study provide the authority with an empirical base from which to design, implement and monitor interventions aimed at achieving this objective. Success in this endeavour will represent a significant and valuable contribution to lion conservation at local, regional and global scales. The task is, however, a daunting one, and, as elucidated by Macdonald *et al.* (2010, p.609):

“The key questions lie beyond biology – can human-lion conflict be mitigated, can incentives and mechanisms be found to ensure community participation, and can the necessary integration be achieved between such constituencies as local communities, rural authorities, private landowners, regional conservation agencies and international donor agencies?”

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LIST OF ACRONYMS

AIC	Akaike's Information Criterion
AIC_c	Akaike's Information Criterion for small sample sizes
CA	Core Area
CI	Confidence Interval
ER	Evidence Ratio
GMA	Game Management Area
HR	Home Range
ISS	Intensive Study Site
MIO	Miombo and Kalahari woodland
MUN	Munga and termitaria woodland
MWU	Mann-Whitney U-Test
NP	National Park
PA	Protected Area
RAI	Relative Abundance Index
SAG	Munga scrub and woodland
TAM	Traditional Asian Medicine
WET	Wetland
WMP	Wilcoxon Matched Pairs Test
ZAWA	The Zambia Wildlife Authority

ANNEXURE A

Table A1. Kernel estimates (km²) of home range (90% isopleths) and core area (50% isopleths) of 15 lions in Kafue National Park, Zambia, 2010-2013. *n* = number of locations (one/day). No range calculated if *n*<60 (Spong 2002). ¹ Two females from one pride collared concurrently. ² Two males from one coalition collared concurrently for 10 months.

Lion	Season and year																	
	Dry 2010			Wet 2010-2011			Dry 2011			Wet 2011-2012			Dry 2012			Wet 2012-2013		
	50%	90%	<i>n</i>	50%	90%	<i>n</i>	50%	90%	<i>n</i>	50%	90%	<i>n</i>	50%	90%	<i>n</i>	50%	90%	<i>n</i>
Females																		
F18	-	-	(40)	27.2	114.6	108	12.5	63.1	70	23.3	122.7	179	18.0	65.0	179	25.7	120.6	174
F21	12.0	65.0	84	37.7	154.7	141	35.8	130.4	151	24.7	148.0	173	24.0	80.9	183	-	-	(52)
F28	32.4	200.4	87	64.4	313.7	178	42.5	293.7	63	56.7	324.8	177	87.2	340.0	182	242.7	931.4	173
F39 ¹	-	-	-	-	-	-	-	-	(47)	37.4	327.1	178	82.4	328.2	184	61.5	539.9	176
F53 ¹	-	-	-	-	-	-	-	-	(38)	53.1	314.0	179	158.9	665.8	181	126.8	618.6	176
F72	-	-	-	-	-	-	-	-	-	-	-	-	133.5	304.6	140	167.2	470.6	177
F77	-	-	-	-	-	-	-	-	-	-	-	-	44.7	274.4	110	69.6	275.6	174
Males																		
M06	-	-	-	-	-	-	-	-	-	-	-	-	173.8	1530.0	62	620.1	2625.7	170
M08	20.9	118.3	65	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
M16	168.3	588.1	90	179.9	708.5	175	92.9	460.8	174	89.2	561.9	182	30.7	240.7	178	30.9	150.4	60
M31	26.8	145.6	61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
M37 ²	-	-	-	-	-	-	-	-	(49)	66.1	427.9	174	98.3	826.7	181	166.2	993.8	171
M43 ²	-	-	-	-	-	-	-	-	-	-	-	-	96.4	379.5	110	104.7	818.5	177
M48	-	-	-	-	-	-	-	-	(42)	183.2	721.8	177	415.5	1283.9	71	-	-	-
M73	-	-	-	-	-	-	-	-	-	-	-	-	64.6	250.1	139	20.1	67.9	173

Table A2. Mean distances from dry season water courses for individual lions in Kafue National Park, and corresponding results of *t*-tests. n: number of locations; m: distance in metres. Random locations are located within the individual's dry season home range.

Lion	2012 Dry Season Random Locations		2012 Dry Season Actual Locations		2012-2013 Wet Season Actual Locations		Random vs Actual		Dry vs Wet	
	n	m	n	m	n	m	t-value	p	t-value	p
	F18	175	1057.6	175	528.3	174	1805.6	-8.56	<0.01	-11.56
F21	173	1138.8	173	610.7	52	1722.5	-7.40	<0.01	-7.28	<0.01
F28	175	4355.5	175	3457.2	173	8420.1	-2.55	0.01	-10.41	<0.01
F39	171	8639.9	171	3502.3	176	4523.2	-6.86	<0.01	-2.10	0.04
F53	175	9718.0	175	6647.7	176	5665.4	-4.97	<0.01	1.64	0.10
F72	134	2247.5	134	1687.0	177	2165.5	-3.24	<0.01	-2.67	0.01
F77	101	3313.2	101	2344.4	174	2549.4	-3.25	<0.01	-0.75	0.45
M06	55	9432.3	55	4527.1	170	8824.5	-4.00	<0.01	-4.94	<0.01
M16	161	2355.0	161	526.6	59	1741.8	-14.33	<0.01	-9.05	<0.01
M37	176	3647.4	176	1991.4	171	2548.0	-6.62	<0.01	-2.15	0.03
M43	106	3091.8	106	1342.5	177	3267.5	-6.82	<0.01	-4.62	<0.01
M73	132	1959.1	132	791.1	173	985.4	-8.60	<0.01	-2.16	0.03

Table A3. Seasonal inundation of lion home ranges in Kafue National Park, Zambia. Dry season data are for the 2012 dry season; wet season data are for the 2012-2013 dry season. * 2011-2012 home ranges used as no data were available for 2012-2013 season.

Lion	Group	Dry Season Home Range					Wet Season Home Range		
		HR Size	Dry Season Inundation		Wet Season Inundation		HR Size	Wet Season Inundation	
		km ²	km ²	%	km ²	%	km ²	km ²	%
F18	Plains	65.0	1.3	2.0	61.2	94.2	120.6	111.4	92.4
F21	Plains	80.9	1.4	1.7	55.8	69.0	148.0*	130.9	88.4
F28	Plains	340.0	1.6	0.5	63.6	18.7	931.4	93.5	10.0
F39	Woodland	328.2	1.7	0.5	2.8	0.9	539.9	2.9	0.5
F53	Woodland	665.8	1.8	0.3	3.2	0.5	618.6	2.8	0.5
F72	Woodland	304.6	1.9	0.6	3.2	1.1	470.6	4.8	1.0
F77	Woodland	274.6	2.5	0.9	11.6	4.2	275.6	6.5	2.3
M06	Plains	1530.0	4.7	0.3	220.7	14.4	2625.7	386.6	14.7
M16	Plains	240.7	2.3	1.0	193.9	80.6	150.4	131.1	87.2
M37	Woodland	826.7	5.2	0.6	19.7	2.4	993.8	35.9	3.6
M43	Woodland	379.5	3.4	0.9	12.6	3.3	818.5	11.6	1.4
M48	Plains	1283.9	2.7	0.2	322.9	25.2	721.8*	310.7	43.0
M73	Woodland	250.1	1.8	0.7	3.1	1.2	67.9	1.3	1.9

Table A4. Overlap of home ranges (90% isopleths) of neighbouring same-sex lions in Kafue National Park, Zambia. * Overlap of core areas (50% isopleths)

Lion pair (lion 1/lion 2)	Season and year	Overlap area (km²)	% lion 1	% lion 2
F18/F21	Dry 2011	22.1	35	17
F18/F21	Dry 2012	9.3	14	12
F18/F28	Dry 2012	6.2	10	2
F39/F77	Dry 2012	28.9	9	11
F53/F77	Dry 2012	42.3	6	16
F18/F21	Wet 2010-11	53.4	47	35
F18/F21	Wet 2011-12	65.8	54	45
F18/F28	Wet 2012-13	16.1	13	2
F28/F39	Wet 2012-13	81.2	9	15
F28/F53	Wet 2012-13	57.2	6	9
F39/F77	Wet 2012-13	41.5	8	15
F39/F72	Wet 2012-13	14.6	3	3
F53/F77	Wet 2012-13	38.9	12	14
F53/F72	Wet 2012-13	49.3	16	11
M16/M08	Dry 2010	87.6	15	74
M16/M31	Dry 2010	103.8	18	71
M06/M16	Dry 2012	186.2	12	77
M06/M37	Dry 2012	216.9	14	26
M06/M43	Dry 2012	60.4	4	16
M16/M48	Dry 2012	145.8	61	11
M16/M48	Wet 2011-12	248.4	44	34
M06/M16	Wet 2012-13	131.7	5	88
M06/M037	Wet 2012-13	498.8	19	50
M06/M043	Wet 2012-13	353.9	14	43
F18/F21*	Wet 2010-11	3.3	12	38
F18/F21*	Wet 2011-12	2.8	12	25
M16/M48*	Wet 2011-12	76.7	86	42
M16/M06*	Wet 2012-13	8.0	26	2

ANNEXURE B



Kafue National Park Water Delineation

Lisanne Petracca

The final products of this analysis were GIS layers of surface water for the wet and dry seasons at Kafue National Park, Zambia. Each layer was derived from multiple Landsat scenes and is at 30-meter resolution. Please see below for more detail on the analysis.

1. I used the USGS Global Visualization Viewer (<http://glovis.usgs.gov/>) to download clear, cloud-free Landsat scenes from the wet season of 2013 and dry season of 2012 in Kafue National Park, Zambia. These are the time periods in which the Kafue Lion Project had its maximum number of collared lions.

The only available images from these dates were from the Landsat 7 satellite, which has a faulty Scan Line Corrector that produces black stripes across each image. I therefore had to select older, stripe-free images from the Landsat 5 satellite to fill the gaps in the Landsat 7 images. Though available imagery was limited, I tried to obtain back-up imagery for dates similar to the dates of the Landsat 7 images.

	Left Side		Right Side	
	Date	Satellite	Date	Satellite
Wet Season 2013	March 22 2013	Landsat 7	March 31 2013	Landsat 7
	Feb 13 2008	Landsat 5	Apr 19 2011	Landsat 5
Dry Season 2012	Oct 13 2012	Landsat 7	Oct 6 2012	Landsat 7
	Oct 19 2011	Landsat 5	Nov 13 2011	Landsat 5
	Nov 17 2010	Landsat 5		

2. The metric I used to derive surface water was the Normalized Difference Water Index (NDWI), derived by McFeeters (1996) and improved upon by Ji et al. (2009). NDWI uses spectral differences between Landsat Bands 2 (green) and 5 (short-wave infrared) to

separate water from soil and vegetation, as water has a distinctively low reflectance of short-wave infrared light. The NDWI equation is as follows:

$$\frac{\text{Band 2} - \text{Band 5}}{\text{Band 2} + \text{Band 5}}$$

3. **Radiometric correction:** I extracted Bands 2 and 5 from each of the 9 images and converted each pixel from digital number (DN) to at-sensor spectral radiance (L_{SAT}), as outlined by Chander et al. (2009):

$$L_{SAT} = \frac{(L_{MAX} - L_{MIN})}{(Q_{CALMAX} - Q_{CALMIN})} * (Q_{CAL} - Q_{CALMIN}) + L_{MIN}$$

LSAT	Spectral Radiance at the sensor's aperture in watts/(meter squared * ster * μm)
QCAL	the quantized calibrated pixel value in DN (i.e. the pixel value)
LMIN	the spectral radiance that is scaled to QCALMIN in watts/(meter squared * ster * μm)
LMAX	the spectral radiance that is scaled to QCALMAX in watts/(meter squared * ster * μm)
QCALMIN	the minimum quantized calibrated pixel value (corresponding to LMIN) in DN
QCALMAX	the maximum quantized calibrated pixel value (corresponding to LMAX) in DN = 255

4. **Atmospheric correction:** I then converted each pixel's at-sensor spectral radiance (L_{SAT}) to at-surface reflectance (P_{surf}), using the following equation from Chander et al. (2009):

$$\rho_{surf} = \frac{\pi * d^2 * (L_{\lambda} - L_{haze})}{ESUN * \cos(\theta)}$$

L_{i,min}	Min non-zero value for each band (of at satellite radiance).
Sun Elevation	Solar elevation from the image header.
ESUN	Table 1 (from Chander 2009).
Day of Year	Table 2
d	Earth-Sun distance, Table 3 (from Chander 2009).
L_{1%}	$L_{1\%} = (0.01 * ESUN_i * \cos\theta) / (p * d^2)$
L_{haze}	$L_{haze,i} = L_{i,min} - L_{i,1\%}$

In order to determine L_{haze, i}

used the dark object subtraction (DOS) method described by Song et al. (2001). The basis of this correction is that a dark body in an image (i.e. a deep lake) should not be scattering energy to the TM sensor, as it is a “perfect” black body and absorbs all energy. Therefore, any radiance for those pixels is due to atmospheric scattering. Since very few objects on the earth’s surface are truly black, the model assumes a 1% minimum reflectance rather than 0%.

Chavez (1996) uses the minimum DN of each band (DN_{i,min}) to determine haze correction values. When using a full Landsat scene, it has been suggested that the darkest DN with at least 1000 pixels is appropriate (Teillet and Fedosejevs 1995; McDonald et al. 1998). Since my bands had already been converted to at-sensor radiance, I used the same rule but applied it to L_{i,min} values rather than DNs.

5. **NDWI:** Following the processing of at-surface reflectance values, I calculated NDWI (see Pg. 1 for equation) for each image. I then subset the NDWI layer to the study area boundaries.

To determine the NDWI threshold for what pixels are classified as water, I used a threshold of 0 as recommended by McFeeters (1996). Water should have positive values, while soil and vegetation should have negative values due to their higher reflectance of short-wave infrared as compared to green light.

6. **Initial NDWI layers:** All “water” pixels from each season were mosaicked within ArcMap to create water layers for the wet and dry seasons in Kafue National Park. I converted the water layers from raster to polygon, and then used the Geometry tool to calculate total area of water in the wet and dry seasons.

	Area (km ²)
Wet season	233.44
Dry season	4.93

I will note that, similar to results by Poley (2013, *unpublished*), the 0.0 NDWI threshold appears to be very good at selecting clear, deep water. It does not appear to select pixels that correspond to turbid, shallow water typical of small streams, or water that contains vegetation. These layers could therefore be considered conservative for Kafue National Park.

7. **Post-classification:** I compared these water layers to .kml files (provided by PI Neil Midlane of the Kafue Lion Project) that approximate various areas of water within Kafue National Park. I determined that the NDWI threshold should be approximately -0.4 to encompass the inundated areas within Kafue that contain vegetation, as a threshold of 0.0 only included clear, deep water. Amended values for inundated area in the wet and dry seasons are below:

	Area (km ²)
Wet season	502.93
Dry season	13.49

This threshold increased water in the wet season by 2.15x and in the dry season by 2.74x. Please see Figure 5.1 in the thesis for the final water layers.

References (Annexure B)

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