Game fencing as a human-wildlife conflict mitigation strategy and its implications for conservation

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Summary

Worldwide, fencing is increasingly being used as a conservation tool to mitigate human-wildlife conflict. However, knowledge of its effectiveness and its impacts on different trophic levels is still very limited. For this dissertation, the effectiveness of two human-wildlife conflict mitigation game fences in Botswana, their impact on predator avoidance behaviour of herbivores and their impact on grass biomass and its key chemical characteristics in formerly overgrazed areas were studied.

A simple albeit effective method was developed enabling stakeholders to identify categories of species that threaten the integrity of fences by digging holes underneath them. Further, the pressure a fence experiences by hole-digging species and the time frame of necessary maintenance actions can be determined, depending on the species present in a particular area. African lions proved to be very opportunistic and utilized holes of even small species such as honey badgers, in order to leave protected areas. Therefore, it is recommended that the fence line studied in Khutse/Central Kalahari Game Reserve should be maintained on a daily basis.

The Makgadikgadi Pans National Park borders one of Botswana’s highest human-wildlife conflict areas. Using a spoor survey method, the effectiveness of the Makgadikgadi game fence in separating humans and wildlife was studied. During the dry season, when there was no surface water available in the Park and the fence prevented access to long stretches of the Boteti River along the National Park boundary, the fence line was under enormous pressure by wildlife, trying to gain access to the river. Livestock moved into the National Park in high numbers during the rainy season, most probably for grazing. Without the implementation of appropriate maintenance, especially during the dry season, the Makgadikgadi game fence cannot be effective in alleviating human-wildlife conflict.

A cost-effective, repeatable and non-invasive spoor method was used to investigate the effects of game fences on predator-prey relationships. A new fence restricted daily herbivore movement, which led to increased localized herbivore densities along the fence, which further attracted lions. Therefore, herbivores were exposed to a potentially increased hunting pressure along the fence. Spatial lion avoidance behaviour by herbivores could neither be detected along a new nor a well-established fence line. Hence, the installation of fences has the potential to have a long-term negative impact on herbivore populations and needs careful consideration especially in small protected areas with small herbivore populations or areas hosting migratory species.

Lastly, the impacts of fencing on grass biomass and its key chemical characteristics were studied in a formerly overgrazed area in Khutse Game Reserve. High levels of grazing by livestock led to higher protein contents, but lower fibre and hemicellulose contents and lower absolute nutrient availability in grasses per unit area. Heavy grazing further had a negative impact on grass biomass, whereas the exclusion of livestock by fencing resulted in a rapid increase of grass biomass, higher fibre and hemicellulose contents and higher absolute nutrient availability after one rainy season. However, in formerly heavily grazed areas there was a high abundance of unpalatable plant species one year after fencing. Therefore, fencing off an overgrazed area had a positive effect on grass biomass, whereas there was no short-term effect on the species composition in formerly overgrazed sites within one year.

The decision whether or not to use fencing as a conservation tool is dependent on many different factors and has to be decided on a case-by-case basis. This dissertation highlights the need to consider whole ecosystems when fencing is deemed the right choice. Appropriate design, alignment and maintenance are the key factors, which will determine whether fencing will be a success or disaster for conservation.

Zusammenfassung

Wildtierzäune werden im weltweiten Artenschutz immer häufiger zur Lösung und Vermeidung von Konflikten zwischen Menschen und Wildtieren eingesetzt. Ihre Effektivität und ihre Auswirkungen auf verschiedene trophische Ebenen sind allerdings nur wenig erforscht. Für die vorliegende Dissertation wurde die Effektivität zweier Wildtierzäune in der Konfliktvermeidung zwischen Menschen und Wildtieren in Botswana, die Auswirkungen dieser Zäune auf das Raubtiervermeidungsverhalten von Herbivoren und die Auswirkungen auf Grasbiomasse und -inhaltsstoffe in ehemals überweideten Gebieten untersucht.

Es wurde eine einfache und dennoch effektive Methode entwickelt, die es Verantwortlichen ermöglicht, Kategorien von Tierarten zu bestimmen, die die Integrität von Zäunen durch das Graben von Löchern unter ihnen hindurch gefährden. Desweiteren kann der Druck, den ein Zaun durch löchergrabende Tiere erfährt, ermittelt und, je nach vorhandenen Tierarten in einem Gebiet, der Zeitrahmen für notwendige Instandhaltungsmaßnahmen festgelegt werden. Da Afrikanische Löwen extrem opportunistisch sind und selbst kleine Löcher unter dem Zaun von der Größe von Honigdachsen nutzten um das Schutzgebiet zu verlassen sollte der untersuchte Wildtierzaun im Khutse/Zentralkalahari Wildreservat täglich instandgehalten werden.

Der Makgadikgadi Pans Nationalpark hat eines der höchsten Konfliktpotenziale zwischen Menschen und Wildtieren in Botswana. Mit einer Spurenzählungsmethode wurde die Effektivität des Wildtierzaunes in der räumliche Trennung von Menschen und Wildtieren untersucht. In der Trockenzeit, wenn im Nationalpark kein Oberflächenwasser verfügbar ist und der Zaun den Zugang zum Fluss Boteti an der Grenze des Parks weitgehend blockiert, stand dieser unter einem sehr großen Druck von Wildtieren, die versuchten an

den Fluss zu gelangen. Während der Regenzeit passierten sehr viele Kühe den Zaun in die entgegengesetzte Richtung, wahrscheinlich um im Nationalpark bessere Weidegebiete zu finden. Der Makgadikgadi Wildtierzaun kann ohne die Einführung von angemessenen Instandhaltungsmaßnahmen den Konflikt zwischen Menschen und Wildtieren vorallem in der Trockenzeit nicht effektiv verhindern.

Eine kosteneffiziente, wiederholbare und nichtinvasive Spurenmethode wurde genutzt, um die Auswirkungen von Wildtierzäunen auf das Verhältnis von Raubtieren und ihrer Beute zu untersuchen. Ein neuer Wildtierzaun blockierte tägliche Wanderbewegungen von Herbivoren, was zu einer lokal erhöhten Herbivorendichte am Zaun führte, welche wiederum Löwen anzog. Folglich waren die Herbivoren entlang des Zaunes einem potenziell höheren Jagddruck durch Löwen ausgesetzt. Weder an einem neuen noch an einem etablierten Wildtierzaun konnte räumliches Löwenvermeidungsverhalten von Herbivoren festgestellt werden. Die Errichtung von Zäunen hat folglich das Potenzial für langfristige negative Auswirkungen auf Herbivorenpopulationen und muss daher vorsichtig abgewägt werden, vorallem wenn es sich um kleine Schutzgebiete oder Gebiete mit migrierenden Tierarten handelt.

Zuletzt wurde die Auswirkung von Wildtierzäunen auf die Grasbiomasse und die wichtigsten chemischen Grascharakteristika in einem ehemals von Kühen überweideten Gebiet im Khutse Wildreservat untersucht. Hoher Weidedruck durch Nutztiere führte zu einem höheren Proteingehalt, einem niedrigeren Rohfaser- und Hemizellulosegehalt und einer geringeren Gesamtnährstoffverfügbarkeit in Gräsern pro Fläche. Er hatte zudem negative Auswirkungen auf die Grasbiomasse, wohingegen der Ausschluss von Kühen durch Zäune nach einer Regenzeit zu einem schnellen Anstieg der Grasbiomasse, einem höheren Rohfaser- und Hemizellulosegehalt und einer erhöhten Gesamtnährstoffverfügbarkeit führte. In dem ehemals stark beweideten Gebiet war die

Zusammenfassung

Dichte an von Kühen gemiedenen Pflanzenarten auch ein Jahr nach der Errichtung des Zaunes jedoch unverändert hoch. Die Errichtung des Zaunes in einem überweideten Gebiet hatte folglich positive Auswirkungen auf die Grasbiomasse, wohingegen im ersten Jahr nach der Errichtung des Zaunes keine Auswirkung auf die Artenzusammensetzung dokumentiert wurde.

Ob Wildtierzäune im Artenschutz genutzt werden sollten hängt von vielen verschiedenen Faktoren ab und muss von Fall zu Fall entschieden werden. Die vorliegende Dissertation verdeutlicht, dass gesamte Ökosysteme berücksichtigt werden müssen, wenn der Einsatz von Zäunen beschlosssen wird. Der Erfolg oder Misserfolg eines Zaunes hängt hauptsächlich von dem verwendeten Design, dem geografischen Verlauf und der angemessene Instandhaltung des Zaunes ab.

Introduction

Global biodiversity is decreasing at an alarming rate, a process which has shown no signs of slowing down in the past years (Butchart *et al.*, 2010). Human activities are generally seen as a major driver for the extinction of many mammal species (Ceballos & Ehrlich, 2002; Dirzo & Raven, 2003; Cardillo *et al.*, 2005), with larger species often more threatened than smaller ones. The African lion (*Panthera leo*) is one of these mammals and its population is declining rapidly. From an estimated number of 200,000 African lions in 1975 (Myers, 1975), less than 100,000 remained by the early 1990s (Nowell & Jackson, 1996) and current population estimates put the continent-wide population at circa 33,000 (Riggio *et al*., 2012). One major cause for this decline is indiscriminate and retaliatory killing as a result of conflict between lions and humans (Bauer, 2008). A study on lethal control of stock-raiding lions in the Laikipia district of Kenya showed that 17 of 18 lions that were tagged for monitoring purposes were killed in retaliation for livestock predation (Woodroffe & Frank, 2005).

In many African countries, livestock and crop farming are the major income sources in rural communities (Powell & Williams, 1995) and substantial numbers of cattle and other livestock are roaming along the borders of National Parks and sometimes even within these protected areas. Where wildlife and humans live in close proximity to each other, conflicts are often inevitable (review: Woodroffe, Thirgood & Rabinowitz, 2005). Livestock predation by lions or other conflict species such as crop-raiding African elephants (*Loxodonta africana*) are common occurrences due to increasing habitat loss as a result of human activities (Bauer, 2008; Blanc, 2008). Many different solutions to promote coexistence of wildlife and humans have been proposed (review: Woodroffe, Thirgood & Rabinowitz, 2005) such as different kinds of compensation and insurance schemes for livestock losses due to carnivores (Dickman, Macdonald & Macdonald, 2011), or chilli and beehive fences as deterrents for elephants (Sitati & Walpole, 2006; King, Douglas-Hamilton & Vollrath, 2011), to name but a few.

Fencing has been widely used as a conservation tool to separate humans and wildlife and promote coexistence (reviews: Breitenmoser *et al.*, 2005; Hayward & Kerley, 2009; Ferguson & Hanks, 2010; Somers & Hayward, 2012). There are many different fence designs for different purposes, starting from natural or living fences, made from plants, to electrified double game fences. The type used varies according to its objective and the available budget and materials (Breitenmoser *et al.*, 2005). Fencing has recently even been proposed as the conservation tool of choice to conserve large carnivores, especially African lions. Packer *et al*. (2013a) suggested that fencing would allow a lion population to be maintained much closer to its estimated carrying capacity. Fencing is further said to reduce maintenance costs of lion populations substantially and almost half the unfenced lion populations are even predicted to become extinct within the next 20-40 years due to edge effects in protected areas and human-wildlife conflict, which could be prevented through fencing (Packer *et al*., 2013a). This proposal caused a storm of protest and Creel *et al.* (2013) pointed out that most fenced lion populations are small and often maintained above carrying capacity, which is not viable for most ecosystems. Focus must lie on population sizes and not densities, since ‘a low-density population of 2000 individuals has more conservation value than a high-density population of 20’ (Creel *et al.*, 2013). They argued further that if management cost-effectiveness is being calculated as the number of lions conserved per dollar and not as lions/km^2 and management expenditure/km^2, unfenced protected areas conserve many more lions than fenced ones. Subsequently, Packer *et al.* (2013b) reanalysed their data concerning management costs per conserved lion and showed that fenced reserves still conserved more lions per dollar than unfenced ones. In order to take into account the contribution of apex predators to ecosystem processes they further argued that population growth rate and population size have to be calculated in relation to carrying capacity (population status) and that both factors are higher in fenced reserves. Woodroffe, Hedges & Durant (2014) recognized the benefits of fencing such as the mitigation of human-wildlife conflict and disease transmission between wildlife and livestock. On the other hand, they pointed out that fencing might cause the extinction of small isolated populations and a decrease in diversity of predators or large bodied species, which would lead to an ecological meltdown (Terborgh, 1988; Terborgh *et al.*, 2001). In countries where wildlife habitats remain extensive and in times of increased climate change, fences can constrain large scale movements in search of food and water and therefore reduce the carrying capacity of these environments. Therefore, they argue fences should only be 'an action of last resort' (Woodroffe, Hedges & Durant, 2014).

In general, fencing should be treated as a high impact measure and pros and cons have to be considered very carefully before implementation (Hayward & Kerley, 2009). Consequences for wildlife can be severe, such as animals getting trapped or entangled, the creation of genetically isolated populations and the use of fence materials to manufacture snares for poaching (Hayward & Kerley, 2009; Gadd, 2012), to name but a few. In order to avoid cutting off migration routes fencing should further not be considered in areas, where migratory species are present (Boone & Hobbs, 2004). Megaherbivores such as African elephants are likely to cause severe damage to fences, and their presence usually involves a considerable amount of maintenance costs (Slotow, 2012). Stakeholders must further take into account that the major expenditures of fencing only arise post-installation, due to the need of extensive genetic management of fenced animal populations and fence maintenance, which can be very challenging financially and logistically (Stein, 1999; Trinkel *et al*., 2008; Frankham, 2009; Trinkel *et al.*, 2010). However, fences can play a prominent role in conservation by mitigating human-wildlife conflict (Angst *et al.*, 2002), reducing edge effects for carnivore populations (Packer *et al.*, 2013a) and they are furthermore successfully being used to "rewild" farm land and to reintroduce wildlife (Hunter *et al.*, 2007; Slotow & Hunter, 2009; Hayward, 2012).

In southern Africa and especially Botswana, fences have a controversial history. In order to fulfill the import conditions of the European Union's beef market and therefore support the country's cattle industry, Botswana has constructed more than 5,000 km of veterinary cordon fences to protect cattle from foot-and-mouth disease (Gadd, 2012), for which buffalo are known to be a host (e.g. Hedger, 1972; Owen & Owen, 1980; Albertson, 1998; Keene-Young, 1999). During the droughts of the 1980s, Botswana's blue wildebeest (*Connochaetes taurinus)* population suffered massive die-offs due to the alignment of the Kuke veterinary cordon fence, which cuts off a natural migration route from the Central Kalahari Game Reserve to essential water resources in the Okavango Delta. Further, several thousand red hartebeest (*Alcelaphus buselaphus*) were reported to have died against the Ghanzi fences west of Central Kalahari Game Reserve during the same drought period (Owen & Owen, 1980; Parry, 1987; Williamson & Mbano, 1988; Boone & Hobbs, 2004; Mbaiwa & Mbaiwa, 2006). Many more reports on carcasses along "deadly" fences can be found in literature, indicating the accumulation of wildlife along fences that cut through migration or daily movement routes (Albertson, 1998; Keene-Young, 1999; Gupta, 2005; reviews: Breitenmoser *et al*., 2005; Mbaiwa & Mbaiwa, 2006). This sudden massive decline in the natural prey base of lions has potentially fuelled the human-lion conflict situation in the surrounding farming areas, as lions have been shown to switch to livestock when natural prey densities decrease (Hemson, 2003). In addition to Botswana's veterinary cordon fences, there are three electrified double game fences in the country. These were installed to stop human-wildlife conflict along the borders of Kgalagadi

Transfrontier National Park (erected in 1995), Makgadikgadi Pans National Park (erected in 2004) and Khutse Game Reserve/Central Kalahari Game Reserve (erected in 2009). This study focusses on the fences in Makgadikgadi Pans National Park and Khutse Game Reserve/Central Kalahari Game Reserve.

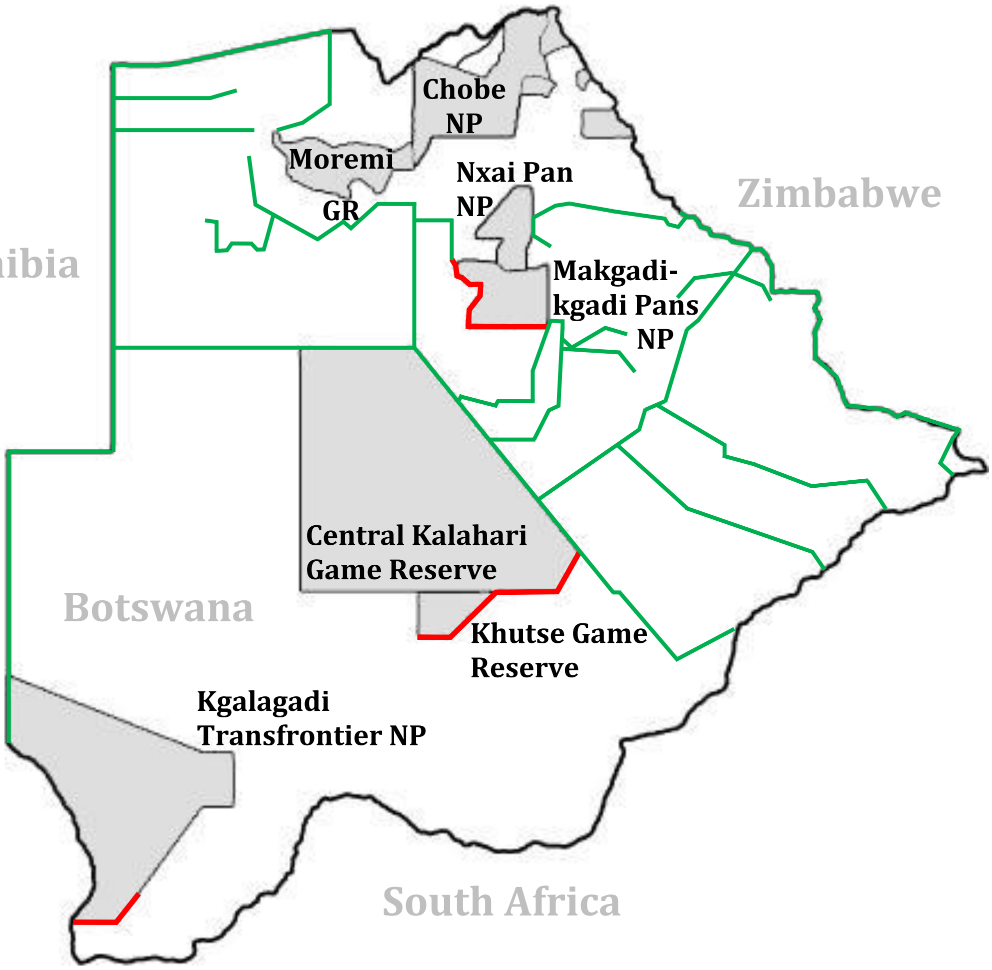

Figure 0.1 Schematic map of Botswana with National Parks (NP, grey) and Game Reserves (GR, grey), game fences (red) and veterinary fences (green).

The Makgadikgadi Pans National Park game fence

In 2004, the Makgadikgadi game fence was built along the western and southern border of the Makgadikgadi Pans National Park in north-eastern Botswana (Figure 0.1) to simultaneously exclude wildlife from farmland and create a new foot-and-mouth disease free "green zone" for the beef export to the European Union. At the western Park boundary, the Boteti River served as a natural barrier between wildlife and livestock until it dried up in 1991 giving livestock access to the National Park. Since then livestock encroached as far as 20 km into the National Park and conflict with wildlife over grazing and water was rampant. In turn, wild animals such as elephants, lions and other predators roamed outside the Park's area, causing damage to fields and livestock (Department of Environmental Affairs and Centre for Applied Research Services, 2010). The Boteti wildlife fence (electrified double game fence) was an attempt to address issues of problem animals like lions and elephants, livestock encroachment into the National Park and foot-and-mouth disease control. It was agreed between the Government and local communities that the fence alignment would provide a "give and take" situation with the fence zig-zaging the dry Boteti riverbed and hence, allowing livestock as well as wildlife access to the remaining water pools. During construction of the fence this plan was altered and for over 110 km it now runs mostly on the eastern side of the Boteti River giving wildlife only very limited access to water (Gupta, 2005). Only three months after installation of the fence, several breaks in the fence and holes underneath it were recorded, which were used for fence line transgressions by elephants or lions respectively (Reed & Sautereau, 2005). Additionally, 115 animal mortalities (88 Burchell's zebra, 18 blue wildebeest, 5 greater kudu, 1 red hartebeest, 1 impala, 1 black-backed jackal, 1 leopard tortoise) were recorded within one month after completion of the fence. Farmers reported a decrease of livestock losses to lions on the one hand, but complained about a loss of grazing and water on the other (Reed & Sautereau, 2005).

The feeding behaviour of lions along the Makgadikgadi fence is highly dependent on the migratory zebra and wildebeest in the area. During the dry season, when these species are abundant along the Boteti River lions primarily feed on migratory natural prey, whereas in the rainy season they mostly feed on livestock (Hemson, 2003). Furthermore, when crops approach harvest maturity during the rainy season conflicts between elephants and humans can arise over potential crop-raiding behaviour. Therefore, human-wildlife conflict levels are highest during this time of the year.

The Khutse Game Reserve and Central Kalahari Game Reserve game fence

The area east of Khutse Game Reserve and south of Central Kalahari Game Reserve in Botswana's South has experienced severe human-carnivore conflict, with farmers loosing up to 20 % of their livestock to predators, especially lions and leopards, each year. In contrast to leopards, livestock predation by lions was mainly focused along the borders of the protected areas (Schiess-Meier *et al*., 2007). In order to reduce livestock predation by excluding predators from human dominated farming areas, the Khutse/Central Kalahari electrified double game fence was installed in 2009 along the southern and eastern border cutline of Khutse Game Reserve and the south-eastern border of Central Kalahari Game Reserve, connecting with the Makalamabedi veterinary fence (Figure 0.1).

Detailed knowledge on the different impacts of fences is still very limited, even though more and more research is being conducted on the topic of fencing (Ferguson & Hanks, 2010; Somers & Hayward, 2012). With this dissertation I am contributing to the growing body of knowledge on the effects and impacts of fencing and will investigate the impacts of fencing on grass biomass and chemistry and on predator avoidance behaviour of large herbivores. Furthermore, I will determine the effectiveness of fencing in separating humans and wildlife and have a close look at the challenges that hole digging animal species pose to the integrity of fences. Using the Khutse/Central Kalahari and the Makgadikgadi game fences as an example the following topics will be investigated:

Permeability of fences

Constructing 100 % exclusion fences intended to completely exclude a certain species from an area is very costly and therefore non-permeability for “traditional conflict species”, such as elephants or lions, is rarely achieved (Ferguson & Hanks, 2010; Somers & Hayward, 2012). The effectiveness of fencing is highly dependent on the fence design, maintenance, ecological aspects of the surrounding habitat (e.g. access to water, soil structure, vegetation cover) and the abundance of wildlife in the area that is likely to damage the structural integrity of a fence. Poor fence maintenance along the borders of protected areas often directly results in an increased permeability of fences and therefore intensifies human-wildlife conflict and negative attitudes towards wildlife in the adjacent farming areas (Funston, 2001; Gupta, 2005; Anthony, 2007; Chaminuka, 2010). However, the degree of maintenance on a certain fence is highly dependent on the length of fencing, the type of damage to the fence, the objective of the fence, the costs of incursion, the costs of management and the total management budget. Different animal species can overcome an obstacle such as a fence in many different ways. They can break entire fence sections down (Graham & Ochieng, 2010; Grant, 2010; Ferguson, Adam & Jori, 2012), jump over it (Van Rooyen, Du Toit & Van Rooyen, 2010), climb certain fence designs (Bonnington *et al.*, 2010; Van Rooyen, Du Toit & Van Rooyen, 2010; Ferguson, Adam & Jori, 2012) or undermine the structural integrity of fences (Dale, 1982; Van Rooyen, Du Toit & Van Rooyen, 2010). Defining the major causes of damage to a fence is vital in order to implement appropriate fence maintenance actions.

Hole digging species are often nocturnal and special skills are required to identify the species by tracks. Chapter One aims to bring light into several fence management issues. Firstly, a reliable manual was developed to identify and categorize hole digging species by the size and shape of holes underneath fences in deep sand habitats such as Khutse Game

Reserve/Central Kalahari Game Reserve and Makgadikgadi Pans National Park in Botswana. Furthermore, with the example of the fence line of Khutse Game Reserve/Central Kalahari Game Reserve, a method is presented to determine the pressure of hole digging a fence experiences by certain species and to give advice on how frequent maintenance actions are required to prevent large predators from transgressing this specific fence line. This approach can be applied to other fences in different habitats in order to plan appropriate management actions in these areas.

The following questions will be answered:

1. How can the pressure a fence experiences by different hole digging species be determined?
2. How frequently are maintenance actions required to prevent large predators from transgressing the Khutse Game Reserve/Central Kalahari Game Reserve fence line?

Design, maintenance and alignment vs. effectiveness of fencing

Game fences, which are not maintained appropriately, can fuel the conflict situation due to easy access for wildlife to human-dominated land and for humans and their livestock to protected areas, in order to prey on livestock or raid crop fields and gain access to better grazing pastures respectively. Furthermore, the design of fences as well as ecological factors such as access to water, vegetation cover or soil structure (rock, deep sand, moving dunes etc.) need to be taken into consideration for the alignment of a game fence, in order to avoid an exclusion fence to be permeable to its target species. Using a method similar to the "Fence Incident Surveillance System" (Ferguson, Adam & Jori, 2012), the permeability and hence the effectiveness of the Makgadikgadi Pans National Park game fence in central Botswana was analyzed. Chapter Two investigates the effectiveness of this particular game fence in separating agropastoralists and potentially stock- and crop-raiding lions and elephants respectively. Furthermore, the importance of fence design, maintenance and alignment will be highlighted and data on seasonal and regional hot spots of fence line transgressions will be provided.

Following questions will be answered:

1. How effective is the Makgadikgadi Pans National Park game fence in excluding elephants and lions from human-dominated area and cattle from the National Park?
2. What is the role of fence maintenance and alignment?
3. Are there seasonal and regional hotspots of fence line transgressions at the Makgadikgadi fence?

Fences as traps and their impact on predator avoidance behaviour by herbivores

Herbivores have been reported to aggregate along game fences and predators have been seen to utilize fences to chase their prey into them (Adendorff & Rennie, 1984; Goodwin, 1985 cited in Hoare, 1992; Albertson, 1998; Van Dyk & Slotow, 2003; Ferguson & Hanks, 2010). Therefore, fences seem to offer both high prey biomass and high prey catchability, which represents preferred hunting conditions for African lions (Hopcraft, Sinclair & Packer, 2005; Nilsen & Linnell, 2006; Hayward *et al.*, 2008; Loveridge *et al*., 2009). Chapter Three investigates the effect of the new Khutse Game Reserve/Central Kalahari Game Reserve game fence and the well-established Makgadikgadi Pans National Park game fence on predator-prey relationships. It determines whether lion prey species get trapped along a newly built game fence, if lions are attracted to this potentially increased prey biomass and whether or not prey species adapt to the increased predation risk and therefore avoid lions spatially, as they do in an open landscape without artificial boundaries (Valeix *et al.*, 2009 a & b). This chapter aims to provide information on how fences can potentially impact herbivore populations.

The following questions will be answered:

1. Do lion prey species get trapped along a newly built game fence?

2. If prey species get trapped: Are lions attracted to this increased prey base?

3. Do lion prey species show spatial predator avoidance along a new compared to a seven-year-old game fence?

Fencing as a tool against overgrazing and bush encroachment

Historically, African grazing systems are characterized by the seasonal movements of migratory wild herbivores. However, due to habitat conversions from wildlife dominated to agricultural areas, cattle have replaced wildlife in many places. Large herbivores have an enormous influence on ecosystem processes and their functionality through direct impacts on plants such as feeding damage or alterations of plant communities through selective feeding behaviour (e.g. Milchunas & Lauenroth, 1993). The combination of grazing and browsing herbivore species (Albon *et al*., 2007; Allred *et al.*, 2012), the timing of grazing (Bullock *et al.*, 2001) and the grazing history (Cingolani *et al*., 2005; Tessema *et al.*, 2011) are important factors to avoid overgrazing or an overabundance of a few specific plant species. Responses to feeding pressure vary from the production of feeding deterrents to an increase in quality (e.g. Skarpe, 1991; Bergstroem, 1992; Bryant, Reichardt & Clausen, 1992; Leriche *et al.*, 2003; Stolter *et al.*, 2005; Fornara & du Toit, 2007; Karban & Baldwin, 2007; Stolter, 2008). The increased grazing pressure due to the replacement of migratory wildlife by cattle in the southern Kalahari (Shugart *et al.*, 2004) can potentially lead to high losses of green leaf biomass, annual net primary production and grass coverage (Perkins, 1996; Verlinden *et al*., 1998; Boone, 2005). These processes support the process of bush encroachment (Roques, O’Connor & Watkinson, 2001; Moleele *et al.*, 2002; Boone, 2005; Joubert, Rothauge & Smit, 2008), which leads to the reduction of grasslands, the invasion of thorn shrubs and thus to reduced carrying capacity for livestock and desertification (Schlesinger *et al.*, 1990). Chapter Four investigates the impact of the new Khutse Game Reserve/Central Kalahari Game Reserve game fence in Botswana on the biomass of grass vegetation and key chemical characteristics by excluding livestock from an area that was formerly overgrazed by cattle. Furthermore, the chapter describes changes under different grazing regimes over time and determines the necessary timespan needed for an area to recover from overgrazing.

The following questions will be answered:

1. How does standing biomass of grass vegetation and key chemical characteristics differ in areas of low and high grazing pressure?
2. If there were differences: How much time does pasture in heavily grazed areas need to recover from overgrazing effects to approach the properties of pasture under low grazing pressure?

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Chapter One

Undermining game fences: Who is digging holes in Kalahari sands?

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Abstract

The effectiveness of game fencing as a tool to promote coexistence between humans and wildlife is highly dependent on the maintenance of fences. It is vital to identify animal species, which dig holes under fences, and their digging behaviour to maintain game fences appropriately. We provide data on some of southern Africa's major hole-digging animal species for a simple albeit effective method enabling stakeholders to categorize species that are digging holes underneath game fences in deep sand habitats by species-specific knowledge on sizes and shapes of holes. Using Botswana's Khutse Game Reserve/Central Kalahari Game Reserve fence as an example, we highlight the temporal aspect in the process of hole digging and enlargement. We present a method to determine the pressure a fence experiences by a number of hole-digging species. Furthermore, we provide data on the time frame of necessary maintenance actions, required to prevent large predators from transgressing this specific fence line. We were especially interested in the effectiveness of fences in excluding African lions from human dominated areas. The predators proved to be very difficult to fence in and extremely opportunistic. They mostly utilized holes that were initially excavated by other, even very small species.

Keywords fencing, hole digging, maintenance

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Chapter One

Introduction

Fencing has been widely used as a conservation tool to separate humans and wildlife to promote coexistence (Hayward & Kerley, 2009; Ferguson & Hanks, 2010; Somers & Hayward, 2012). Its effectiveness is highly dependent on the fence design, maintenance, ecological aspects of the surrounding habitat (e.g. soil structure, vegetation cover) and the abundance of wildlife in the area that is likely to damage the fence. To gain a broader understanding on the effects of wildlife-caused damage, it is vital to have a detailed look at the fences themselves. Particular focus should be on damage that will counteract the effectiveness of fences and transgression frequencies of different animal species. Bonnington *et al.* (2010), Ferguson, Adam & Jori (2012) and K. M. Kesch, D. T. Bauer & A. J. Loveridge (in prep.) developed methods to monitor the permeability of fences to wildlife enabling detailed studies of fences themselves. Funston (2001) pointed out significant differences between South Africa/Namibia and Botswana concerning the financial and temporal investment in the maintenance of the Kgalagadi Transfrontier National Park fence and the resulting difference in the permeability of the fence and therefore livestock predation in the areas surrounding the park. Poor fence maintenance and thus the increased conflict with wildlife are often the cause for negative attitudes towards protected areas by neighbouring communities (Gupta, 2005; Anthony, 2007; Chaminuka, 2010). However, the degree of maintenance efforts on a certain fence is highly dependent on the length of fencing, the type of damage to the fence, the objective of the fence, the costs of incursion, the costs of management and the total management budget.

Fences are built to withstand pressure by a variety of animal species. Some species, such as elephants, have the ability to break down entire sections (Graham & Ochieng, 2010; Grant, 2010; Ferguson, Adam & Jori, 2012) or are known to be exceptional jumpers (e.g. kudus)

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and can clear fences of remarkable height (Van Rooyen, Du Toit & Van Rooyen, 2010). Primates and a number of carnivore species are able to climb certain fence designs and are generally very difficult to exclude entirely from restricted areas (Bonnington *et al*., 2010; Van Rooyen, Du Toit & Van Rooyen, 2010; Ferguson, Adam & Jori, 2012). Furthermore, there are species that are known to undermine the structural integrity of fences such as hyaenas (Dale, 1982; Van Rooyen, Du Toit & Van Rooyen, 2010). To maintain a game fence appropriately, the knowledge of which animal species are causing damage to a fence in a certain area is vital. However, when it comes to smaller hole-digging animals, special skills are required to identify the species and implement suitable damage prevention actions. As these species are often cryptic and nocturnal, their occurrence can best be determined by the presence of tracks.

This study aims to bring light into several fence management issues. Firstly, we developed a reliable manual in cooperation with experienced San trackers, who are well known for their outstanding tracking abilities (Stander *et al.*, 1997). The manual helps to identify and categorize hole-digging species by the size and shape of holes underneath fences in deep sand habitats. Further, with the example of the fence line of Khutse Game Reserve/Central Kalahari Game Reserve in southern Botswana, this study presents a method to determine the pressure of hole digging a fence experiences by certain species and gives advice on how frequent maintenance actions are required to prevent large predators from transgressing this specific fence line.

Methods

Study sites

The study was carried out along two game fences in Khutse Game Reserve (KGR)/south-eastern Central Kalahari Game Reserve (CKGR) and Makgadikgadi Pans National Park (MPNP), Botswana. The country is characterized by a cold dry season from April to September and a hot rainy season from October to March.

Located between 20 – 21 °S and 24 – 26 °E (Thomas & Shaw, 1991), the MPNP is 4,900 km² in size. The annual rainfall averages 450 mm (Meynell & Parry, 2002), and annual temperatures range between a minimum of 6.9 – 19.9 °C and a maximum of 25.3 – 35.2 °C (Alexander *et al.*, 2002). The area west of the Park is one of the highest human–wildlife conflict areas in Botswana (Ecological Support Services, 2002). In 2004, an electrified double game fence (2.7 m wire netting fence with the lowest of four electrified wires 10 cm off the ground; 1.5 m wire netting cattle fence) was installed, crisscrossing the Boteti river bed, which forms the western boundary of the park.

The KGR (2,600 km^2) is situated between 23 – 24 °S and 24 – 25 °E (Thomas & Shaw, 1991) in southern Botswana and borders the CKGR (52,000 km^2) to the north. The average annual rainfall is 300 mm (de Vries, Selaolo & Beekman, 2000), and average monthly temperatures range between 8.5 and 35.5 °C (Thomas & Shaw, 1991). In October 2009, an electrified double game fence (same design as in MPNP) was completed to stop livestock predation by African lions (*Panthera leo*, Linnaeus) in the area. The fence alignment follows the southern and eastern border of KGR and around the south-eastern corner of CKGR, resulting in a total length of about 300 km.

Potential hole-digging species (>5 kg) along both fences include lion, brown hyaena (*Hyaena brunnea*, Thunberg), spotted hyaena (*Crocuta crocuta*, Erxleben), cheetah

(*Acinonyx jubatus*, Schreber), leopard (*Panthera pardus*, Linnaeus), caracal (*Caracal caracal*, Schreber), serval (*Leptailurus serval*, Schreber), bat-eared fox (*Otocyon megalotis*, Desmarest), black-backed jackal (*Canis mesomelas*, Schreber), wild dog (*Lycaon pictus*, Temminck), warthog (*Phacochoerus africanus*, Gmelin), aardvark (*Orycteropus afer*, Pallas), honey badger (*Mellivora capensis*, Schreber) and porcupine (*Hystrix africaeaustralis*, Peters).

Hole count survey and hole sizes by species

With the help of experienced San trackers, data were collected on a stretch of 120 km fence line in KGR/CKGR (October 2009 - July 2010) and 95 km fence line in MPNP (November 2010 - September 2011). The San people are well known for their outstanding tracking abilities (Stander *et al.*, 1997). The trackers participating in this study spent most of their lives in the CKGR as hunters and gatherers, following an ancient tradition of tracking and spoor (tracks/signs) reading. Further, they had extensive tracking experience in various research projects, and their skills were thoroughly tested (D. T. Bauer, M. Schiess-Meier, D. R. Mills and M. Gusset, in prep.; M. Schiess-Meier, unpublished data).

The fence line was driven with an average speed of 10 - 15 km h^{-1} with trackers sitting on the roof and on the bonnet of a 4x4 vehicle, scanning for tracks on the road ahead and for holes underneath the fence. Data were collected in the early morning hours, when the road and soil surface at the fence were still undisturbed by vehicles, rain or wind. All holes underneath the fence, of which the species that initially dug or enlarged the hole in order to transgress the fence line could be reliably determined by tracks (spoor, fur, scratch marks of claws or quills), were numbered. Furthermore, GPS coordinates and measurements of holes (depth, width) were also recorded. Depth was defined as the distance from the lowest horizontal wire of the fence to the deepest point of the hole. Width was described by the distance from one edge of the hole to the other edge, on soil surface level (Figure 1.1).

The cross section of the hole between its deepest point and the lowest fence wire was defined as hole size (HS; in cm^2). Hole sizes were calculated using the formula for half a circle's surface area: HS = $1/2(p*r^2)$. Every hole's radius r is given by the mean between the depth and half the width of each hole (Figure 1.1). Performing a Mann–Whitney U test (two-tailed), we tested for differences between species, and the holes were grouped into different hole size categories. The same test was performed for depths and widths of all holes and compared between species. To further distinguish between holes of different species, we had a detailed look at the overall shapes of holes, concentrating on the following criteria: slope, angle to fence, edges of the hole at the deepest point.

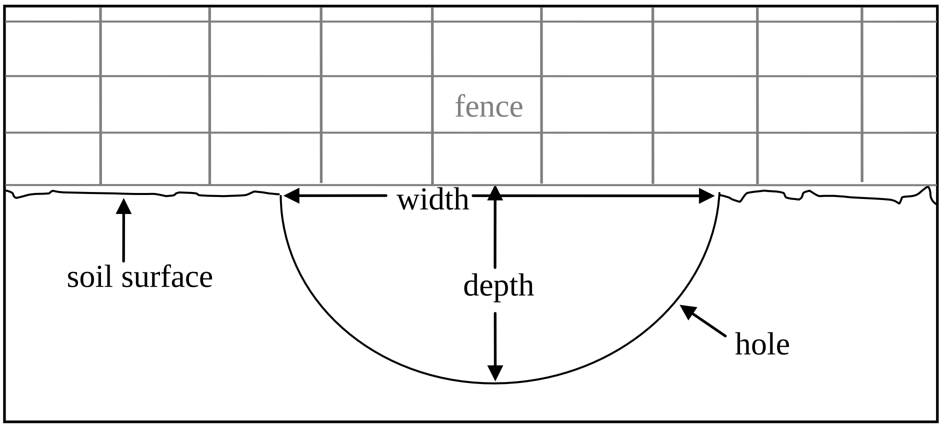

Figure 1.1 Schematic diagram of a hole under the fence with measurements (width, depth).

Species-specific time frames for the establishment of holes

In KGR/CKGR, all holes were filled with soil on a monthly basis to simulate maintenance, and weekly and monthly densities of new holes were calculated to describe the general and species-specific pressure the fence experiences by hole-digging species every week/month. The general term 'density of new holes' (DNH) was defined as the number of new holes per 100 km week^{-1} and month^{-1}. The term ‘density of new holes by species x’ (DNHS) is the number of new holes dug/caused by a certain species x per 100 km week^{-1} and month^{-1}. At the same time, existing holes were monitored weekly for enlargements by species classified in a larger hole size category. Besides recording tracks in the holes, the width and depth of every hole were measured to monitor enlargement even without visible tracks, following the hole size category method. In MPNP, new and pre-existing holes were only recorded to determine which species enlarged them.

All species were classified differently, depending whether they initiated the hole-digging process themselves or enlarged pre-existing holes: ‘enlarging specialists’ (mostly enlarge existing holes), ‘opportunists’ (initiate digging process but also enlarge holes) and ‘digging specialists’ (mostly initiate hole-digging process themselves).

Data were tested for normality with the Kolmogorov-Smirnoff test and tested for differences performing a two-tailed Mann-Whitney U test.

Results

We were able to record and analyse data for lion, brown hyaena, aardvark, porcupine, honey badger and black-backed jackal.

Hole sizes by species

The comparison of hole sizes between species revealed four different hole size categories (Table 1.1). The underlying statistics are presented here:

1 lion (**>1500 cm^2**; lion-hyaena: $Z = -4.856$, $n = 154$, $P < 0.001$; lion-aardvark: $Z = -9.293$, $n = 193$, $P < 0.001$; lion-porcupine: $Z = -10.695$, $n = 432$, $P < 0.001$; lion-honey badger: $Z = -7.267$, $n = 95$, $P < 0.001$; lion-jackal: $Z = -9.112$, $n = 121$, $P < 0.001$).

2 hyaena (**900-1500 cm^2**; hyaena-aardvark: Z = -8.076, n = 231, P < 0.001; hyaena-porcupine: Z = -10.076, n = 470, P < 0.001; hyaena-honey badger: Z = -6.343, n = 133, P < 0.001; hyaena-jackal: Z = -9.43, n = 159, P < 0.001).

3 aardvark and porcupine (**650-900 cm^2**; aardvark-porcupine: Z = -0.457, n = 509, P = 0.648; aardvark-honey badger: Z = -2.417, n = 172, P = 0.016; aardvark-jackal: Z = -5.409, n = 198, P < 0.001; porcupine-honey badger: Z = -2.47, n = 411, P = 0.014; porcupine-jackal: Z = -5.993, n = 437, P < 0.001).

4 honey badger and jackal (**400-650 cm^2**; honey badger-jackal: Z = -0.968, n = 100, P = 0.333).

A more detailed investigation of the depths and widths of the holes showed the necessity to take more than one measurement into account in order to distinguish between different species (Table 1.1). For example, while honey badger and jackal belong to the same hole size category, their holes do not show any difference in the depths (Z = -0.387, n = 100, P = 0.699), but there is a significant difference in the widths (Z = -3.084, n = 100, P = 0.002).

Besides measurements, the overall shape of the hole can be very useful to determine between species. There are species-specific differences in the shape of holes of black-backed jackal, honey badger, porcupine and aardvark (Figure 1.2). Jackal holes are very narrow, and the deepest point forms a V-shape in the middle of the hole. A honey badger hole is more of a box shape and often bends to one side. Furthermore, while all other species dig perpendicular to the fence, honey badgers generally do not show this characteristic. Whereas porcupine holes are generally shallow and wide, aardvarks tend to dig more in a U-shape, and distinctive claw marks are usually present in the edges at the deepest point of the holes.

Table 1.1 Comparison of hole sizes (HS), hole depths (HD) and hole widths (HW) between species. Values include median, 1st & 3rd quartile, sample size n and level of significance (Sig).

	HS (cm^2)	Sig	HD (cm)	Sig	HW (cm)	Sig
lion (n = 58)	median = 1842.7 1.quartile = 1413.7 3.quartile = 2482.3		median = 32.5 1.quartile = 29 3.quartile = 35		median = 70 1.quartile = 57.3 3.quartile = 93	
		***		*		***
hyaena (n = 96)	median = 1275.9 1.quartile = 942.9 3.quartile = 1640.1		median = 28 1.quartile = 24 3.quartile = 34		median = 54 1.quartile = 45.8 3.quartile = 66	
aardvark (n = 135)	median = 726.1 1.quartile = 567.1 3.quartile = 962.2		median = 23 1.quartile = 19 3.quartile = 28.5		median = 39 1.quartile = 34 3.quartile = 44	
		ns		***		***
porcupine (n = 374)	median = 709.3 1.quartile = 537.6 3.quartile = 942.9		median = 20 1.quartile = 17 3.quartile = 23		median = 45 1.quartile = 47 3.quartile = 57	
		*		ns		***
honey badger (n = 37)	median = 567.1 1.quartile = 402.1 3.quartile = 831		median = 21 1.quartile = 15 3.quartile = 24	ns	median = 35 1.quartile = 31 3.quartile = 42	
		ns		ns		**
jackal (n = 63)	median = 481.1 1.quartile = 421.2 3.quartile = 636.2		median = 20 1.quartile = 18 3.quartile = 23		median = 28 1.quartile = 25 3.quartile = 37	

ns, not significant.
*P < 0.05, **P < 0.01, ***P < 0.001.

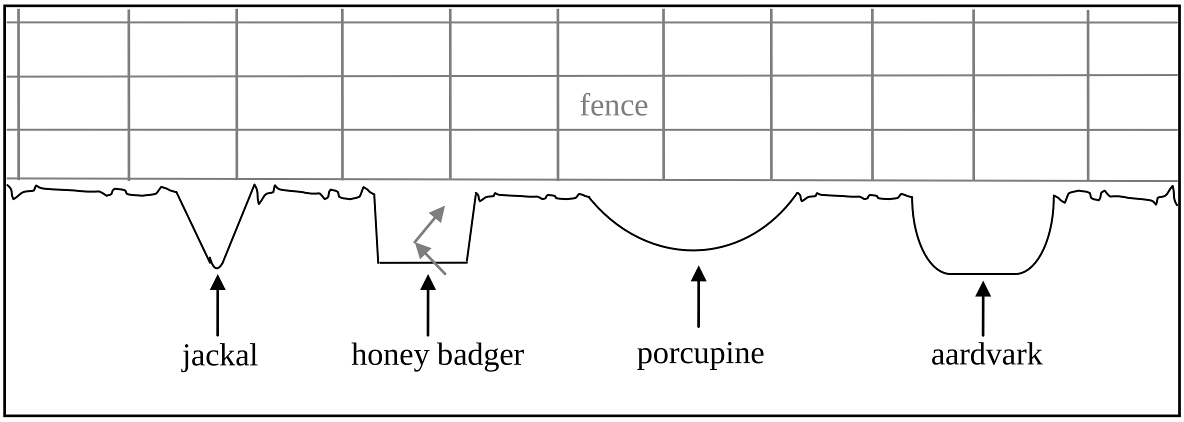

Figure 1.2 Diagram of hole shapes of black-backed jackal, honey badger, porcupine and aardvark.

Kesch, K. M., Bauer, D. T. & Loveridge, A. J. (2014) Undermining game fences: Who is digging holes in Kalahari sands? *Afr. J. Ecol.* 52, 144-150.

Species-specific time frames for the establishment of new holes

We recorded 371 newly dug holes and followed the hole enlargement process on 68 (18.3 %) of them. The hole digging species, of which we had sufficient data, were classified by their digging behaviour:

‘enlarging specialists’ (hole size category 1): African lion. Lions mostly enlarged pre-existing holes and only initiated the digging process in 36 % of the cases.

‘opportunists’ (hole size category 2): brown hyaena. Hyaenas initiated the hole-digging process themselves in 67.4% of the cases, but also enlarged pre-existing holes (32.6 %).

‘digging specialists’ (hole size category 3 & 4):black-backed jackal, honey badger, porcupine, aardvark. These species mostly initiated the digging process themselves (jackal: 100 %, honey badger: 100 %, porcupine: 94.8 %, aardvark: 89.6 %).

We were able to calculate monthly and weekly DNH and DNHS for porcupine, brown hyaena, black-backed jackal and aardvark for the KGR/CKGR fence (Table 1.2). The overall DNH was 66.2 holes per 100 km per month. The DNHS for porcupine and hyaena increased with every week of data collection, whereas the DNHS for jackal and aardvark decreased after 3 weeks of data collection. A decrease in the DNHS occurs when the number of new holes is smaller than the amount of old holes that have been enlarged by larger species and therefore belong to a different DNHS. Unfortunately, there was not enough data to integrate lion and honey badger into the calculations of DNHS.

Discussion

This study provides data on a first set of six animal species for a simple albeit effective method enabling stakeholders to determine categories of species that are digging holes underneath game fences and their digging behaviour in deep sand habitats (Table 1.1). We determined four different hole size categories: (1) lion; (2) brown hyaena; (3) aardvark & porcupine; and (4) honey badger & black-backed jackal (Table 1.3). Species-specific hole shapes were described, and the categories were classified as either ‘enlarging specialists’ (category 1), ‘opportunists’ (category 2) or ‘digging specialists’ (categories 3 & 4). However, further research is needed to describe shapes and measurements of holes and the digging behaviour of additional species in various habitats and soil types. The presented data set must therefore be seen as a start to help stakeholders to identify the type of digging behaviour and the species involved at their specific fence based on hole sizes and shapes. This study allows them to match measurements with hole size categories and certain digging behaviour and therefore plan their fence maintenance efforts accordingly.

Table 1.2 Density of new holes (DNH) and density of new holes per species x (DNHS) for porcupine, brown hyaena, black-backed jackal and aardvark 1, 2, 3, 4 and 5 weeks after filling of holes and percentage of DNH/DNHS after one month in Khutse Game Reserve/Central Kalahari Game Reserve.

weeks after filling holes	**hole density = no. of holes/100 km ± SE (% of total holes after 5 weeks)**				
	total	hole density porcupine	hole density hyaena	hole density jackal	hole density aardvark
1	25.7 (38.8 %)	22.6 (48.3 %)	3.6 (25.9 %)	1.3 (32 %)	0 (0 %)
2	41.9 (63.3 %)	25.8 (55.2 %)	9.3 (67.7 %)	3.5 (86.4 %)	1.7 (100 %)
3	49 (74 %)	33 (70.7 %)	11.5 (83.3 %)	2.9 (73.6 %)	0 (0 %)
4	58.8 (88.8 %)	41.9 (89.7 %)	11.8 (85.2 %)	3.5 (86.4 %)	1.7 (100 %)
5	66.2 ± 7.7	46.7 ± 6.2	13.8 ± 3.9	4 ± 1.4	1.7 ± 0.7

To plan fence maintenance actions or classify the extent of direct and facilitated fence permeability, stakeholders can use the method of calculating weekly/monthly DNH and DNHS in their areas. The DNH and DNHS are a measure to describe the hole-digging pressure on game fences by specific species. In the case of KGR/CKGR, aardvark, jackal and hyaena did not initiate many new holes within the first week after simulated maintenance (filling of all the holes underneath the fence with sand). However, within the first week, the DNHS of porcupines almost reached 50 % of the total DNHS after 1 month.

Table 1.3 Hole size categories, transgression time frames and recommended maintenance time frames for the Khutse Game Reserve/Central Kalahari Game Reserve fence.

	black-backed jackal (*Canis mesomelas*)	honey badger (*Mellivora capensis*)	porcupine (*Hystrix africaeaustralis*)	aardvark (*Orycteropus afer*)	brown hyaena (*Hyaena brunnea*)	African lion (*Panthera leo*)
HS category 1 (1500-3000 cm^2)						X
HS category 2 (900-1500 cm^2)					X	
HS category 3 (725-900 cm^2)			X	X		
HS category 4 (500-725 cm^2)	X	X				
time to transgress	0-1 week	0-1 week	0-1 week	0-1 week	0-1 week	1-2 weeks
maintenance	daily	daily	daily	daily	daily	daily

Partially dug holes of black-backed jackal, honey badger, aardvark or brown hyaena were hardly ever encountered during the study. We therefore assume that these species are very likely to dig a hole under a fence in one night. The first complete lion holes were found about two weeks after simulated maintenance. However, many incomplete lion holes and scratch marks along long stretches of fence were recorded and made us assume that lions avoided digging when possible and rather walked long distances to find a suitable hole. Interestingly, they were recorded to use holes down to the size of honey badger holes and were able to lift the entire fence construction up while squeezing through a hole (K. M. Kesch, pers. observation). Hence, despite digging the largest holes underneath game fences, lions seem very reluctant to initiate the digging process themselves and are completely opportunistic in the utilization of different species' (even very small) holes to transgress the fence line. Therefore, this species is very difficult to fence in, and special attention is required in areas where there are 'digging specialists' present. Hoare (1992) only categorized lions as 'potential climbers'. However, this and other studies (Reed & Sautereau, 2005; Ferguson, Adam & Jori, 2012) show that they dig or enlarge holes under electrified fences to exit protected areas.

Different fences obviously have different objectives and hence require different maintenance efforts. The extent of these efforts is dependent on a variety of factors, such as the total fence management budget, the costs of incursions compared with the costs of maintenance, the length of the fence, the DNH and the types of digging species present. In our case study in KGR/CKGR, where lions caused the major part of livestock predation outside the protected area (Schiess-Meier *et al.*, 2007), the fence was supposed to be an impermeable exclusion fence and separate lions from human-dominated areas completely. As lions were recorded to squeeze through holes down to the size of honey badgers, maintenance efforts have to be planned according to the appearance time frame of these holes. In practice, this means that the fence should be patrolled and repaired on a daily basis (Table 1.3). Further, to improve the design, the fence should be partly buried into the ground.

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Author contribution

I hereby confirm that Kristina Kesch conceived, designed and performed the experiments, analysed the data and wrote the paper.

Hamburg,

Jörg Ganzhorn

Prof. Dr. Joerg Ganzhorn

Chapter Two

Tools to monitor fence permeability: The importance of maintenance and alignment for the effectiveness of fences

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Abstract

Game fences are widely used to mitigate human-wildlife conflict and, where fencing is deemed the right choice, appropriate design, alignment and maintenance are the keys to success. We studied the effectiveness of the Makgadikgadi Pans National Park game fence along the Boteti River in central Botswana, one of the highest human-wildlife conflict areas in the country, using a spoor survey method and counting holes made by transgressing animals. We investigated the fence's effectiveness in separating humans and wildlife, as evidenced by the fence line transgression frequencies of different hole digging and conflict species. Since the fence prevents access to long stretches of river along the National Park boundary, fence line transgressions for lion (*Panthera leo*), elephant (*Loxodonta africana*) and all the digging species were higher during the dry season, when there was no surface water available in the Park. Conversely, cattle crossed the fence and moved into the National Park in high numbers during the rainy season, probably to access grazing. Wildlife damage to the fence was highest in the dry season and without the implementation of prompt and constant maintenance and repair, game fences such as the Boteti fence cannot be effective in alleviating human-wildlife conflict.

Keywords alignment, fencing, holes, human-wildlife conflict, maintenance, spoor survey

Chapter Two

Introduction

Game fences have recently been proposed as the conservation tool of choice to conserve large carnivores, especially African lions (*Panthera leo*; Packer *et al*., 2013 a & b), causing considerable controversy (Creel *et al.*, 2013; Woodroffe, Hedges & Durant, 2014). Regardless of their potential to solve human-wildlife conflict by separating people and wild animals, fencing must generally be seen as a high impact measure and pros and cons have to be considered very carefully before implementation (Hayward & Kerley, 2009). Consequences for wildlife can be severe, such as animals getting trapped or entangled, the creation of genetically isolated populations and the use of fence materials to manufacture snares for poaching (Hayward & Kerley, 2009; Gadd, 2012), to name but a few. In order to avoid cutting off migration routes, fencing should further not be considered in areas, where migratory species are present (Boone & Hobbs, 2004). Megaherbivores such as African elephants (*Loxodonta africana*) are likely to cause severe damage to a fence, which will involve considerable maintenance costs (Slotow, 2012). Nevertheless, well-constructed and well maintained fences can alleviate human-wildlife conflict, reduce edge effects for carnivore populations (Packer *et al.*, 2013a) and are often used as a conflict solution (reviews: Breitenmoser *et al*., 2005; Hayward & Kerley, 2009; Ferguson & Hanks, 2010; Somers & Hayward, 2012).

The installation of a game fence is a costly enterprise and maintenance can be very challenging financially and logistically, especially in large fenced areas. Where fencing is deemed the right choice, managers must take into account that the bulk of expenses related to fencing only arise after its installation, due to the need of fence maintenance and the extensive management of fenced animal populations. Many fenced reserves in South Africa, where it seems that substantial funds for appropriate management of fenced animal populations are available, are struggling with inbred animal populations (Stein, 1999; Trinkel *et al*., 2008; Frankham, 2009; Trinkel *et al*., 2010).

For many species including elephants, lions and leopards non-permeability of fences is often very difficult to achieve and the effectiveness of fences is highly dependent on maintenance (Hoare, 1992; Hayward *et al.*, 2007; Hunter *et al.*, 2007; Davies-Mostert, Mills & Macdonald, 2009; Bonnington *et al.*, 2010; Ferguson, Adam & Jori, 2012; Slotow, 2012; Kesch, Bauer & Loveridge, 2014). Game fences, which are not maintained appropriately, can further fuel the conflict situation due to predators being attracted to accumulations of prey along the fence (Chapter Three of this manuscript) and easy access to human-dominated land. To determine if and to what extent fences are permeable to certain animal species and therefore the fences' effectiveness as a conflict solution, the "Fence Incident Surveillance System" (FISS; Ferguson, Adam & Jori, 2012) and Bonnington's (2010) spoor method enable stakeholders to calculate frequencies of fence line crossings.

Using a method similar to the FISS, we studied the permeability and hence the effectiveness of the Makgadikgadi Pans National Park game fence in central Botswana. One of the major reasons for the installation of this fence was the resolution of conflict between agropastoralists, and lions and elephants (Gupta, 2005). Since this fence appears to be permeable to many different animal species (Reed & Sautereau, 2005) this study investigates whether it is effective in excluding lions and elephants from human-dominated area. Furthermore, we highlight the importance of fence maintenance and alignment and provide data on seasonal and regional hot spots of fence line transgressions for the Makgadikgadi fence.

Chapter Two

Methods

Study site

Located between 20 and 21 degrees South and 24 and 26 degrees East, the Makgadikgadi Pans National Park (MPNP) is 4,900 km² in size. The region has one wet (October - March) and one dry season (April - September) and annual rainfall averages 450 mm (Meynell & Parry, 2002). Temperatures range annually between a mean minimum of 6.9 - 19.9 °C and mean maximum temperature of 25.3 - 35.2 °C (Alexander *et al.*, 2002). MPNP is home to the largest remaining zebra (*Equus burchelli antiquorum)* and wildebeest (*Connochaetes taurinus)* migration in southern Africa. With the first rains the animals move from their dry season range along the Boteti River east to the big Makgadikgadi Saltpans, where rainwater accumulates at the surface during the rainy season. The area west of the Boteti River, which forms the western park boundary, is one of the highest human-wildlife conflict areas in Botswana, with the major conflict species being lion (killing livestock) and elephant (crop raiding; Department of Environmental Affairs and Centre for Applied Research, 2010). Mitigating this conflict was one of the major reasons for an electrified double game fence (2.7 m high electrified fence and 1.5 m high cattle fence) being installed in 2004, crisscrossing the dry Boteti riverbed (Gupta, 2005). In 2008 - after almost 20 years - the river started to flow again, creating a permanent water source for people and wildlife in the area but also causing short circuits and flooding of the fence at some sections.

The section of the fence north of Khumaga village crisscrosses the Boteti River in several places, giving wildlife access to water. By contrast, the section between the villages of Khumaga and Sukwane runs exclusively on the eastern side of the Boteti River, excluding wildlife from the water source (Figure 2.1).

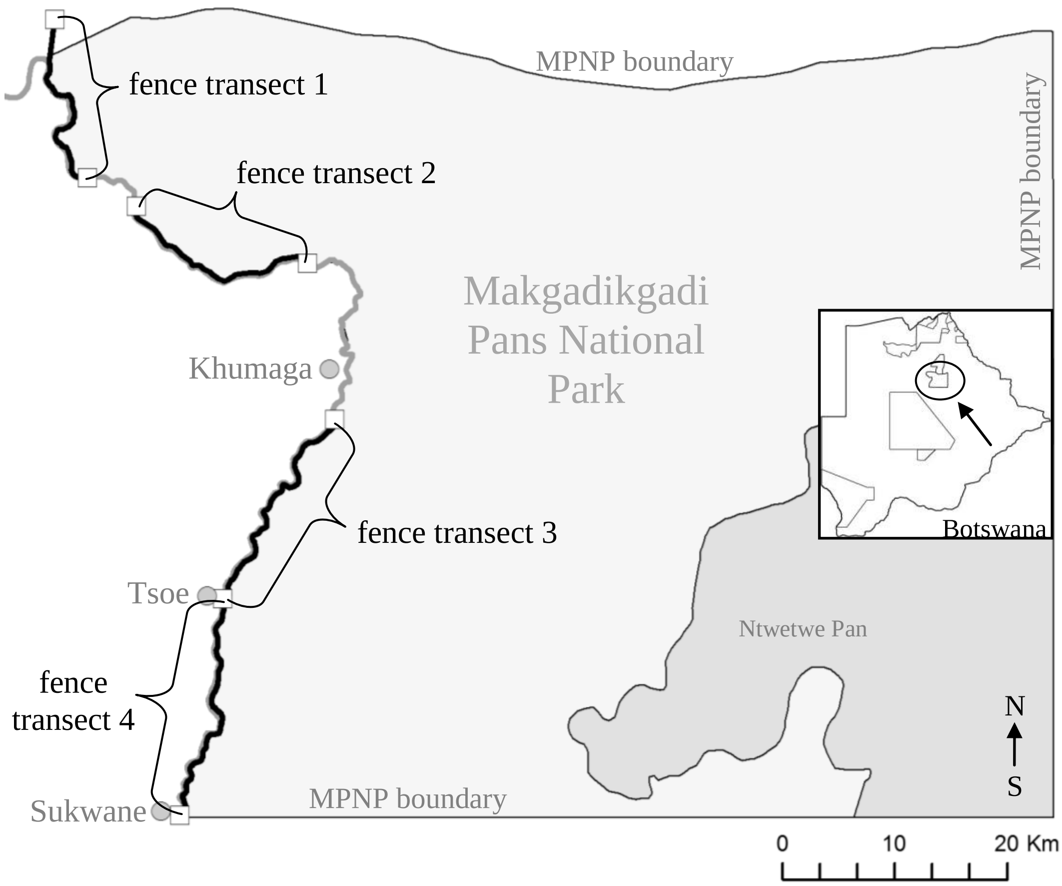

Figure 2.1 Map of Makgadikgadi Pans National Park with park boundaries, villages, fence transects, start/end of transects represented by squares.

Spoor and break count survey

With the help of an experienced San tracker, data were collected in the rainy (November 2010 - April 2011) and dry season (June - October 2011). The maintenance roads along the inside of the MPNP fence line were surveyed in four transects (mean length ± SD = 21.6 ± 2 km), with a total length of 86.4 km (Figure 2.1). Due to the fence alignment (see above), transects were grouped into a northern (transects I & II) and a southern section (transects III & IV, Figure 2.1) for data analysis.

Transects I-IV were each driven 11-12 times and a total distance of 965 km was covered in 46 days of data collection. Each day of data collection, data were recorded for one transect.

Data collection was conducted during the early morning, when the road was still undisturbed by vehicles and when no rain or wind occurred during the night before. The fence line was driven with an average speed of 10-15 km/h with the driver, one person on the roof and one person on the bumper scanning for holes and breaks underneath and in the fence. Recorded data included GPS-coordinates for every hole or break, fresh tracks (from the last 24 hours) transgressing the fence line for five hole digging species (aardvark (*Orycteropus afer*), porcupine (*Hystrix africaeaustralis*), honey badger (*Mellivora capensis*), black-backed jackal (*Canis mesomelas*), brown hyaena (*Hyaena brunnea*); Kesch, Bauer & Loveridge, 2014) and three conflict species (lion, elephant, cattle; Ecological Support Services 2002), number of adult individuals and direction of travel for conflict species. Brown hyaenas were classified as digging species but not as conflict species, as they have been shown not to actively hunt livestock (Maude 2005).

The reliability and accuracy of San trackers have been described in detail by Stander *et al.* (1997). The San tracker participating in this study had extensive tracking experience in various research projects and hunting outfitters and was familiar with the data collection procedure.

Fence line transgressions

"Transgression frequency" was introduced as a standardized term for the pressure a fence experiences by different animal species trying to transgress a fence line. It was defined as the number of fence-line transgressions per 100 km of fence line per 24h and was calculated for each day of data collection, where all spoor not older than 24 hours was identified by the San tracker and recorded. From this data set, species-specific mean transgression frequencies and standard errors could be determined for the total length of the fence line, per area (by only taking the northern or southern transects into account), per direction of travel (in or out of the park), for the whole study period and per season. In order to determine the general transgression pressure that the fence experiences by certain species, every spoor crossing the fence line within the past 24 hours before data collection was recorded. Hence, it is possible that individuals were recorded repeatedly when crossing the fence line more than once within 24 hours.

Data were tested for deviation from normality using the Kolmogorov-Smirnov test and for equality of variances using the Levene test. Pair wise comparisons were evaluated with a two-tailed t-test.

Seasonal and spatial presentation of fence line transgression incidents

In order to determine species- and season-specific hot spots of fence line transgressions, all recorded fence line transgression incidents of lion, elephant and cattle was presented in three seasonal figures.

Results

Fence line transgressions

Lions and elephants crossed the fence line more often during the dry season, but the seasonal difference was not significant (Table 2.1). Lions transgressed 100 km of fence line approximately 21 times (10 times going out of the park) every 24 hours in the dry season and 13 times (6 times going out of the park) in the rainy season. However, during the rainy season, lions showed more activity in the northern section of the fence than in the southern section ($t = -2.306$, $n = 36$, $p = 0.027$).

Table 2.1 Transgression frequencies (number of transgressions/100 km and 24 h) of hole digging species (aardvark, porcupine, honey badger, black-backed jackal, brown hyaena) and potential conflict species (lion, elephant, cattle) in total, north and south of Khumaga and rainy vs. dry season. Frequencies given as mean ± standard error, significance levels and p-values.

species			rainy season	statistics	dry season	statistics	rainy vs. dry
digging species	total	total	82.91 ± 10.64		152.10 ± 27.91		t = -2.317, n = 50, p = 0.033
		north	73.65 ± 10.92	t = 0.866 n = 36 p = 0.394	184.27 ± 38.27	t = -1.597 n = 14 p = 0.136	
		south	92.16 ± 18.36		96.57 ± 23.32		
aardvark	*(Orycteropus afer)*	total	16.33 ± 3.89		9.15 ± 3.22		t = 1.089, n = 50, p = 0.281
		north	8.91 ± 3.61	t = -1.983 n = 36 p = 0.058	10.34 ± 4.77	t = 0.480 n = 14 p = 0.640	
		south	23.74 ± 6.55		7.02 ± 3.28		
porcupine	*(Hystrix africaeaustralis)*	total	42.06 ± 7.62		89.28 ± 23.33		t = -1.924, n = 50, p = 0.073
		north	41.10 ± 9.63	t = -0.123 n = 36 p = 0.903	111.36 ± 33.30	t = 1.304 n = 14 p = 0.217	
		south	43.01 ± 12.08		49.53 ± 18.67		
honey badger	*(Mellivora capensis)*	total	7.51 ± 2.14		4.83 ± 1.72		t = 0.741, n = 50, p = 0.462
		north	7.09 ± 2.95	t = -0.195 n = 36 p = 0.847	5.12 ± 2.31	t = 0.212 n = 14 p = 0.836	
		south	7.94 ± 3.19		4.33 ± 2.75		
black-backed jackal	*(Canis mesomelas)*	total	6.97 ± 1.52		35.48 ± 11.12		t = -2.541, n = 50, p = 0.024
		north	8.71 ± 2.60	t = 1.149 n = 36 p = 0.260	45.09 ± 16.41	t = 1.176 n = 14 p = 0.262	
		south	5.23 ± 1.55		18.19 ± 6.27		
brown hyaena	*(Hyaena brunnea)*	total	10.04 ± 1.65		13.36 ± 3.85		t = -0.931, n = 50, p = 0.356
		north	7.84 ± 1.81	t = -1.351 n = 36 p = 0.187	12.36 ± 3.31	t = -0.516 n = 14 p = 0.628	
		south	12.25 ± 2.72		17.51 ± 9.42		
lion	*(Panthera leo)*	total	13.44 ± 3.25		21.04 ± 13.44		t = -0.778, n = 50, p = 0.440
		north	20.51 ± 5.39	t = -2.306 n = 36 p = 0.027	4.24 ± 2.67	t = 0.786 n = 18 p = 0.256	
		south	6.36 ± 2.93		51.29 ± 35.54		
elephant	(Loxodonta *africana*)	total	80.53 ± 17.59		132.28 ± 37.19		t = -1.421, n = 50, p = 0.162
		north	51.77 ± 22.52	t = 1.677 n = 36 p = 0.103	53.94 ± 29.29	t = -4.371 n = 14 p = 0.001	
		south	109.29 ± 25.87		273.30 ± 42.04		
cattle		total	112.19 ± 28.58		0.00 ± 0.00		t = 3.295, n = 50, p < 0.001
		north	66.01 ± 30.50	t = 1.648 n = 36 p = 0.108	0.00 ± 0.00	no statistics	
		south	158.07 ± 46.79		0.00 ± 0.00		

Elephant movements resulted in approximately 132 (70 going out of the park) transgressions of 100 km fence line every 24 hours in the dry season and 81 (43 going out of the park) transgressions in the rainy season. In the dry season, elephants utilized the southern fence section significantly more than the northern section ($t = -4.371$, $n = 14$, $p = 0.001$).

With 112 transgressions of 100 km fence line every 24 hours, cattle transgressed the fence line significantly more often in the rainy season, with no transgressions being recorded in the dry season.

Seasonal and spatial presentation of fence line transgression incidents

The here presented figures show raw data, which are not corrected for different sampling efforts and therefore seasons cannot be compared to each other. The figures purely serve the comparison of transgression pressure on different fence sections within one season.

During the dry season, lions mainly crossed the fence line in the south of the fence. Most transgressions were focussed on an area of about 30 km around Tsoe village. In contrast, transgressions by lions during the rainy season were mostly focussed on the north of the fence line and here especially on an area northwest of Khumaga and close to the northern boundary of the park (Figure 2.2).

Elephant transgressions in the dry season are mainly focussed on the south of the fence, with a high number of transgressions all the way from Khumaga village to Sukwane village. Furthermore, transgressions were recorded in an area northwest of Khumaga. During the rainy season, there was an unaltered high number of transgressions in the south. However, in the north of the fence, more transgressions were recorded in a section close to the northern park boundary (Figure 2.3).

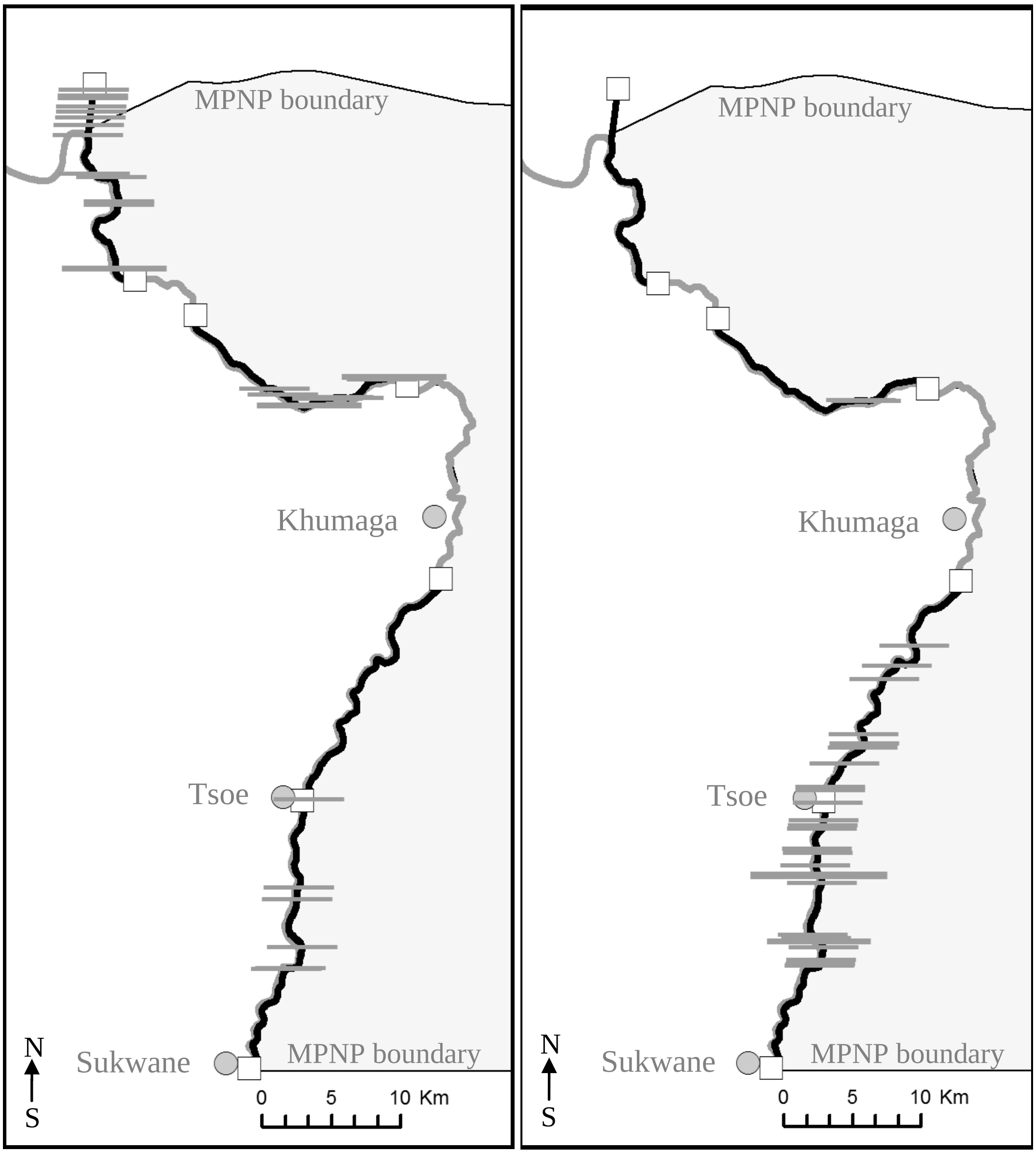

Figure 2.2 Fence line transgressions by African lions during the rainy (left) and dry season (right). Transgression events represented by grey circles (small circles: 1-4 transgressions, medium size circles: 5-9 transgressions, large circles: >10 transgressions), villages (full squares), start/end of transects (open squares).

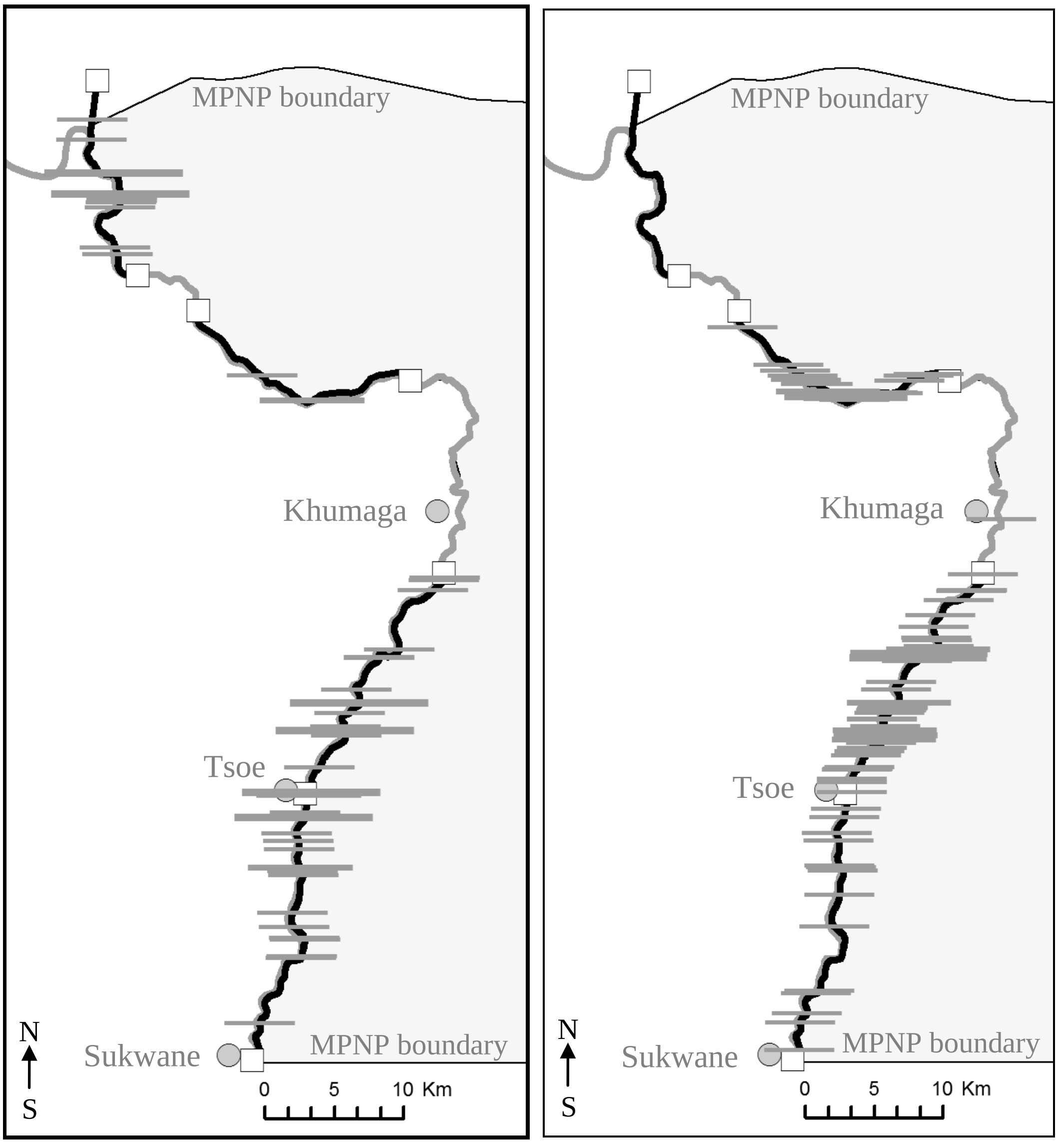

Figure 2.3 Fence line transgressions by African elephants during the rainy (left) and dry season (right). Transgression events represented by grey lines (short lines: 1-9 transgressions, medium lines: 10-19 transgressions, long lines: >20 transgressions), villages, start/end of transects (open squares).

During the rainy season, fence line transgressions by cattle were mainly recorded in the south and the far north of the fence. No transgressions were recorded in the dry season (Figure 2.4).

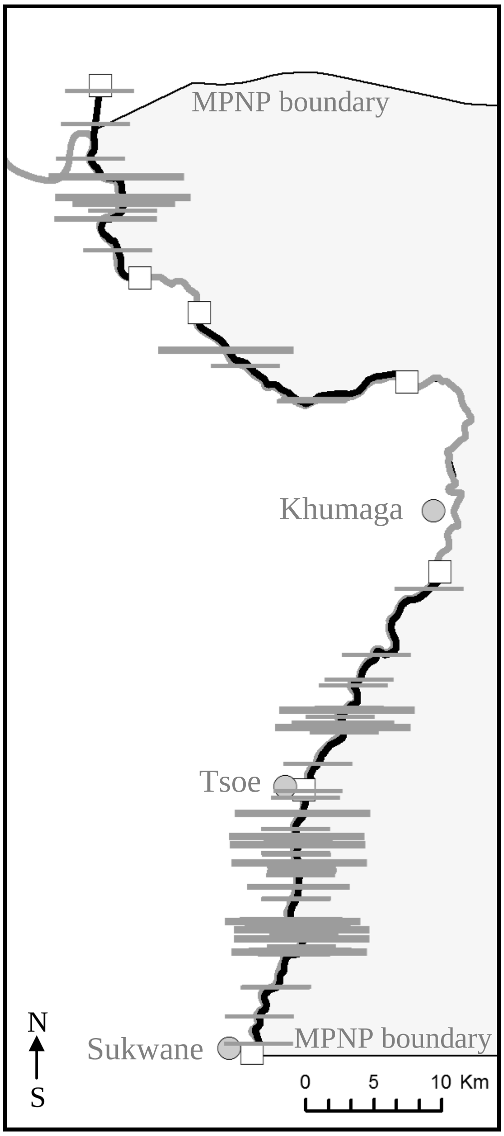

Figure 2.4 Fence line transgressions by cattle during the rainy season. Transgression events represented by grey lines (short lines: 1-9 transgressions, medium lines: 10-19 transgressions, long lines: >20 transgressions), villages, start/end of transects (open squares).

Discussion

Digging species in general, and especially black-backed jackal, caused higher transgression pressure on the fence in the dry season, when surface water is scarce, but did not show any spatial difference between the northern and southern fence sections. During that time of the year, the Boteti River represents the only reliable water source and along most parts of the river, the fence line blocks access. The resulting holes underneath the fence are being utilized by conflict species such as lions to transgress the fence line into human-dominated landscape (Kesch, Bauer & Loveridge, 2014).

Lions transgressed the fence line more often in the dry season than in the rainy season (21 (10 times out of the park) vs. 13 times (6 times out of the park) per 100 km and 24 hours), which is probably due to the lack of surface water in the dry season. During this time of the year, most fence line transgressions by lions were found along a 30 km stretch of fence around Tsoe village. During this time of the year the migrating zebra and wildebeest as the lions' major food source at the Boteti River (Hemson, 2003) are mostly located in an area north of Khumaga village where the fence allows access to the river. Therefore, the lions in this area have no need to cross the river in order to find food or water, whereas lions further south still cross the fence line in high numbers. During the rainy season, lions were more active in the northern section of the fence, especially in an area northwest of Khumaga village and at the northern Park boundary. At that time of the year the zebra and wildebeest have left the Boteti River and migrated east. Therefore, lions often leave the security of the National Park to feed on livestock (Hemson, 2003). The area northwest of Khumaga village has several sandbanks within the river, which seem to offer relatively easy river crossings (pers. observation) and might be the reason for lions to focus on this area. Furthermore, the fence does not follow the Boteti River in the area close to the northern Park boundary. Therefore, in this area the fence is the only boundary lions have to cross in order to get into human- and livestock-dominated area, which could be the reason for this second transgression hotspot.

In the dry season, elephant transgression numbers were higher than in the rainy season (132 transgressions (70 going out of the park) vs. 81 transgressions (43 going out of the park) per 100 km and 24 hours), when there is surface water available in the park. During both seasons, an unaltered high number of elephant transgressions was recorded in the south of the MPNP fence. This part of the fence has been exclusively installed on the National Park's side of the Boteti River and therefore does not give wildlife any access to water, which is probably the reason for this high number of elephant transgressions year-round. Elephants are water dependent (Western, 1975) and require 80-160 liters of water per day (Douglas-Hamilton *et al.*, 2001). Elephant damage to a fence is therefore inevitable, if it blocks off their access to water as the MPNP fence does. Crop raiding being more of an issue during the rainy than the dry season (personal communication K. Evans, 16.01.2014) supports the theory of the high elephant transgression numbers during the dry season being due to the blocked off access to water.

In the rainy season, cattle caused 112 (57 going into the park) transgressions along the western border of MPNP every 24 hours and 100 km. The Boteti River represents a drainage system of the Okavango Delta, where flood waters only arrive from the Angolan highlands during the dry season. As a result, the water level of the Boteti River is highest during the dry season and may be too high for cattle to cross into the park during that time of the year. Surprisingly, about three quarters of all fence line transgressions by cattle were recorded either in the southern section or the far north of the fence, where the fence line runs exclusively on the eastern side of the Boteti River and cattle have unfettered access to water outside the Park. Therefore, our results suggest that cattle roam and are actively herded (pers. observation) into the National Park in large numbers not for water, but for grazing.

The MPNP fence, as many other game fences in Africa, was primarily installed to separate livestock and crops from lions and elephants respectively, which cannot be achieved when the fence line is permeable to these species and cattle. It is especially vulnerable to transgressions by wildlife leaving the National Park in search of water during the dry season, when surface water is scarce inside the Park. During the time of data collection, no maintenance was carried out on the fence and therefore animals could easily cross through breaks in the fence and holes underneath it, which were caused by elephants and digging species. Further, due to the alignment of the fence, elephant damage is inevitable due to the species' dependence on water. In order to stop digging species threatening the integrity of the fence it is recommended to sink the fence 1 m into the ground. Further, the reelectrification and realignment of the fence so that it gives wildlife access to water, especially in the southern section, would also help to reduce elephant caused damage to the fence and lower the costs of much needed maintenance for it to be effective.

Further, there are reports of lion, elephant and other herbivore movements between the MPNP and the Central Kalahari/Khutse Game Reserve complex, which lies south-west of the Park (Hemson 2003; Mbaiwa & Mbaiwa 2006; Chase 2009), and a natural corridor between the two protected areas has been predicted, especially for young dispersal male lions (N.B. Elliot, unpublished data). Fencing and protection of a wildlife corridor between the Boteti River and the Central Kalahari Game Reserve might allow genetic exchange between the two areas, provide access to the Boteti River in drought periods and reduce the human-wildlife conflict by decreasing breakages due to animals trying to move through human-dominated land between the two protected areas.

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Author contribution

I hereby confirm that Kristina Kesch conceived, designed and performed the experiments, analysed the data and wrote the paper.

Hamburg,

Jörg Ganzhorn

____
Prof. Dr. Joerg Ganzhorn

Fences of fear: Lion-prey relationships along game fences

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Abstract

Fencing has been used widely to delineate boundaries and mitigate human-wildlife conflict, but little is known about the effect of game fences on predator-prey relationships. A cost-effective, repeatable and non-invasive spoor method was used to investigate whether African lion prey species aggregate along fences and if lions are attracted by this possibly increased prey base. Furthermore, the initial and long-term impact of fences on spatial predator avoidance behaviour by lion prey species was determined. Our results suggest that new fences restrict daily herbivore movement behaviour, which leads to increased localized herbivore densities. Lions appear to be attracted by this high prey density along the fences and herbivores do not show spatial avoidance behaviour of lions, either along a new or along a seven-year-old fence. For the herbivore species we have data from, fences not only seem to have an initial but also a long-term negative influence on predator avoidance behaviour. We conclude that the installation of fences has the potential of adverse impacts on herbivore populations and needs careful consideration especially in small protected areas with small herbivore populations or areas hosting migratory species.

Keywords African lion (*Panthera leo*), Botswana, fencing, Kalahari, lion-prey relationships, predation pressure, spoor counts

Chapter Three

Introduction

Humans have used fences to delineate boundaries and to mitigate conflicts with wildlife on a global scale (reviews: Breitenmoser *et al*., 2005; Hayward & Kerley, 2009; Ferguson & Hanks, 2010; Somers & Hayward, 2012). Fencing can have positive consequences for people and wildlife by mitigating resource competition between wildlife and livestock and therefore have a positive impact on primary production and alleviating human-wildlife conflict (Chapter Four in this manuscript; Hayward & Kerley, 2009). Fences have the potential of creating disease free zones (Gadd, 2012) and reducing edge effects for carnivore populations. Further, fences have been proposed as the conservation tool of choice to conserve large carnivores (Packer *et al*., 2013 a & b). However, where fences are used to delineate boundaries of wildlife areas they can also have significant negative impacts. Cutting off migration routes can lead to mass die-offs of migrating animals and the degradation and fragmentation of natural habitats and therefore to genetically isolated animal populations (Hayward & Kerley, 2009; Somers & Hayward, 2012; Woodroffe, Hedges and Durant, 2014). The reduction of edge effects can lead to carnivore populations being maintained at unsustainably high population densities (Creel *et al.*, 2013). Furthermore, herbivores have been reported to aggregate along game fences, while predators have been seen to utilize fences to chase their prey into them (Adendorff & Rennie, 1984; Goodwin, 1985 cited in Hoare, 1992; Albertson, 1998; Van Dyk & Slotow, 2003; Rhodes & Rhodes, 2004; Ferguson & Hanks, 2010).

African lions (*Panthera leo*) preferably select areas of both high prey biomass (Nilsen & Linnell, 2006; Hayward *et al.*, 2008; Loveridge *et al*., 2009) and high prey catchability (Hopcraft, Sinclair & Packer, 2005) and game fences would appear to provide both. In a landscape free of artificial barriers, lion prey species avoid their predators spatially and move into open area when lions are in their vicinity (Valeix *et al.*, 2009 a & b). However, little is known about the effect of artificial barriers such as game fences on predator avoidance behaviour by herbivores.

This study investigates whether lion prey species were trapped along a newly built game fence in Botswana and whether this resulted in an increase in lion presence, due to increased prey availability and abundance. As a result of habituation of prey to the presence of predators, we expected prey species to be alert to and avoid the parts of the fence line frequented by lions. Data collection for this study was carried out along two different fence lines in Botswana, one newly built and one seven-years-old. Along the newly built fence line we expected no spatial avoidance of lions by prey species. On the seven-year-old game fence we investigated whether or not lion prey species had adapted to the increased predation risk and therefore avoided lions spatially, as they would in a landscape free of barriers (Valeix *et al.*, 2009 a & b). This study aims at providing information on how fences can influence predator-prey relationships and therefore have a possible negative influence on prey populations.

Methods

Study sites

The study was carried out on two game fences in Khutse Game Reserve (KGR)/south-eastern Central Kalahari Game Reserve (CKGR) and Makgadikgadi Pans National Park (MPNP), Botswana.

The KGR (2,600 km^2) is situated between 23 - 24 °S and 24 - 25 °E (Thomas & Shaw, 1991) in southern Botswana, bordering the CKGR (52,000 km^2) in the north. The semi-arid climate is characterized by a cold dry season (April - September) and a hot rainy season

(October - March), average annual rainfall of 300 mm (de Vries *et al.*, 2000) and average monthly temperatures between 8.5 °C and 35.5 °C (Thomas & Shaw, 1991). In October 2009, an electrified double game fence (2.7 m wire netting fence with four electrified wires; 1.5 m wire netting cattle fence) was completed along the southern and eastern border of KGR and around the south-eastern corner of CKGR, resulting in a barrier of about 300 km, intended to stop livestock predation by African lions (Figure 3.1).

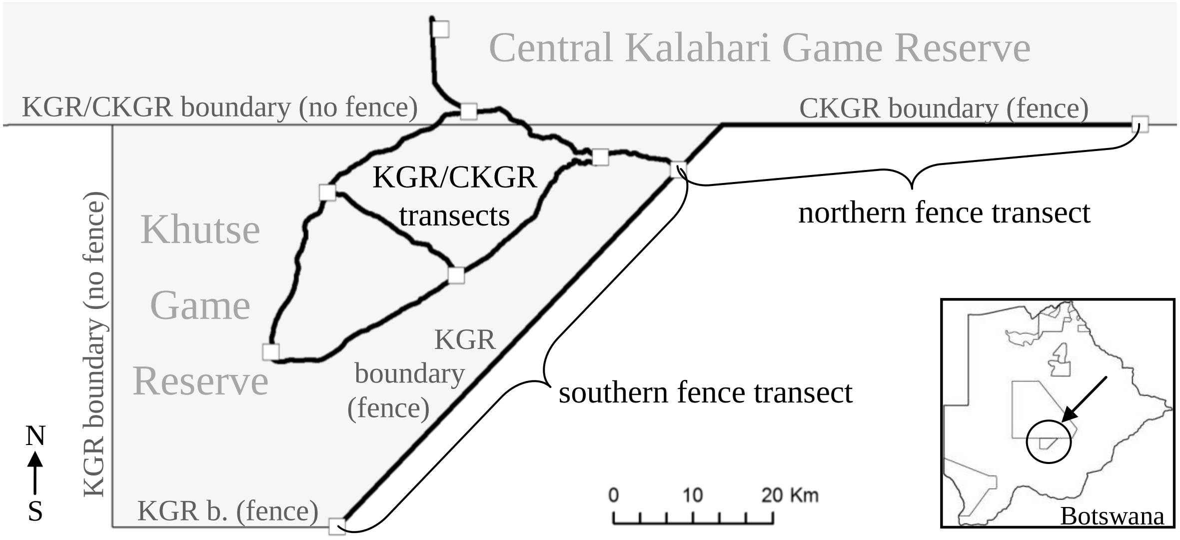

Figure 3.1 Map of Khutse Game Reserve/southern Central Kalahari Game Reserve with fence line, Khutse/Central Kalahari transects and fence transects, start/end of transects represented by squares

The MPNP (4,900 km²) is situated between 20 - 21 °S and 24 - 26 °E (Thomas & Shaw, 1991), annual rainfall averages 450 mm (Meynell & Parry, 2002) and annual temperatures range between a mean minimum of 6.9 - 19.9 °C and a mean maximum of 25.3 - 35.2 °C (Alexander *et al*., 2002). The western park boundary is formed by the Boteti River, along which an electrified double game fence (same design as in KGR) was installed in 2004 (Figure 3.2).

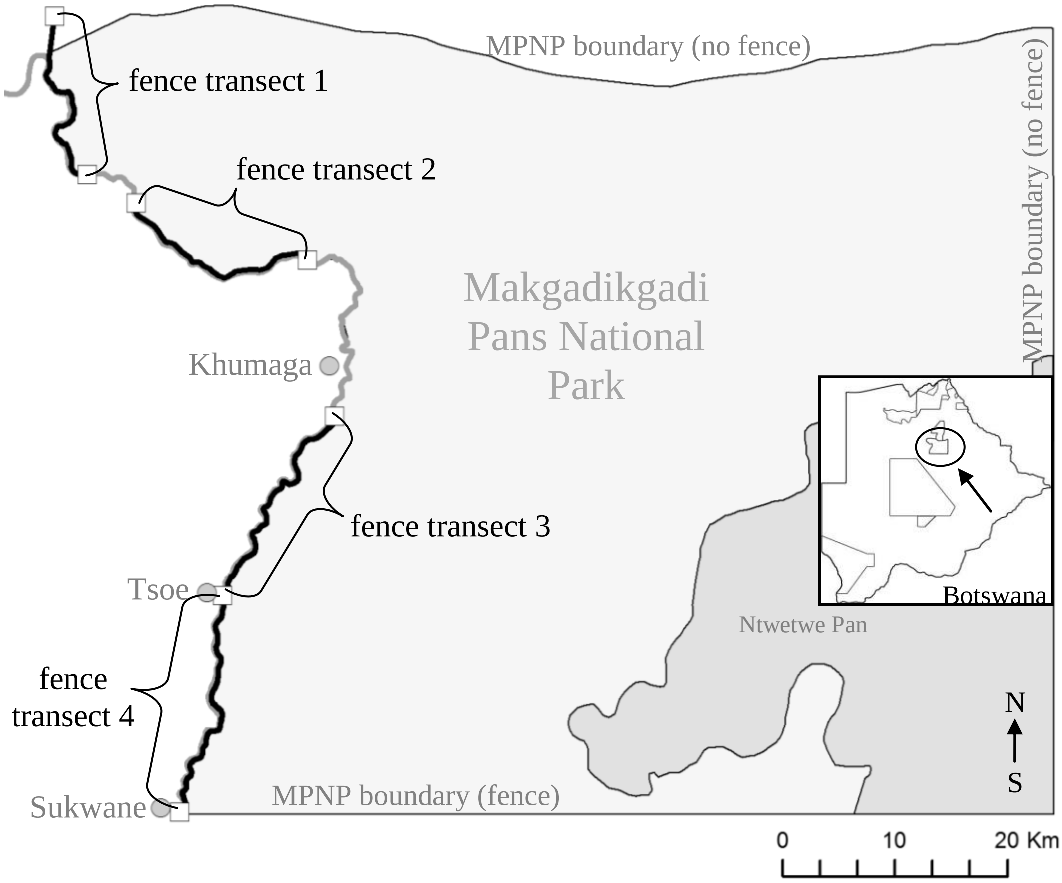

Figure 3.2 Map of Makgadikgadi Pans National Park with park boundaries, fence transects, villages, start/end of transects represented by squares

Along the KGR/CKGR fence, potential natural prey species for lions include eland (*Taurotragus oryx*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx gazella*), red hartebeest (*Alcelaphus buselaphus caama*), blue wildebeest (*Connochaetes taurinus*), ostrich (*Struthio camelus*), springbok (*Antidorcas marsupialis*) and warthog (*Phacochoerus aethiopicus*) (Ramsauer, 2006). Along the Boteti River, potential prey includes giraffe, greater kudu, impala (*Aepyceros melampus*) and cattle. Further, the MPNP hosts a seasonal mass migration of Burchell's zebra (*Equus burchelli*) and blue wildebeest, with the animals being in the Boteti area during the dry season (Hemson, 2003; Maude, 2010).

Spoor counts

Between October 2009 and June 2010, just after the installation of the KGR/CKGR fence, and between November 2010 and September 2011, seven years after the MPNP fence had been installed, spoor (track) surveys for adult lions and their potential prey species were conducted in three different study sites (see below). Sandy roads served as transects and although hard clay soil around the numerous saltpans within KGR/CKGR was common, this type of substrate accounted for less than 5 % of the total transect length.

Data were recorded during early mornings when the roads were “fresh” (no vehicle tracks) and when no wind or rain occurred during the night before. A 4x4 vehicle was driven with an average speed of 10 - 15 km/h with experienced San trackers sitting on the bonnet and on the roof, both scanning the road for tracks. Track incidences from the last 24 hours were recorded including the number of animals as well as the track length on the road using a Global Positioning System (GPS). Intersecting roads were covered with a temporal separation of at least three days and the same transects were not covered on consecutive days to avoid double counting of the same tracks.

The San people are well known for their outstanding tracking abilities (Stander *et al.*, 1997). The trackers participating in this study spent most of their lives in the CKGR as hunters and gatherers, following an ancient tradition of tracking and spoor (tracks/signs) reading. Further, they had several years of tracking experience for research projects and in the hunting safari business, and their skills were thoroughly tested (Bauer *et al.*, 2014).

Study site 1: inside KGR/CKGR

Eight road transects (mean length ± SD = 21.3 ± 1.9 km) inside KGR/CKGR were covered repeatedly, with a total length of 193 km. Separate data collection for different aspects of this study resulted in different total sampling distances per study aspect. In order to determine lion spoor density a total of 2,260.4 km were covered, whereas 360 km were covered to calculate herbivore travel distances (Table 3.1).

Table 3.1 Number of different transects, number of repeats per transect, transect length and total distance covered for different aspects of the study

	no. of transects	transect repeats	mean transect length in km (range)	total transect length in km
Herbivore travel distance KGR/CKGR fence	6	13	20	1,560
Herbivore travel distance KGR/CKGR	8	17	21.3 (16.2 – 32.9)	360
P. leo spoor counts KGR/CKGR fence	20	13	6	1,560
P. leo spoor counts KGR/CKGR	8	100	21.3 (16.2 – 32.9)	2,260
Spatial predator avoidance KGR/CKGR fence	30	13	4	1,560
Spatial predator avoidance MPNP fence	39	10	2	780

Study site 2: along the KGR/CKGR fence

Due to an artificial waterhole along the CKGR section of the fence the KGR/CKGR fence was divided into a northern and a southern section (Figure 3.1). Further, the KGR entrance gate with houses of employees of the Department of Wildlife and National Parks represented a physical and acoustic barrier between the two areas. The maintenance roads along the inside of the fence with a total length of 120 km were driven thirteen times each, resulting in a total transect length of 1,560 km. These roads were divided into different transect lengths for different aspects of the study (Table 3.1).

In order to calculate herbivore travel distances, the fence line was divided into six 20 km transects. Twenty 6 km transects were covered thirteen times in order to calculate lion spoor densities. In order to avoid recording spoor of the same individuals twice while determining spatial predator avoidance by herbivores, the fence line was divided into discrete sections that were analyzed separately, depending on distances lion prey species travelled along the fence. Pilot analysis revealed that ostrich travelled the longest distances along the KGR/CKGR fence (mean ± SE: ostrich = 2.9 ± 0.3 km, red hartebeest = 1.1 ± 0.1 km, gemsbok = 2.6 ± 0.4 km, greater kudu = 1.8 ± 0.2 km). The upper quartiles of distances covered along the fence by all analyzed herbivore species were below the 75 % quartile of ostrich (75 % quartiles: ostrich = 4.1 km, red hartebeest = 1.8 km, gemsbok = 3.4 km, greater kudu = 2.6 km). Therefore the length of the fence sections was set at 4 km.

Study site 3: along the MPNP fence

In order to avoid recording spoor of the same individuals twice, four maintenance roads were divided into discrete sections that were analyzed separately, depending on distances lion prey species travelled along the fence. Cattle travelled the longest distances (mean ± SE: cattle = 3.1 ± 1 km; greater kudu = 0.3 ± 0.08 km; giraffe = 0.9 ± 0.3 km). The upper quartiles of all analyzed prey species were below the 75 % quartile of cattle (75 % quartiles: cattle = 2.1 km, greater kudu = 0.3 km, giraffe = 0.9 km). The length of the fence sections was therefore set at 2 km. Thirtynine 2 km transects were each covered ten times, resulting in a total transect length of 780 km.

<u>Data analysis and statistics</u>

Prey travel distances along the KGR/CKGR fence and inside KGR/CKGR

Data collection was carried out along the KGR/CKGR fence and inside KGR/CKGR. Apart from being flanked on one side by the game fence, the maintenance road along the fence was similar to the roads inside the reserve. Distances travelled along roads inside the reserve and along the fence were compared. If an animal merely crossed the road, the travel distance was defined to be 1 m. In order to investigate whether there was a difference in the density of lion prey species between the KGR- and the CKGR-part of the fence due to an artificial waterhole at the CKGR-part we further calculated and compared distances from one spoor encounter to the next for both parts of the fence.

Data were tested for deviation from normality using the Kolmogorov-Smirnov test and for equality of variances using the Levene test. Pair wise comparisons were evaluated with a two-tailed t-test.

Lion spoor density along the KGR/CKGR fence and inside KGR/CKGR

Adult lion spoor densities were calculated following Stander (1998). Coefficients of variation (CV) and 95 % confidence intervals were calculated after every increase of the data set. The desired CV, as an indicator of precision, was set at 20 % (Stander, 1998). Funston *et al.* (2010) showed that 30 carnivore track incidences will usually ensure a CV < 20 %. Spoor densities were calculated for the northern and southern section of the KGR/CKGR fence, both fence sections combined and for the inside of the reserve. As set out above, distances between spoor encounters were determined, from which means and variances could be calculated.

Data were tested for deviation from normality using the Kolmogorov-Smirnov test and for equality of variances using the Levene test. Pair wise comparisons were evaluated with a two-tailed t-test.

Spatial predator avoidance along the KGR/CKGR and MPNP fences

The “long-term risk of predation” by lions was defined as the long-term probability of lion presence at a site (Valeix *et al.*, 2009b), which was calculated over a period of nine and eleven months in KGR/CKGR and MPNP respectively. In order to determine if this influenced the spatial distribution of lions’ prey species, the long-term probability of lion and herbivore presence was determined for different sections of the fence line and herbivore species.

During regular data collection on transects, all sections of both fence lines (Table 3.1) were monitored for the presence of lion tracks and tracks of their prey species. Each fence section could either score 1 for the presence or 0 for the absence of spoor per species and day of data collection. For each section and species the mean percentage of spoor presence was calculated over all days of data collection for the whole study period. We then tested for correlations between the fence section-specific percentage of spoor presence of lions (long-term lion encounter risk) and prey (probability of prey occurrence) over the whole study period with Spearman correlations.

Some lion prey species are known to increase their group sizes when the long-term encounter risk of the predators increases (Valeix *et al*., 2009a). Hence, in order to avoid assuming a positive correlation between lion and prey presence due to non-spatial avoidance behaviour, tracks of groups were counted as one track incident.

Results

Prey travel distances along the KGR/CKGR fence and inside KGR/CKGR

Sufficient data for species-specific analyses were recorded for ostrich, red hartebeest, gemsbok and greater kudu, which were defined as the four key prey species for lions along the KGR/CKGR fence line. Comparing travel distances along the fence line and along the roads within the reserve revealed that all four species showed significantly longer travel distances along the fence line (Table 3.2).

Generally, we found significantly longer distances between prey spoor encounters in the south (spoor density = 11.1 spoors/100 km, n = 127 spoors on 780 km of transect), than in the north (spoor density = 16.9 spoors/100 km, n = 164 spoors on 780 km of transect) of the fence (Table 3.2).

Lion spoor density along the KGR/CKGR fence and inside KGR/CKGR

There was no significant difference in the distances between lion spoor encounters along the KGR/CKGR fence (spoor density = 1.8 spoor/100 km, CV = 18.7 %, n = 26 spoors on 1,560 km of transect) and within the reserve (spoor density = 1.3 spoor/100 km, CV = 21.2 %, n = 75 spoor on 2,260 km of transect; Table 3.2). However, comparing distances between spoor encounters from the northern and southern fence sections revealed a much lower spoor density in the south (spoor density = 0.3 spoor/100 km, CV = 81.7 %, n = 2 spoors on 780 km of transect) than in the north (spoor density = 4.2 spoor/100 km, CV = 15.8 %, n = 24 spoors on 780 km of transect). Since we only recorded two track incidences in the south we could not test this statistically. Distances between lion spoor encounters in the northern section of the fence were significantly lower than within the reserve (Table 3.2).

After 75 spoor encounters within the reserve the CV was still above 20 %, whereas the CV for the northern section of the fence line dropped below 20 % after only 10 spoor encounters.

Table 3.2 Herbivore travel distances (in m), distances between prey spoor encounters and distances between lion spoor encounters (in km) in Khutse Game Reserve/Central Kalahari Game Reserve. Values: mean ± standard error, n = xx.

	travel distance (m)		distances between spoor encounter at fence (km)		*P. leo* distance between spoor encounter (km)	
	reserve	fence	north	south		
S. camelus (ostrich)	45 ± 17 n = 14	2852 ± 337 n = 100	20 ± 3 n = 37	24 ± 4 n = 38	reserve (n = 75) 76 ± 6	fence (n = 26) 56 ± 9
	(t = -8.309, p < 0.001)		(t = 0.784, p = 0.436)		(t = 1.691, p = 0.094)	
O. gazella (gemsbok)	118 ± 32 n = 74	2619 ± 353 n = 74	59 ± 8 n = 19	34 ± 5 n = 31	north fence (n = 24) 24 ± 4	south fence (n = 2) 1. spoor = 599 km 2. spoor = 60 km
	(t = -7.056, p < 0.001)		(t = -2.948, p = 0.005)		(no statistics available)	
A. buselaphus (red hartebeest)	1 ± 0 n = 9	1893 ± 228 n = 108	15 ± 2 n = 61	25 ± 6 n = 43	reserve (n = 75) 76 ± 6	north fence (n = 24) 24 ± 4
	(t = -8.284, p < 0.001)		(t = -1.802, p = 0.078)		(t = 7.036, p = < 0.001)	
T. strepsiceros (greater kudu)	46 ± 27 n = 11	1812 ± 249 n = 80	30 ± 3 n = 45	40 ± 9 n = 28		
	(t = -7.064, p < 0.001)		(t = 1.124, p = 0.269)			
P. leo prey			6 ± 0 n = 162	9 ± 1 n = 140		
			(t = 3.922, p < 0.001)			

Spatial predator avoidance along the KGR/CKGR and MPNP fences

Spoor of individual lions and their four key prey species (ostrich, gemsbok, red hartebeest, greater kudu) was analyzed along the fence line of KGR/CKGR. Besides gemsbok, all other prey species' probabilities of occurrence were positively correlated with the long-term lion encounter risk (ostrich: $r_s = 0.614$, $n = 30$, $p < 0.001$; red hartebeest: $r_s = 0.630$, $n = 30$, $p < 0.001$; greater kudu: $r_s = 0.459$, $n = 30$, $p = 0.011$; Figure 3.3). In contrast, the occurrence probability of gemsbok was not correlated to the long-term lion encounter risk ($r_s = -0.189$, $n = 30$, $p = 0.317$; Figure 3.3).

Along the MPNP fence, sufficient data for species-specific analyses were collected for greater kudu, giraffe and cattle. None of the prey species' probabilities of occurrence were correlated with the long-term lion encounter risk (greater kudu: $r_s = 0.011$, $n = 39$, $p = 0.947$; giraffe: $r_s = -0.211$, $n = 39$, $p = 0.196$, cattle: $r_s = 0.034$, $n = 39$, $p = 0.835$; Figure 3.4).

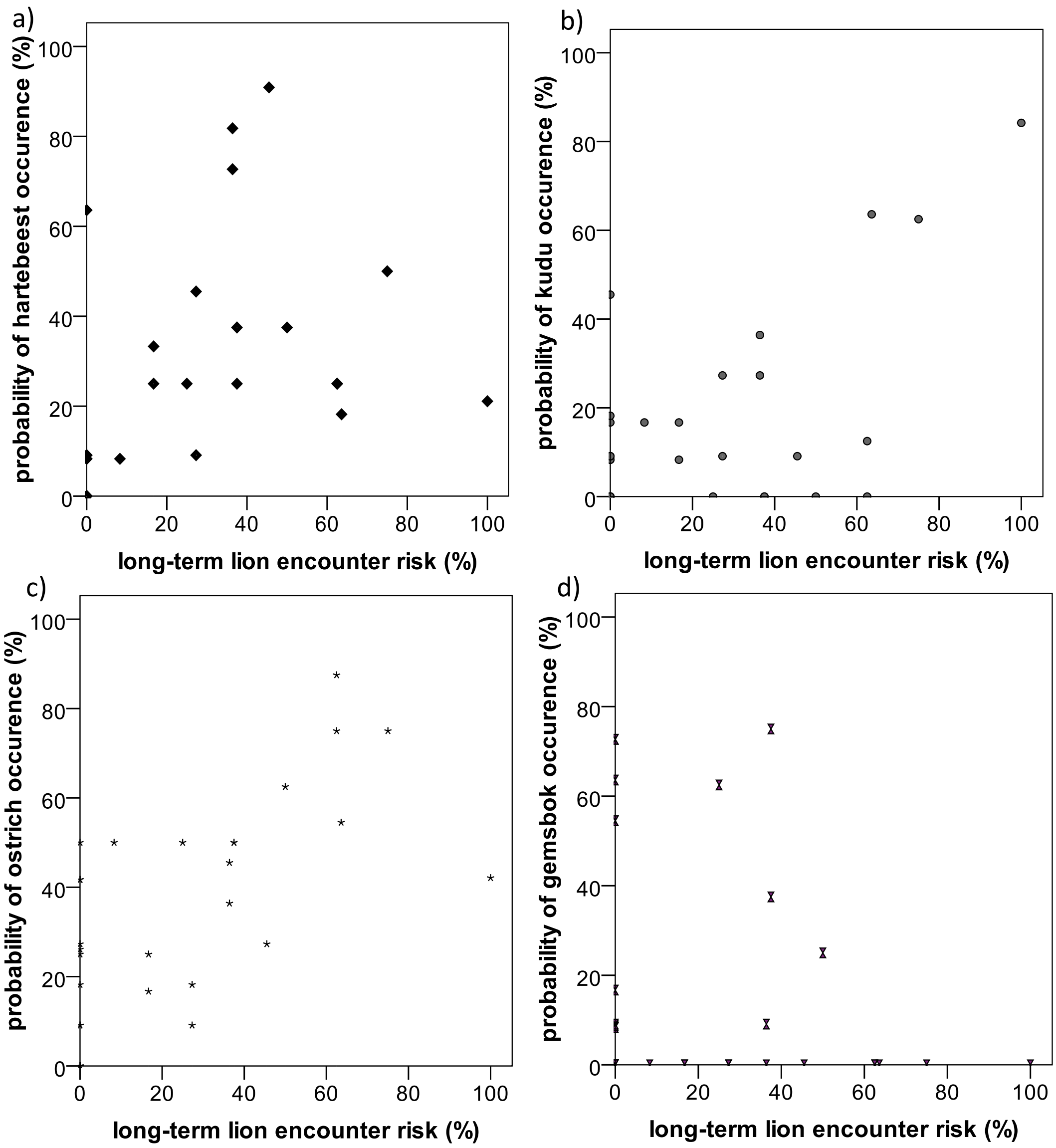

Figure 3.3 Probability of prey occurrence in dependency of the long-term lion encounter risk along the Khutse Game Reserve/Central Kalahari Game Reserve fence for a) red hartebeest, b) greater kudu, c) ostrich and d) gemsbok.

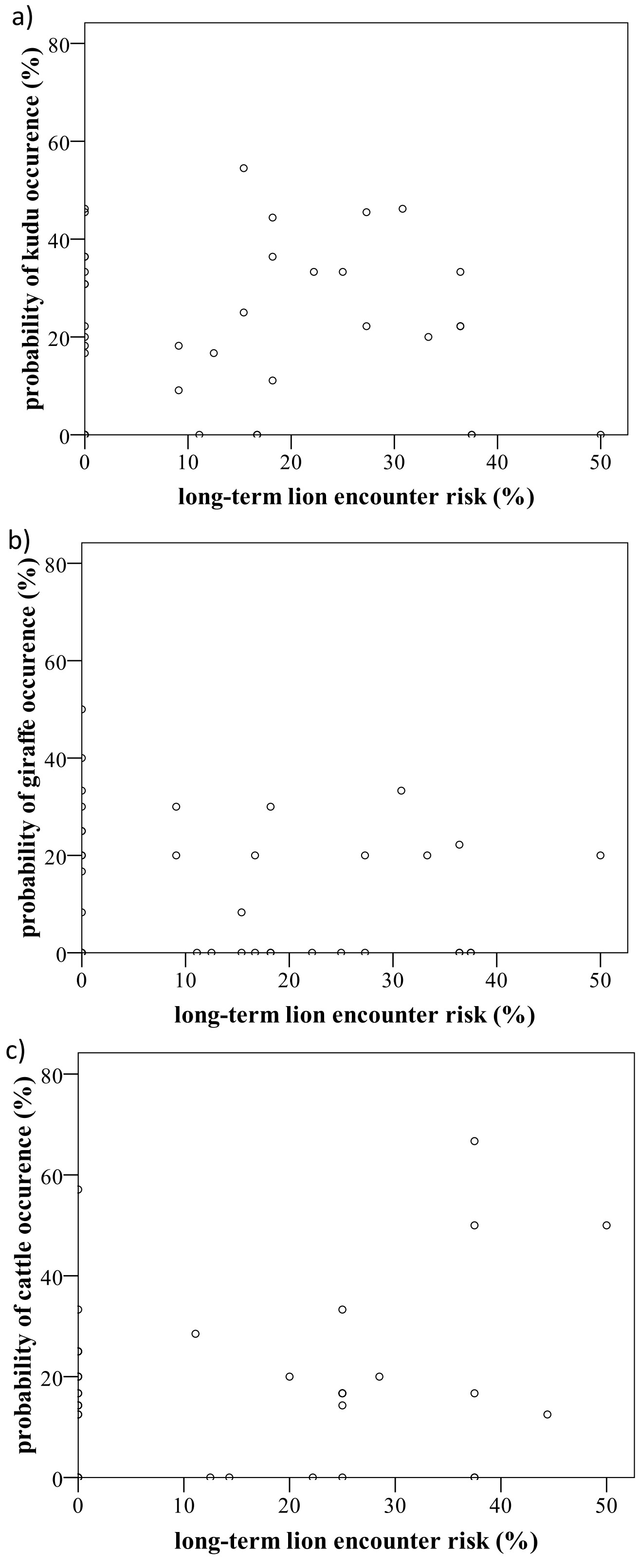

Figure 3.4 Probability of prey occurrence in dependency of the long-term lion encounter risk along the Makgadikgadi Pans National Park fence for a) greater kudu, b) giraffe and c) cattle.

Discussion

Game fences represent considerable artificial barriers in the landscape and are known to be used by predators to trap and capture prey animals (Adendorff & Rennie, 1984; Albertson, 1998; Van Dyk & Slotow, 2003; Rhodes & Rhodes, 2004; Ferguson & Hanks, 2010). They have the potential to create a new kind of edge effect for herbivore populations by offering their predators a hunting advantage. Therefore this study investigated whether lion prey species were trapped at a new fence, whether lions were attracted by this increased prey density and whether or not prey species had learned to avoid lions spatially, seven years after fencing.

Our results suggest that new fences restrict daily movement behaviour of greater kudu, gemsbok, red hartebeest and ostrich. As other studies suggest (Goodwin, 1985 cited in Hoare, 1992; Albertson, 1998), the animals appear to be trapped and therefore accumulate along fences, which was particularly true for the northern section of the KGR/CKGR fence, where there is a pumped waterhole and several bore holes at cattle-posts in the livestock dominated area, in close vicinity to the fence. In this area, we further found higher densities of lion tracks compared to the inside of the reserve and the predators seem to be attracted by higher prey densities, as a previous study in northern Botswana suggests (Albertson, 1998). In contrast to Funston *et al.*'s (2010) suggestion that 30 carnivore track incidences will usually ensure sufficient precision with a CV < 20 %, we still calculated a CV > 20 % after 75 lion spoor encounters within the reserve. However, along the northern section of the game fence, the CV dropped below 20 % after only 10 lion spoor encounters. This supports the suggestion that lions regularly frequented the area of higher prey density and presumably higher prey catchability along the northern fence section. In comparison, lion spoor encounters were less frequent and very irregular inside the reserve, where prey aggregations were less predictable.

As expected, we did not find spatial avoidance of lions by their prey species at the new KGR/CKGR fence. In fact, for most of the tested prey species we even found positive correlations between the percentage of days with spoor being detected and the long-term lion encounter risk. This result supports the hypothesis that lions were attracted by animals trapped along the new game fence in KGR/CKGR, where prey animals had not yet adapted to the new barrier and therefore did not show spatial avoidance behaviour of the predators. Out of all analyzed species, gemsbok and kudu are the preferred lion prey within the study area (Lerch & Truessel, 2007; pers. comm. C. Graf) and gemsbok was the only species whose spatial distribution did not show a correlation with the long-term lion encounter risk. This is probably due to the species' independence of water as most gemsbok tracks were found in the far south of the fence line, where there are no pumped waterholes and where we did not find much lion activity.

Along the seven-year-old MPNP fence, there was no spatial correlation between prey species and lions. Hence, lion prey species did still not actively avoid the predators along the fence, which they do in landscapes without artificial barriers (Valeix *et al.* 2009, a & b). This is most probably due to the Boteti River representing the only reliable water source in the area and herbivores as well as carnivores are attracted to this resource. Therefore, it seems that the fence alignment along the river and the fence blocking off access for wildlife in most areas disables lion prey species to avoid their predators spatially along the MPNP fence. Other studies have demonstrated that even years after completion carcasses are still frequently found along game fences (Adendorff & Rennie, 1984; Van Dyk & Slotow, 2003; Reed & Sautereau, 2005; Ferguson & Hanks, 2010). Animals are thought to learn about a new barrier and eventually how to avoid increased hunting pressure along fences. Some species such as giraffe though, are known to adapt very slowly to a new boundary and continue to be trapped and entangled in game fences (Goodwin, 1985 cited in Hoare, 1992; Albertson 1998).

Our results suggest that fences not only have an initial but also a long-term negative influence on predator avoidance behavior by herbivores, at least in areas where the fence alignment does not take ecological factors such as access to essential water resources into account. Seven years after completion of a fence line lion prey species had not developed spatial avoidance behaviour of lions and had therefore not fully adapted to a potentially increased hunting risk along the fence. Hence, fences have the potential to create a new kind of edge effect to herbivore populations. In order to avoid potentially adverse impacts on these populations, especially in small protected areas with small herbivore populations or areas hosting migratory species, careful consideration should be taken of the consequences of increased vulnerability of prey species to predation along artificial barriers when planning new fences and their alignment. Further research is needed on the impact of fences on herbivore population numbers and predator avoidance behaviour on a temporal level or by increasing of group sizes.

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Author contribution

I hereby confirm that Kesch conceived, designed and performed the experiments, analysed the data and wrote the paper.

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Changes in forage biomass and quality after exclusion of livestock in the southern Kalahari

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Abstract

In many southern African grazing systems, wild-ranging wildlife has been replaced by livestock, which often leads to overgrazing and, as a result, bush and shrub encroachment is a major problem in these areas. It leads to the reduction of grasslands, the invasion of thorn shrubs, a reduced carrying capacity for livestock, desertification and socio-economic problems in arid and semi-arid regions as previously profitable areas become economically unviable. This study aims to determine how standing biomass of grass vegetation and its key chemical characteristics differ between low and high grazing pressure. Furthermore, it determines the required time period needed for pasture in heavily grazed areas to recover from overgrazing effects and approach the properties of pasture under low grazing pressure. The results showed that grazing leads to lower fibre and hemicellulose and higher protein content, but lower absolute nutrient availability in continuously grazed areas. Heavy grazing further had a negative influence on grass biomass, whereas the exclusion of livestock resulted in a rapid increase of grass biomass, higher fibre and hemicellulose contents and higher absolute nutrient availability after one rainy season. Furthermore, a high abundance of unpalatable plant species was found in the heavily grazed area. In order to prevent overgrazing and subsequent negative impacts like bush encroachment or desertification in areas where cattle substitutes wild-ranging herbivores, it is necessary to

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implement rotating grazing systems and lower stocking rates, as well as the use of a combination of different wild and domestic herbivores for sustainable development.

Keywords bush encroachment, chemical components in grass, desertification, fencing, grass biomass, livestock, overgrazing

Introduction

Fifty percent of the worldwide terrestrial surface is used as rangeland, a large amount of which is populated with wild-ranging herbivores (Gordon, 2006). Due to their influence on plants, which play an important role in ecosystem processes and functionality, the impact of large herbivores is enormous. Different herbivore species are supported by different habitats with varying plant communities, which are mainly driven by abiotic factors (e.g. soil characteristics and climate). However, herbivores influence plants in different ways and at different scales, from direct impact through feeding damage to alteration of plant communities through selective feeding behaviour (e.g. Milchunas & Lauenroth, 1993). Furthermore, feeding damage can alter the chemical composition of plants, leading to such wide-ranging consequences as changes in litter quality. While some plant species respond to grazing or browsing by producing feeding deterrents, others compensate by increasing growth of high quality items (e.g. Skarpe, 1991; Bergstroem, 1992; Bryant, Reichardt & Clausen, 1992; Leriche *et al.*, 2003; Stolter *et al.*, 2005; Fornara & du Toit, 2007; Stolter, 2008). Changes in the chemical composition of plants due to feeding damage might lead to changes in utilization by subsequent herbivores (Skarpe, 1991; Bergstroem, 1992; Stolter, 2008). The composition of plant primary compounds (e.g. nitrogen) as a nutritional source for herbivores, and plant secondary compounds (e.g. tannins) as defence mechanisms against browsing, might indicate the attractiveness of plants to utilization by herbivores.

Therefore, the impact of herbivores on plants can lead to cascading responses throughout different trophic levels, from the soil microbial community (e.g. Hobbs, 1996; Bardgett, Wardle & Yeates, 1998; Hamilton & Frank, 2001; Van der Wal *et al*., 2004) up to apex predators (e.g. Huntley, 1991; Häggström & Larsson, 1995; Krebs *et al.*, 1995; Turchin *et al.*, 2000). Hobbs (1996) described three feedbacks from herbivores to plant communities: a) the regulation of process rates, b) the modification of spatial mosaics, and c) the possible control of transition between alternative ecosystem states. The magnitude of herbivores' impact on plant systems depends on a variety of factors, such as intensity and timing of grazing or browsing, herbivore species composition, competition between herbivore or plant species, as well as abiotic factors (e.g. climate).

African grazing systems are historically shaped by the seasonal movements of wild ranging large herbivores. However, due to changes in land-use, large areas are now continuously grazed by cattle. Although bush encroachment is also assumed to be a natural process in savannah succession (Ward, 2005), it is enhanced through overgrazing by livestock, in combination with fire suppression, climatic effects and lack of browsers (e.g. Skarpe, 1990; Moleele *et al.*, 2002; Joubert, Rothauge & Smit, 2008). Bush or shrub encroachment is a major problem in southern Africa as it leads to the reduction of grasslands, the invasion of thorn shrubs and ultimately to the reduction of livestock carrying capacity. Bush encroachment is caused mainly by different *Acacia* species in concert with some other plant species, such as *Dichrostachys cinerea, Euclea undulata, Grewia flava, Lycium namaquense* (Skarpe, 1990; Moleele & Perkins, 1998). It causes socio-economic problems in arid and semi-arid regions as previously profitable areas are no longer economically viable (Smit, 2004). Furthermore, in arid regions, high grazing pressure could lead to the loss of soil fertility by erosion resulting in desertification of formerly productive grassland (Schlesinger *et al.*, 1990).

The Kalahari Transect Wet Season Campaign in 2000 documented increased grazing pressure in the southern Kalahari, bordering and affecting the Khutse Game Reserve (KGR) and the southern border of Central Kalahari Game Reserve (CKGR), where cattle replaced migratory wildlife (Shugart *et al.*, 2004). High livestock grazing is known to cause high losses of green leaf biomass, annual net primary production and grass coverage (Perkins, 1996; Verlinden *et al*., 1998; Boone, 2005). These processes, in turn, support the process of bush encroachment (Roques, O'Connor & Watkinson, 2001; Moleele *et al.*, 2002; Boone, 2005; Joubert, Rothauge & Smit, 2008).

In 2009, a game fence was installed along the borders of KGR and CKGR, in order to protect livestock from predation by African lions. Prior to fence construction, livestock was grazing the eastern border of KGR and the southeastern border of CKGR, resulting in overgrazing. The exclusion of livestock from the game reserves after fencing allowed the effects of livestock grazing on grass biomass production and its chemical composition to be studied, and changes under different grazing regimes over time to be monitored. Taking advantage of this experimental setup, we posed the following questions:

1. How does standing biomass of grass vegetation and key chemical characteristics differ between low and high grazing pressure?

2. If there were differences: How much time does pasture in heavily grazed areas need to recover from overgrazing effects to approach the properties of pasture under low grazing pressure?

Chapter Four

Methods

Study site

The study was carried out in Khutse Game Reserve (KGR)/south-eastern Central Kalahari Game Reserve (CKGR), Botswana. The KGR (2,600 km^2) is situated between 23 - 24 °S and 24 - 25 °E, within the Kweneng District in southern Botswana, bordering the CKGR (52,000 km^2) in the north. The semi-arid climate is characterized by a cold dry season (April - September) and a hot rainy season (October - March), average annual rainfall of 300 mm (de Vries, Selaolo & Beekman, 2000) and average monthly temperatures between 8.5 °C and 35.5 °C (Thomas & Shaw, 1991). The landscape is predominantly flat and characterized by tall grass, open salt pans and thorn bush thickets with scattered acacia trees. In October 2009, an electrified double game fence (2.7 m wire netting fence with four electrified wires; 1.5 m wire netting cattle fence) was completed along the southern and eastern border of KGR and around the south-eastern corner of CKGR, resulting in a barrier of about 300 km, intended to stop livestock predation by African lions (*Panthera leo*). More details on the fence and its effects on native wildlife are provided by Kesch, Bauer & Loveridge (2014).

Grass sampling

Three sampling sites were installed in three different areas: Site 1 (23°21'54" S, 24°37'24" E) is located outside the protected area and therefore outside the fenced area. It was characterized by intensive grazing by livestock, mainly cattle, which was supposed to have remained stable throughout the study. Site 2 (23°21'48" S, 24°37'16" E) is located inside the reserve and therefore inside the fenced area. Prior to the installation of the fence, the area was subject to a similar grazing pressure by livestock as Site 1. Due to the exclusion of livestock after the construction of the fence, grazing pressure was reduced to a similar intensity as at Site 3, starting in October 2009. Site 3 (23°20'33" S, 24°32'55" E) is located 8 km inside KGR. It is characterized by low grazing pressure by wildlife such as greater kudu (*Tragelaphus strepsicerus*), gemsbok (*Oryx gazella*) and red hartebeest (*Alcelaphus buselaphus*). The grazing pressure is supposed to have remained stable throughout the study.

At each site we established a grid of 7 x 3 sampling plots (each sampling plot 10 x 10 cm^2), spaced at regular distances of 20 m, resulting in 21 sampling plots per site. Plots were sampled in June 2009 (dry season), September 2009 (dry-wet), December 2009 (wet), March 2010 (wet-dry) and June 2010 (dry 2). During each sampling month, all grass material in each of the 21 sampling plots (10 x 10 cm^2) per site was cut 5 cm above the ground. In order to avoid sampling the same plots again, transects were shifted north by 1 m every three months. Grass biomass was measured as wet weight immediately after cutting and as dry mass after drying in the sun until the samples had reached a constant weight.

Chemical analyses

Chemical analyses were run separately for the pooled plant material harvested from each sample of the 10 x 10 cm^2 plots if enough plant material was available. Neutral Detergent Fiber (NDF) and Acid Detergent Fiber (ADF) represent components of the cell wall. ADF consists of cellulose, lignin and minerals. Whereas cellulose is digested by symbionts in the rumen and delivers their main energy, lignin is indigestible for most ruminants. NDF consists of ADF plus hemicellulose, which is digestible by all herbivores. Hemicellulose (HC) is calculated by subtracting ADF from NDF. Nitrogen in grass is mostly contained in protein and can be converted to crude protein by multiplication with the standard factor of 6.25 (Robbins, 1983). Analyses of these components were carried out at the chemical laboratory of the Department of Animal Ecology and Conservation at the University of Hamburg in Germany. Analyses follow the procedures described by Stolter *et al.* (2005). At some plots and dates the plant material collected was insufficient for chemical analyses. In this case, two to three samples were combined per site and date.

The amount of protein and hemicellulose per unit area was calculated by multiplying the dry biomass per 100 cm² sample with the average concentrations of protein or hemicellulose for the plot and date.

Statistics

We applied non-parametric Kruskal Wallis Analysis of Variance (X^2) to the analyses of biomass production and the amount of protein and hemicellulose per unit area as measurements of dry biomass deviated from normality. For the different sites and sampling times, the concentrations of NDF, ADF, hemicellulose and crude protein did not deviate from normality. For the concentrations of chemical components we applied parametric ANOVA with post-hoc tests as provided by IBM SPSS 22.0.

Results

Biomass

Biomass of Site 1 (high grazing pressure by livestock) was always significantly lower than at Site 3 (low grazing by wildlife) (Table 4.1). Site 2 did not differ from Site 1 prior to the construction of the fence, but differed significantly from Site 3. After construction of the fence and the onset of the rainy season, biomass at Site 2 increased compared to Site 1.

The difference in biomass between Sites 1 and 2 started to be significant only after the wet season in June 2010 (measurement in the subsequent dry season). At this time, biomass at Site 2 was no longer statistically different from biomass at Site 3. The standing biomass of grass remained stable at Sites 1 and 3 throughout the year.

Table 4.1 Grass biomass (dry weight) and chemical composition in three different areas of grazing pressure. Values for biomass, protein and HC per 100 cm² are medians and quartiles based on dry mass of plants in grams cut in 21 x 100 cm² plots per site and month. Values for chemical components are means ± standard deviation (in % of dry mass); N = sample size for the samples available for chemical analyses. Values for HC and Protein per 10 cm² were calculated as the median biomass times the mean concentration of HC or Protein, respectively. Statistics are based on Kruskal-Wallis-Analysis of Variance for biomass, protein and HC per 100 cm² (X^2) and ANOVA (F-values) for chemical items. Different superscripts indicate different median / mean values according to post-hoc tests. Significance levels are marked with asterisks: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Item	Season / year	**Site 1** livestock	**Site 2** livestock → no livestock	**Site 3** no livestock	Statistics
Biomass [g / 100cm²]	Dry / 2009	3-4^a-8	5-10^a-23	10-25^b-96	X^2 = 22.62***
	Dry-wet / 2009	0-2^a-8	0-2^a-8	4-24^b-33	X^2 = 13.43***
	Wet / 2009	0-3^a-8	0-13^a-28	9-31^b-51	X^2 = 16.72***
	Wet-dry /2010	0-3^a-8	7-15^a-29	12-26^b-60	X^2 = 16.51***
	Dry / 2010	0-2^a-6	15-24^b-46	29-33^b-71	X^2 = 26.88***
NDF [%]	Dry / 2009	68.3 ± 7.2	71.7 ± 4.1	72.2 ± 3.4	F = 2.61
	Dry-wet / 2009	64.8^a ± 6.6	72.7^b ± 3.5	71.5^{ab} ± 3.7	F = 7.54**
	Wet / 2009	57.8^a ± 14.8	71.8^b ± 6.5	76.0^b ± 4.7	F = 13.99***
	Wet-dry /2010	70.1^a ± 10.9	77.4^b ± 4.3	77.1^{ab} ± 3.8	F = 5.80**
	Dry / 2010	71.0 ± 11.1	76.3 ± 4.0	73.7 ± 4.8	F = 2.56
ADF [%]	Dry / 2009	45.2 ± 5.1	44.8 ± 6.0	42.1 ± 4.3	F = 1.67
	Dry-wet / 2009	39.9 ± 2.7	42.3 ± 4.9	42.3 ± 3.6	F = 1.22
	Wet / 2009	35.1^a ± 5.6	43.2^b ± 4.8	46.1^b ± 4.8	F = 15.31***
	Wet-dry /2010	43.0^a ± 5.4	42.9^a ± 3.2	47.2^b ± 4.6	F = 5.64**
	Dry / 2010	44.6 ± 6.3	43.1 ± 2.8	43.3 ± 5.0	F = 0.32
HC [%]	Dry / 2009	23.1^a ± 7.5	26.9^{ab} ± 6.8	30.1^b ± 1.6	F = 5.42**
	Dry-wet / 2009	24.9^a ± 7.0	30.3^b ± 2.6	29.2^{ab} ± 2.5	F = 4.23*
	Wet / 2009	22.6^a ± 10.4	28.5^{ab} ± 6.4	29.8^b ± 2.1	F = 4.13*
	Wet-dry /2010	27.0^a ± 7.8	34.4^b ± 2.6	29.9^a ± 3.8	F = 10.28***
	Dry / 2010	26.4^a ± 11.7	33.2^b ± 3.1	30.4^{ab} ± 2.3	F = 5.13**

Table 4.1 continued from page 102

HC [g / 100cm²]	Dry / 2009	0.7-0.9^{a}-1.8	1.2-2.7^{b}-6.2	3.0-7.5^{b}-28.7	X^2 = 26.64***
	Dry-wet / 2009	0-0.5^{a}-2.0	0-0.6^{a}-2.3	1.2-7.2^{b}-9.6	X^2 = 13.46***
	Wet / 2009	0-0.7^{a}-1.7	0.1-3.7^{b}-7.9	2.5-9.2^{b}-15.2	X^2 = 18.84***
	Wet-dry /2010	0-0.8^{a}-2.2	2.2-5.2^{b}-9.8	3.6-7.8^{b}-17.8	X^2 = 17.66***
	Dry / 2010	0-0.5^{a}-1.6	4.8-8.0^{b}-15.1	8.8-10.0^{b}-21.6	X^2 = 28.23***
Protein [%]	Dry / 2009	6.0^{a} ± 2.6	4.7^{ab} ± 1.9	3.5^{b} ± 0.6	F = 7.25**
	Dry-wet / 2009	6.3^{a} ± 3.2	3.9^{b} ± 1.8	3.2^{b} ± 0.5	F = 8.68***
	Wet / 2009	9.9^{a} ± 3.8	5.4^{b} ± 2.7	4.6^{b} ± 3.3	F = 9.11***
	Wet-dry /2010	7.2^{a} ± 3.2	4.8^{b} ± 0.9	4.2^{b} ± 1.1	F = 11.51***
	Dry / 2010	6.7^{a} ± 3.1	3.7^{b} ± 1.1	3.7^{b} ± 0.7	F = 13.27***
Protein [g / 100cm²]	Dry / 2009	0.1-0.2^{a}-0.5	0.2-0.5^{a}-1.1	0.4-0.9^{b}-3.3	X^2 = 13.03***
	Dry-wet / 2009	0-0.1^{a}-0.5	0-0.1^{a}-0.3	0.1-0.8^{b}-1.1	X^2 = 10.29**
	Wet / 2009	0-0.3^{a}-0.7	0-0.7^{ab}-1.5	0.4-1.4^{b}-2.3	X^2 = 9.19**
	Wet-dry /2010	0-0.2^{a}-0.6	0.3-0.7^{ab}-1.4	0.5-1.1^{b}-2.5	X^2 = 10.94**
	Dry / 2010	0-0.1^{a}-0.4	0.5-0.9-1.7	1.1-1.2^{b}-2.6	X^2 = 21.28***
Sample size	Dry / 2009	N = 14	N = 16	N = 16	
	Dry-wet / 2009	N = 8	N = 8	N = 17	
	Wet / 2009	N = 10	N = 13	N = 17	
	Wet-dry /2010	N = 11	N = 20	N = 19	
	Dry / 2010	N = 8	N = 21	N = 21	

NDF = Neutral detergent fiber; ADF = Acid detergent fiber; HC = hemicellulose

Fiber

For most of the year, fiber contents varied between sites (Table 4.1). At the transition between dry and wet season (dry-wet), there was a tendency of a lower content of all fiber fractions at Site 1. In December (wet), at the beginning of the wet season, fiber concentrations were significantly lower at Site 1 than at the other sites.

Crude Protein

Crude protein concentrations were always significantly higher at the site with heavy grazing pressure (Site 1) than at Site 3. Site 2 resembled Site 3 throughout the study.

Absolute nutrient availability

In absolute terms, the amount of protein and hemicellulose available in plant biomass per unit area were always highest at Site 3 and remained high at this site year-round. Prior to fencing, Site 2 resembled Site 1 but shifted towards Site 3 after the installation of the fence (Table 4.1).

Differences within grass species between sites

In June 2010 (dry 2), species were identified at plots that consisted of a single grass species. Due to the restricted sample size the comparison of different chemical components was only feasible for Spear grass (*Heteropogon contortus*) (Table 4.2). The differences between sites within the species match the pattern of the samples, where different grass species had been pooled. Acid detergent fiber was lowest and protein was highest at the site with highest grazing pressure (Table 4.2).

Table 4.2 Chemical composition of Spear grass *Heteropogon contortus* collected in June 2010 (dry 2) at sites of different grazing pressure. N = sample size; significance levels are marked with asterisks: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Chemical compound	**Site 1** (n = 3) livestock	**Site 2** (n = 2) livestock → no livestock	**Site 3** (n = 11) no livestock	F (differences between sites)
Grazing pressure	high	low	low	
NDF [%]	76.0 ± 3.7	71.6 ± 42.1	76.9 ± 2.5	2.28
ADF [%]	42.3 ± 1.5	42.1 ± 1.5	47.0 ± 3.0	4.65*
HC [%]	33.7 ± 3.3	29.5 ± 3.5	30.0 ± 2.1	2.98
Protein [%]	6.1^{a} ± 0.6	4.6^{ab} ± 0.1	3.5^{b} ± 0.9	13.13***

Differences between grass species per site

The comparison of the chemical composition between grass species within a given site was restricted to species for which more than one sample was available in June 2010 (dry 2). This limited feasible comparisons of grass species to Site 2 (*Heteropogon contortus, Pogonarthia squarrosa, Eragrostis contortus* and *Anthephora pubescens*). Protein concentrations differed significantly between species. All other components measured were not significantly different (Table 4.3).

Table 4.3 Chemical composition (in %) of different grass species collected in June 2010 (dry 2) at site 2 (livestock excluded after October 2009) of low grazing pressure. N = sample size; significance levels are marked with asterisks: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Chemical compound	Spear grass (*Heteropogon contortus*	Herringbone grass (*Pogonarthria squarrosa*)	Lehmann's love grass (*Eragrostis contortus*)	Wool grass (*Anthephora pubescens*)	F (differences between species)
N	2	2	12	3	
NDF [%]	71.6 ± 42.1	77.8 ± 2.1	78.2 ± 2.9	74.2 ± 3.6	2.85
ADF [%]	42.1 ± 1.5	46.2 ± 1.0	43.5 ± 2.6	42.8 ± 2.3	0.42
HC [%]	29.5 ± 3.5	31.7 ± 1.1	34.6 ± 2.2	31.3 ± 5.1	2.88
Protein [%]	$4.6^{ab} \pm 0.1$	$3.4^{a} \pm 0.7$	$3.1^{a} \pm 0.5$	$5.7^{b} \pm 1.5$	11.92***

Discussion

The first objective of the study was to describe how grass vegetation differs in standing biomass and key chemical characteristics under low and high grazing pressure. Over an annual cycle, plants from the heavily grazed area always contained higher concentrations of protein than plants from areas of low grazing pressure. This might be due to the consumption of most of the available biomass by grazing animals in the area of high grazing pressure, so that only the little plant material left can become moribund in the dry season. Not eaten grasses (e.g. left-over grasses or grasses under low grazing pressure) start to die off at the beginning of the dry season, resulting in the common phenomenon of high fiber proportions in the remaining standing biomass (Georgiadis & McNaughton, 1990; Biondini, Patton & Nyren, 1998). This is most evident at Site 1 at the beginning of the wet season in December. Here, the low fiber content might reflect the high proportion of new growth and the lower proportion of old grass due to heavy grazing by livestock year-round. The findings of higher concentrations of protein at the site with higher grazing pressure are underpinned by the intra-species comparison of *Heteropogon contortus* growing on the three different sites. However, at Site 3 (no livestock) the relatively lower quality of fodder (concerning protein) in the area of low grazing pressure is compensated by the high biomass available. As a result, the total amount of protein available per unit area is much higher in the area of low grazing pressure than in the areas of high grazing pressure.

Apart from the “left-over hypothesis” described above that leads to more moribund grass at sites with low grazing activity, another reason for higher nitrogen concentration on heavily grazed sites might be the fertilization by dung and urination of herbivores (Hobbs, 1996; Hamilton *et al.*, 1998; Wilsey, 2002; Rufino *et al.*, 2006). Additionally, a Fabaceae species, *Elephantorrhiza elephanthina*, was abundant at Site 1. This plant family is known for the ability to fix nitrogen and thus improve soil quality. Furthermore, the nitrogen concentration in plants is directly connected to nutrient cycling below-ground. Holland & Detling (1990) and Hamilton & Frank (2001) found that grazed plants decreased root carbon inputs into the soil via rhizosphere. This resulted in lower carbon availability to decomposers and a subsequent increase in plant-available nitrogen. This might be an explanation for the ability of plants to react to browsing or grazing with higher nitrogen content, which is often related to compensation growth. This phenomenon is also known from other grass (Fanselow *et al.*, 2011) and woody plant species such as *Salix* species (Stolter *et al*., 2005) and *Acacia nigricans* (Fornara & du Toit, 2007). Thus, the higher nitrogen content in plants growing under high grazing pressure may not simply result from relatively higher proportion of new growth on the overall plant biomass. Higher nitrogen concentration in leaves might also positively influence the nutrient turnover by enhancing the quality of litter, which might be easier to decompose. However, in overgrazed areas (e.g. Site 1), this litter is not available, and the impact of grazing on soil fertility might be dependent on the grazing history of the area. Another reason for the differences between sites could stem from differences in plant species composition. The same plant species differed in chemical composition between sites, while different plant species had different chemical properties when growing at the same site (e.g. *Heteropogon contortus*). Since we collected "fodder" per unit area without discriminating between plant species and parts, we cannot identify the reasons for the chemical differences between sites.

For the second objective, we assessed how much time the pasture in heavily grazed areas requires in order to recover from overgrazing effects and approach the chemical properties of pasture under low grazing pressure. The results showed that, in terms of grass biomass, a formerly heavily overgrazed area in the Kalahari needed one rainy season to recover from overgrazing. Biomass production of sampling Site 2 (just inside the fence) increased dramatically with the beginning of the rainy season. Already in December 2009 (wet) there was no longer any significant difference between the formerly overgrazed area and the low grazing area inside the reserve. By the end of the rainy season in March 2010 (wet-dry), the biomass at Site 1 (high grazing livestock) and Site 2 (fenced for about nine months) began to differ significantly. At first glance these results sound encouraging but we must keep in mind that this is only due to grass biomass.

Based on qualitative assessments, plant species composition within Site 2 remained very different from the low grazing control area inside the reserve. While *Heteropogon contortus* (Spear grass) dominated the species' composition in the low grazing area, *Eragrostis lehmanniana* (Lehmann's love grass) represented the main species in the formerly overgrazed area. Lehmann's love grass typically grows in areas with past disturbance (Van Oudtshoorn, 1999). As such, it is an indicator for formerly overgrazed areas, which has been confirmed in this study. It is a valuable fodder grass and often used to resow sandy or loamy soil in arid regions (Van Oudtshoorn, 1999). In contrast, Spear grass is one of the most common grasses in southern Africa. It is only palatable in early summer, can grow in poor soils and is very resistant to fire (Van Oudtshoorn, 1999). Other studies found an increase in unpalatable plants (Díaz *et al.*, 2007) or plants with high grazing tolerance (Todd & Hoffman, 1999) as a response to grazing. This was also obvious for Site 1, where *Elephantorrhiza elephantina*, a medicinal plant seemingly avoided by cattle and known to become abundant in overgrazed areas (Van der Walt & le Riche, 1999), was the dominant deciduous scrub. This dominance might underscore the importance of different herbivores (grazers and browsers in combination) to avoiding underutilization or high abundance of specific plants. Milchunas & Lauenroth (1993) found that changes in dominant species are most evident during early years of comparisons between grazed and ungrazed areas. However, changes in plant composition seem to be more sensitive to changes in ecosystem-environmental independent variables than changes in grazing variables (Milchunas & Lauenroth, 1993; Hendricks *et al.*, 2005; Anderson & Hoffman, 2007). Furthermore, the timing of grazing (Bullock *et al.*, 2001), the grazing history (e.g. duration/intensity and duration/resource availability; Cingolani, Noy-Meyr & Díaz, 2005; Tessema *et al.*, 2011) and herbivore species composition (Albon *et al*., 2007; Allred *et al.*, 2012) seem to be important for changes in plant community structure. Since ours was a short-term study, we mainly concentrated on short-term changes such as plant-chemistry and biomass. Further investigations regarding long-term changes in plant community structure would be very beneficial for understanding grazing-plant interactions in this area.

The results of our study show that grazing leads to higher protein contents in continuously grazed areas. This result might depend on the ability of the plant to respond to grazing (grazing tolerance) and to assess essential nutrients. Heavy grazing had a negative influence on biomass production of grasses, simply because all grasses were consumed by cattle. The exclusion of livestock resulted in a rapid biomass increase even after years of grazing, which underscores the potential of the plants to recover from heavy grazing. Within the timeframe of our study, changes in plant composition were not to be expected after the installation of the fence. However, we found differences between different grazing regimes, with a high abundance of unpalatable plant species at the grazed site. In anthropogenic grazing systems, where cattle substitute wild-ranging herbivores, natural long distance movements are no longer possible. To prevent overgrazing and subsequent negative impacts such as bush encroachment or desertification and to promote sustainable development, it is necessary to implement management strategies, including rotating grazing systems and lower stocking rates, as well as the use of different herbivores (e.g. a combination of cattle, goats and wildlife; e.g. Albon *et al*., 2007; Dickhoefer *et al.*, 2010). Here, fences can be of much use in excluding herbivore species from certain areas, therefore giving the vegetation time to recover.

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Author contribution

I hereby confirm that Kristina Kesch conceived, designed and performed the experiments, analysed the data and contributed to the writing of the paper.

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Discussion

Around the world, fencing is being used for varying purposes. While Australia was one of the first countries to use large scale fencing as a tool for pest control (McKnight, 1969; Dickman, 2012), North America mainly utilizes fences for re-wilding projects (Donlan *et al.*, 2005) and to reduce road accidents with deer (Clevenger, Chruszcz & Gunson, 2001). India on the other hand has only recently started to consider fencing in conservation (Hayward & Somers, 2012). In Africa, fences are mostly being used to mitigate a large variety of human-wildlife conflict, ranging from livestock- or crop-raiding carnivores and elephants respectively (Ferguson & Hanks, 2010) to disease transmission between wildlife and livestock (Gadd, 2012), but also to “rewild” farm land and for the reintroduction of wildlife (Hunter *et al.* 2007; Slotow & Hunter, 2009; Hayward, 2012). Within the continent, there are many different reasons for and approaches to fencing. While fencing in East and Central Africa is very limited, southern Africa is crisscrossed with fences (Hayward & Somers, 2012; Lindsey *et al.*, 2012). Zimbabwe has historically used fencing to contain diseases such as foot-and-mouth disease in certain areas and to control the spread of the tsetse fly (Foggin, 2010). Densely populated countries such as South Africa are using fencing mainly in order to control human-wildlife conflict around many isolated protected areas, but also to delineate boundaries between private properties in order to control ownership over wildlife (Lindsey, 2010). Botswana on the other hand is a less densely populated country with vast areas of wilderness remaining. However, it still has a history of fencing to control foot-and-mouth disease and the country is criss-crossed with about 5,000 km of veterinary cordon fences (Gadd, 2012). Furthermore, fences in Botswana are also being used to control conflict between humans and wildlife at the borders to protected areas (Funston, 2001; Kesch, Bauer & Loveridge, 2014). Despite all these differences in the use of fences, their effectiveness is highly dependent on their design, their alignment and their maintenance, no matter what purpose they have been built for. I had the opportunity to study two different game fences in Botswana to determine their impacts on vegetation, lion-herbivore relationships and their effectiveness in human-wildlife conflict control, which they were built for.

Permeability of fences

Depending on their location, fences can be under enormous pressure by different animal species trying to transgress them. These species have been grouped as “heavy non-jumping species”, “medium weight non-jumping species”, “jumping species”, “species burrowing or squeezing through small gaps” and “potential climbers” (Hoare, 1992). Heavy and medium weight non-jumping species such as elephant or gemsbok can cause considerable damage to the structure of the fence by breaking it down in order to gain access to the other side or by being chased into the fence by predators respectively (personal observation, Ferguson, Adam & Jori, 2012; Figure 5.1). Furthermore, species like leopard and primates are prone to climb certain fence designs in order to get to the other side (Hoare, 1992). Chapter One of this manuscript showed how burrowing or digging species such as honey badgers and hyaenas can cause severe damage to the integrity of a fence that is not buried into the ground and how their holes are subsequently used by conflict species such as lions to transgress fence lines. Previously described methods such as the “Fence Incident Surveillance System” (FISS) explain how to determine different species that are damaging the fence or crossing the fence line (Bonnington *et al.*, 2010, Ferguson, Adam & Jori, 2012). In order to be able to apply the FISS, stakeholders must have access to trackers with detailed spoor reading skills, which is very rare in most cases. Therefore, Chapter One described a simple albeit effective method enabling stakeholders to identify species and their type of digging behaviour and therefore the extent of direct and facilitated fence permeability involved at their specific fence, solely by the size and shape of holes underneath fences. Digging species were classified as either "enlarging specialists", "opportunists" or "digging specialists", depending on their digging behaviour. The terms "DNH" (density of new holes) and "DNHS" (density of new holes per species x) were introduced as a measure to describe the hole-digging pressure on game fences. Therefore, fence maintenance can be planned more economically according to the type of species that are challenging the fence.

Figure 5.1 Elephant bull crossing the Makgadikgadi fence line.
(photo credit: Kristina Kesch)

Different fences obviously have different objectives and hence require different maintenance efforts (reviews: Ferguson & Hanks, 2010; Somers & Hayward, 2012). Exclusion fences that are designed to exclude a certain species from a certain area are supposed to be 100% impermeable to this species but can be permeable to others. In South Africa, a single strong cable 30 cm above the ground was used to limit the movement of rhino but allowed other species to move freely. Similarly, a single electrified strand 2 m above the ground limited elephant movement, while other species were not being restricted (Slotow, 2012). In Tanzania, different fence designs showed different levels of permeability to different mammal size classes (Bonnington *et al.*, 2010). Sawyer *et al.* (2013) pointed out the effect of other semi-permeable barriers such as human development on migratory ungulates and distinguished between "connectivity" and the "functional attributes" of a migration route. A semi-permeable barrier such as a human development area will normally ensure connectivity between different areas but functional attributes such as access to stopover sites, movement corridors and escape terrain for predator avoidance can be compromised, depending on the permeability level of the human development area. Ideally, a barrier should be as permeable as possible and prevent only movement of the targeted species. Therefore, fence design and the extent of maintenance should always be adapted to the purpose of a particular fence and has to be decided on a case-by-case basis.

Design, maintenance and alignment vs. effectiveness of fencing

Without the implementation of appropriate maintenance a game fence cannot be effective as a human-wildlife conflict solution. Funston (2001) showed how different approaches to maintenance efforts between countries had an impact on the effectiveness of the Kgalagadi Transfrontier National Park boundary fence, which runs through Botswana, South Africa and along the border to Namibia. Despite the game fence in Botswana being the newest and highest fence between the three countries, a lack of maintenance lead to the highest lion transgression rates along the Park's boundary. Another example is the western boundary fence of Kruger National Park, South Africa. It consists of five different fence designs and none of them has been proven to be 100% effective in constraining the transgressions of elephant, lion, hyaena and buffalo (Keet *et al.*, 2010; Ferguson, Adam & Jori, 2012). Chapter Two investigated the effectiveness of the Makgadikgadi Pans National Park western boundary fence, Botswana, in separating lions and elephants from human-dominated areas housing livestock and crop fields. The study showed that the fence is under enormous pressure by species transgressing the fence line year-round. During the dry season this is probably due to the limited access to the Boteti River, which is fenced out of the Park in most areas and, at the same time, represents the only reliable water source in the area. A daily frequency of 21 transgressions per 100 km was found for lion and 132 transgressions per 100 km for elephant along this fence during the dry season. In the rainy season cattle had a daily transgression frequency of 112 transgressions per 100 km, whereas there were no transgressions recorded during the dry season, presumably due to high water levels of the Boteti River. During the time of data collection no maintenance was carried out on this fence, which resulted in high transgression frequencies. The high numbers of cattle transgressing in and out of the Park offer lions very easy access to livestock and hence conflict levels remain high (personal observation).

Different fence designs result in different efficacy levels (review: Hayward & Kerley, 2009). In order to constrain the transgression of digging species a fence must be buried into the ground and its base should consist of rocks or concrete. Climbing species can be excluded from certain areas by the use of electric wires and overhangs. Overhangs will also exclude jumping species, as does sheer height of a fence (Hoare, 1992; Dickman, 2012). The most challenging species to fence in or out are megaherbivores such as elephants, which have the ability to damage a fence by pure strength. Here, different fence designs result in different levels of success, but traditionally electrification of fences and strong supporting poles play a crucial role in most of them (Kioko *et al.*, 2008; Ferguson, Adam & Jori, 2012; Slotow, 2012). However, more recently new elephant-proof fence designs have been developed, such as bee-hive and chilli fences (Sitati & Walpole, 2006; King, Douglas-Hamilton & Vollrath, 2011), which successfully deter elephants from crop fields by using natural deterrents. Furthermore, the alignment of fences plays a considerable role and ecological factors such as access to water, vegetation cover and soil structure (rock, deep sand, moving dunes etc.) have to be taken into account. In the case of the Makgadikgadi Pans National Park, the fence blocks off the access to the Boteti River in most places, whereby the river is the only reliable water source for wildlife in the area. Therefore, elephant damage is inevitable due to the species' dependence on water (Western, 1975). However, even with the perfect fence design for a particular area and purpose, a fence cannot be effective without the implementation of appropriate maintenance efforts. Inevitably, a fence will be damaged by elephants, digging species and animals getting entangled in the fence as well as theft of fence material by humans.

Fences as traps and their impact on predator avoidance behaviour by herbivores

Game fences represent considerable artificial barriers in the landscape and some species are known to adapt very slowly to new boundaries and continue to be trapped and entangled in fences (Goodwin, 1985 cited in Hoare, 1992; Albertson 1998). Reports on carcasses along fences are common and predators are known to use fences to trap and capture their prey (Adendorff & Rennie, 1984; Albertson, 1998; Van Dyk & Slotow, 2003; Rhodes & Rhodes, 2004; Reed & Sautereau, 2005; Ferguson & Hanks, 2010). Chapter Three of this manuscript demonstrated the potential threat fences can pose to herbivore populations due to predators using fences for hunting, an often underestimated challenge with fencing. Fences do not only have the potential of constraining seasonal migration patterns but also daily movement behaviour. Therefore, animals get trapped by fences and predators are attracted by this accumulation of prey. In an open landscape without artificial barriers, lion prey species are known to actively avoid the predators on a spatial level (Valeix *et al.*, 2009 a & b). This kind of predator avoidance behaviour was neither found at a new nor at a well-established game fence in Botswana. Therefore, Chapter Three suggested that fences seem to have a long-term negative influence on herbivores' ability to adapt to an increased hunting risk.

Figure 5.2 Greater kudu caught and died in a farm fence.
(photo credit: Tarina Josefowicz)

In Botswana, the construction of fences caused a mass die-off of ungulates migrating from the Kalahari Desert to the Okavango Delta during the droughts of the 1980s (Owen & Owen, 1980; Parry, 1987; Williamson & Mbano, 1988; Boone & Hobbs, 2004; Mbaiwa & Mbaiwa, 2006). Where migratory animals get trapped along fences an increase in lion populations has been reported since they take advantage of the trapped and weakened prey species along the fence (Albertson, 1998). Carnivores are likely to learn how to use fences for hunting. In Pilanesberg National Park and Shambala Private Game Reserve, South Africa, wild dogs have been reported to kill larger prey than usual due to the use of fences

(Van Dyk & Slotow, 2003; Rhodes & Rhodes, 2004). Hence, fencing creates a new kind of edge effect for herbivores by offering their predators a hunting advantage prey animals don't seem to be able to adapt to. In order to reduce threats to herbivore populations, this needs careful consideration when planning new fences, especially in small protected areas with small herbivore populations or areas hosting migratory species.

Fencing as a tool against overgrazing and bush encroachment

Fencing the borders of protected areas and therefore fencing certain herbivores in or out can reduce the carrying capacity of an area and lead to herbivore population declines (Ben-Shahar, 1993). Furthermore, the impact of herbivore grazing on vegetation cover can be severe and habitats can change drastically. Cassidy, Fynn & Sethebe (2013) studied the effect of a veterinary cordon fence on bush encroachment and found a much higher cover of woody vegetation on the livestock dominated side of the fence, where cattle is grazing the area heavily. Overgrazing is a very destructive process as certain woody plants with shallow root systems are favoured in the accumulation of rain water, which leads to bush encroachment and desertification (Schlesinger *et al.*, 1990; Skarpe, 1990). Chapter Four showed that heavy grazing leads to lower grass biomass, lower fibre contents in grasses and a lower absolute nutrient availability per unit area. The exclusion of livestock from a formerly overgrazed area had a positive effect on the primary production of grasses. Only one rainy season was needed for the grass biomass to recover from heavy grazing pressure and grasses showed higher fibre contents and a higher absolute nutrient availability. However, in heavily grazed areas there was still a high abundance of unpalatable plant species one year after fencing.

In order to prevent overgrazing and subsequent negative impacts like bush encroachment or desertification in anthropogenic grazing systems, where cattle substitutes wild-ranging herbivores, it is therefore necessary to implement sustainable management strategies. These should include rotating grazing systems, where grazing areas are separated from each other by fences and the vegetation is given time to recover. Furthermore, the use of different herbivores (e.g. a combination of cattle, goats and wildlife) would be ideal for sustainable development (e.g. Dickhoefer *et al.*, 2010).

Fencing is mostly being applied to solve conflict situations between humans and wildlife and its impacts on other trophic levels are often being ignored. This dissertation highlights the importance of taking whole ecosystems into account when fencing is being considered, in order to avoid severe consequences on trophic levels, which were not even targeted by the fence.

Conclusions

Fencing is a high impact measure and can be a great success or have disastrous effects in conservation. Whether or not fencing is the right choice has to be decided on a case-by-case basis and is dependent on many different factors.

The construction of fences through migration routes had devastating effects on population numbers of different herbivore species in Africa and kangaroos in Australia (review: Hayward & Kerley, 2009). As Woodroffe, Hedges & Durant (2014) pointed out, fencing should generally be avoided in countries, where there are vast areas of wilderness remaining and where essential resources like permanent water are far away from each other, such as in Botswana. Here, veterinary cordon fences had devastating effects when they caused a mass die-off of water dependent ungulate species because fences were built without considering animal migration routes to essential water resources (Owen & Owen, 1980; Parry, 1987; Williamson & Mbano, 1988; Boone & Hobbs, 2004; Mbaiwa & Mbaiwa, 2006). Despite these past experiences, there were further plans of constructing fences through the largest remaining herbivore migration in southern Africa by extending the Makgadikgadi western and southern boundary fence in Botswana along the Park's eastern border, and thereby cutting off the migration route (Gupta, 2005).

Fencing is often being used to control diseases such as foot-and-mouth disease or bovine tuberculosis (Foggin, 2010; Gadd, 2012). However, reports on permeable fences are common (Reed & Sautereau, 2005; Dube *et al.*, 2010; Ferguson, Adam & Jori, 2012; Chapter One & Two of this manuscript) and therefore their effectiveness in controlling the spread of diseases is questionable. After the failure of veterinary fences due to theft of fence material in Zimbabwe, veterinarians are calling for a foot-and-mouth disease vaccination program for cattle in high risk areas, combined with fences to keep buffalo and cattle separated (Foggin, 2010). The development of vaccinations is ongoing but can be seen as an effective alternative to fencing or could be used in combination with fences for the control of foot-and-mouth disease (Barteling & Vreeswijk, 1991; Keeling *et al.*, 2003; Parida, 2009).

On the other hand, in densely human populated countries such as South Africa or countries where protected areas are situated far away from each other, there is no real alternative to fencing. Where dispersal of animals is impossible because distances between protected areas are extensive and will only result in conflict and put lives at risk, fences are a useful tool to mitigate conflict situations and protect both humans and wildlife. Fencing can also assist with the creation of new protected areas such as Pilanesberg National Park in South Africa. Here, reserves housing dangerous wildlife have to be fenced by law (Hayward & Somers, 2012). In such countries fences could be of further use as the problem of genetic isolation and inbreeding could be tackled with a new approach of creating fenced animal corridors between wildlife areas. However, in order to avoid an increase of human-wildlife conflict due to escaping wildlife, maintenance is the key to success for such corridors.

Where fencing is deemed the right choice, there are three major points that have to be taken into account:

1. The design of fences is imperative for their effectiveness (review: Hayward & Kerley, 2009). Fences can act as deadly traps to species other than the target species. Tortoises have been reported to get trapped between the lowest electrical wire and the fence itself and get electrocuted. Pangolins and snakes die on that same electrical wire when they touch it and curl up around it (Beck, 2010). Fences are further being used as look-out posts by birds of prey (Chavez-Ramirez *et al.*, 1994), which could lead to an increased hunting pressure on rodents along fence

lines. Burying a fence into the ground and building a base out of rocks or concrete will contain digging species in a particular area. Electric wires, overhangs and height can exclude climbing and jumping species (Hoare, 1992; Dickman, 2012) and elephant movements can be contained by bee-hive and chilli fences (Sitati & Walpole, 2006; King, Douglas-Hamilton & Vollrath, 2011).

2. The appropriate alignment of fences is imperative for its effectiveness and therefore, many different ecological factors have to be taken into account, such as access to water, soil structure (rock, deep sand, moving dunes etc.), vegetation cover or topography of a particular area. As the Makgadikgadi example has shown, water dependent megaherbivores will break fences, when these are limiting their access to water. Another example is the Kgalagadi Transfrontier National Park game fence, where its effectiveness is compromised by moving dunes, which can either cover or undermine the fence by blowing sand onto and away from it (Herrmann, Funston & Babupi, 2001).
3. Lastly, fences cannot be effective without the implementation of appropriate maintenance, which has to be decided on a case-by-case basis and depends on the purpose of a fence. Ideally, a fence should be as permeable as possible and prevent only movement of the targeted species. Therefore, fence design and the extent of maintenance should always be adapted to the purpose of a certain fence and it has to be acknowledged that each situation is unique. However, a non-maintained fence, which does not fulfil its purpose is a waste of funding and can pose a great danger to wildlife in its area.

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Declaration of oath

I hereby declare on oath that the work in this dissertation is my own and that I have not used other than the acknowledged resources and aids.

Maun, 2nd of June 2014

Kristina Kesch