TESTING THE EFFICACY AND POTENTIAL CONSEQUENCES OF FENCING AS A WILDLIFE MANAGEMENT TOOL

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ABSTRACT

This dissertation examines how various anthropogenic barriers affect wildlife movement, and in particular, how fencing affects movement and behavior of both migratory prey and predators in semi-porous environments. I chose to examine this subject as our planet's last remaining ecosystems are threatened by human encroachment due to population pressure, agriculture, and a myriad of other ecological stressors. In order to mitigate the encroachment, conservation fencing is rapidly becoming the norm even though constraining wildlife movement is fraught with ecological issues. My interest in conservation fencing was to examine the potentially hidden or understudied consequences of its usage.

The introduction discusses human-wildlife conflicts and the role of fences. Chapters 1 and 2 review the literature concerning animal movement and landscape ecology and set the general framework from which follows the series of specific studies in Chapters 3-6. Chapter 3 compares basic monitoring methods that lie at the core of the studies that follow. In this chapter, a comparison of traditional track monitoring to modern camera trapping methods demonstrated the power of mechanical vigilance but also the importance of timely monitoring for managerial decisions. Chapter 4 examines the effectiveness of fence-gaps, a wildlife management tool designed to compromise between complete isolation by fencing and an open landscape. The results of this study showed that most of the species *in situ* have indeed discovered these fence-gaps. Chapter 5 explores the potentially unintended consequences of the creation of fence-gaps as these structures funnel migration movement and thus could act as prey-traps. Using a spatial analysis of carcass locations, the results of this study demonstrated that predation locations did not cluster near the fence-gaps.

Chapter 6 examines predation near the perimeter fencing and within fenced areas designed to exclude elephant. Results showed that lion predation was not over-represented near the perimeter fences and that exclosures provided good hunting grounds for lion but these exclosures did not create prey-traps. The dissertation concludes that fencing is a useful conservation tool that requires reliable monitoring to understand how wildlife functions with fencing, and to permit managers to react to issues through an adaptive management framework.

Dedication

To my wife Susan Rimmer, who gave me the unconditional love and support to leave my career in finance and pursue this crazy dream of becoming a biologist in my middle age;

To my son Alex and my daughter Kristina, for their love and support. Thank you for your curiosity of the natural world and for making me strive to be a better person;

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GENERAL INTRODUCTION: Fencing And Wildlife Conservation

Human-Wildlife Conflicts and Fencing

As population pressure and human-wildlife conflicts increase, there are fewer pristine ecosystems where wildlife can move through the landscape unfettered by anthropogenic barriers. The focus of this dissertation is to examine how fencing is used as a tool to segregate people and wildlife and to test the efficacy of certain measures put into place to help mitigate certain downsides of fencing. Other than to claim ownership of the land and the wildlife that inhabit it, the major reason for fencing wildlife is to reduce human-wildlife conflicts, i.e. keeping people safe from wildlife, and keeping wildlife safe from people. My focus and examples are primarily African, as some of the planet's most spectacular long-range migration happens on that continent (Harris, Thirgood, Hopcraft, Cromsight, & Berger, 2009) and fencing is being increasingly used to segregate wildlife and people and threatens these historical migrations (Naidoo, Du Preez, Stuart-Hill, Jago, & Wegmann, 2012; Newmark, 2008; Spinage, 1992).

Protecting People

Protecting people (including their crops and livestock) from wildlife is arguably the primary reason for erecting a wildlife-proof fence. Crop raiding by wildlife, mostly by elephants (Chiyo, Cochrane, Naughton, & Basuta, 2005; Graham, Douglas-Hamilton, Adams, & Lee, 2009) or by primates (Naughton-Treves, Treves, Chapman, & Wrangham, 1998; Siex & Struhsaker, 1999), and livestock depredation by carnivores are two of the major human-wildlife conflicts that can lead to a negative and confrontational attitude of local people towards conservation efforts (Hill, 2000; R. Hoare, 2000). Farmers are far less tolerant to elephants that can destroy their fields than are pastoralists and conversely, pastoralists are less tolerant of large predators that can depredate their livestock (Gadd, 2005; Kikoti, Griffin, & Pamphii, 2010).

Crop Raiding

Crop raiding behavior by elephants can be difficult to predict (Kioko, Muruthi, Omondi, & Chiyo, 2008) although some temporal patterns and some spatial aspects are predictable (Sitati, Walpole, Smith, & Leader-Williams, 2003) such as seasonality (Jackson, Mosojane, Ferreira, & Van Aarde, 2008). Farmers do not have a reliable system that predicts when and where elephants will encroach. Therefore, farmers need to constantly be on alert, either by actively guarding their fields throughout the nights or by erecting passive barriers such as fences. Active guarding (enhanced by banging pots, lighting fires, shouting), although fairly effective, requires constant vigilance and comes with a cost of diminished daytime productivity. Elephants increase crop raiding more often during moonless nights and during heavy rains, corresponding with less active guarding (Barnes et al., 2007) and reduced predator activity. Fencing is thus front and center to the discussion surrounding solutions to crop raiding (Hayward & Kerley, 2009; King, Lawrence, Douglas-Hamilton, & Vollrath, 2009; Kioko et al., 2008). Some of the proposed solutions are expensive (e.g. electrical fences), require excessive resources or expertise (translocation of problem animals) and do not necessarily address the root cause (O'Connell-Rodwell, Rodwell, Rice, & Hart, 2000). Culling of problem animals (mostly males) is used as a last resort as it can lead to issues of diminishing effective population size (Sukumar, 1991). De-tusking problem animals is costly and elephants learn to use different techniques to breach the fencing (Mutinda et al., 2014). Low-tech solutions (such as ditches, thorn fences, hedges) do not work very well (Sitati, Walpole, & Leader-Williams, 2005). Alternative solutions showing promise include greasing rope with chili oil (Sitati & Walpole, 2006) and the use of bee-fences, where log hives are suspended from rope fences (King, Douglas-Hamilton, & Vollrath, 2011). One of the secondary benefits from bee-fences is that the farmers can collect and sell the honey. However, electrical fencing is still considered the best option to protect crops (Sitienei, Jiwen, & Ngene, 2014; Thouless & Sakwa, 1995).

Human Fatalities

Elephant and other large mammals can also directly attack and kill humans they encounter (Bury, Langlois, & Byard, 2012; Das & Chattopadhyay, 2011). Fatal or near fatal lion attacks often happen on the periphery of conservation areas, where prides are displaced by other larger prides or competing predators (Packer, Ikanda, Kissui, & Kushnir, 2005; Yamazaki & Bwalya, 1999). There is also evidence that agro-pastoralists regularly attempt to chase off and scavenge prey from lion and leopard, leading to fatal attacks to the scavenging parties (Treves & Naughton-Treves, 1999). Fencing can help segregate predator populations from local communities and reduce the likelihood of this type of incidental contact and dangerous opportunistic scavenging.

Livestock Depredation

Livestock depredation is a critical issue to pastoralist communities and is the main driver of the retaliatory killing of predators (Packer et al., 2013). Pastoralists have traditionally used livestock enclosure made of thorny acacia branches (called bomas) or long wood poles to protect their livestock at night from predators, however these enclosures are not always effective (Kolowski & Holekamp, 2006). Lion, hyena, leopard, wild dog, and cheetah are all predators of domestic livestock (Bauer, de Iongh, & Sogbohossou, 2010; Martins, Horsnell, Titus, Rautenbach, & Harris, 2011; Ott, Kerley, & Boshoff, 2007; Rust, Whitehouse-Tedd, & MacMillan, 2013; Tumenta et al., 2013; Woodroffe, Lindsey, Romanach, Stein, & Ole Ranah, 2005). When these predators roam outside of protected areas, they are under constant persecution (Bagchi & Mishra, 2006; R. E. Hoare & Williamson, 2001; Maclennan, Groom, Macdonald, & Frank, 2009). Pastoralists have historically not been tolerant to predators such as lion, leopard or hyena, and have speared, poisoned, trapped or otherwise hunted predators outside of protected areas (Groom, Funston, & Mandisodza, 2014; Schnitzler, 2011). Lion populations are prey density dependent inside protected areas whereas they are human population dependent outside protected areas (Packer et al., 2013). Lions in mixed-use habitat prefer to hunt wild prey inside protected areas but will venture outside to hunt domestic livestock in times of primary prey scarcity (Valeix, Hemson, Loveridge, Mills, & Macdonald, 2012). Where lions are not fenced-in, in Northern Kenya for example, the rate of retaliatory killing and poisoning of lion threatens this species with near-term extirpation (Hazzah, Mulder, & Frank, 2009). In order to discourage this retaliatory killing, the Kenyan government and private conservancies have developed compensation schemes where pastoralists receive the market rate for livestock lost due to predators. The government has also developed a paid lion guardian program, hiring members from local pastoral community to act as lion protectors in hope to effect a substantial drop in the rate of retaliatory killing (Hazzah et al., 2014; Maclennan et al., 2009). In other jurisdictions, fencing lions is seen as the only solution. In South Africa, fencing is an integral and compulsory part of all new lion re-introduction programs (Hunter, 2007). Keeping predators confined to fenced conservancies is a sub-optimal solution and an admission of failure of humanity's tolerance for wildlife (Hayward & Kerley, 2009), however it may offer the best solution for the future (Creel et al., 2013; Miller & Funston, 2014; Watson, 2013).

Collisions

Another major contributor to human-wildlife conflicts that can be partially addressed by fencing is wildlife-vehicle collisions (WVC). In countries with an extensive road infrastructure, WVC are the major cause of conflicts with people and are responsible for mortality and great economic costs (Bissonette, Kassar, & Cook, 2008). As well, roads act as barriers to movement and are one the major threats to carnivore populations (Noss, Quigley, Hornocker, Merrill, & Paquet, 1996). In India and in Africa, elephant are often killed by trains (Singh & Satheesan, 2002; Whitehouse & Kerley, 2002) and the collisions can cause serious delays, and sometimes derailments. Even inside protected areas in Tanzania, collisions are common (Drews, 1995). In North America, fences have been shown to be effective at reducing the number of collisions (A. P. Clevenger, Chruszcz, & Gunson, 2001; Olsson & Widen, 2008; VerCauteren, Lavelle, & Hygnstrom, 2006).

Although fences are efficient at reducing WVC, they also create a barrier effect that stops historical migration, thus restricting gene flow and reducing the available habitat for the fenced species. Ecologists have combined fencing with specially designed eco-passages (either underpasses or overpasses, depending upon the targeted species) to try and mitigate the barrier effects of fencing. In the last decade, eco-passages have proved useful for a variety of species including small underpasses designed for frogs and toads(Leresche, Cherix, & Pellet, 2009), salamanders(Pagnucco, Paszkowski, & Scrimgeour, 2012), and turtles(Dodd Jr, Barichivich, & Smith, 2004), large overpasses for deer, elk and moose (A. P. Clevenger & Waltho, 2005), large underpasses for bear, wolf and cougar(Anthony P. Clevenger & Waltho, 2000), panther (Foster & Humphrey, 1995) and other carnivores (Grilo, Bissonette, & Santos-Reis, 2008) , arboreal passages for canopy dwelling mammals (Weston, Goosem, Marsh, Cohen, & Wilson, 2011) and elephant underpasses (Straziuso, 2011).

Disease

Fences also offer protection from the two-way transmission of disease between domestic stock and wild stock. Disease transmission from wildlife into livestock or human populations can be difficult to control where reservoirs of disease are varied and prevalent diseases in wildlife (Biet, Boschiroli, Thorel, & Guilloteau, 2005; Karesh, Cook, Bennett, & Newcomb, 2005). Bovine tuberculosis and rabies are two of the most common and virulent and wildlife plays a large part in their persistent re-emergence (Bengis et al., 2004; Chomel, Belotto, & Meslin, 2007; Lembo et al., 2008; Palmer, 2007). Vigilant monitoring of disease in wildlife populations can lead to an early and efficient response through culling (Donnelly et al., 2006; Morner, Obendorf, Artois, & Woodford, 2002). When possible, fencing can also be used as a method to prevent contact between wild and domestic populations (Ferguson & Hanks, 2012; Hargreaves et al., 2004). Wildlife populations are also susceptible to infections that are prevalent in domestic livestock (Giacometti, Janovsky, Belloy, & Frey, 2002; Messenger, Barnes, & Gray, 2014; Posautz, Loncaric, Kubber-Heiss, Knoll, & Walzer, 2014). Segregating wild and domestic populations is an effective tool for the prevention of both zoonoses and zooanthroponoses.

Protecting Wildlife

Poaching

Fencing also protects wildlife from people. Poverty is widespread throughout most of Africa and is one of the main drivers of poaching (Challender & MacMillan, 2014). Poaching can take many forms: the illegal harvest of wild plants, the capture and sale of live wild animals, and the trade in body parts of protected species. Regulation has not been successful as the implementation of the regulations is subject to lax enforcement and corruption (Rowcliffe, de Merode, & Cowlishaw, 2004). Trade bans on elephant tusks have been partially effective to curtail poaching at the international scale, but have not been very successful at the domestic level, where there is an unregulated local market (Lemieux & Clarke, 2009). The trade ban on rhino horn has not been effective as the global rhino population has declined by over 97% (Berger, 1994). The demand for rhino horn, both in traditional Chinese medicine throughout Asia or as traditional knife handle material in Yemen, is rising as a consequence of higher regional income levels (E. Martin & Vigne, 2007; Vigne, Martin, & Okita-Ouma, 2007). The price of rhino horn in 2013 was higher than gold, and could fetch upwards of $65,000 per kilo (Douglas & Alie, 2014). Thus, in areas of high poverty the rewards from poaching can be substantial. Wildlife managers have to resort to extreme measures of protection, such as electrified fencing, 24-hr armed patrols and "shoot on sight" policies to deter potential poachers (Messer, 2010). The militarization of conservation is not without its critics (Duffy, 2014), but as population of rhinos continues to drop, the value of the horns continues to rise and this has attracted organized criminal syndicates (Milledge, 2007). Calls for legalizing trade in rhino horn (Biggs, Courchamp, Martin, & Possingham, 2013; Di Minin et al., 2015; Ferreira, Pfab, & Knight, 2014), in an attempt to remove the criminal syndicate element and also benefit from the increasing demand, are not viewed as implementable without jeopardizing the survival of the remaining population (Collins, Fraser, & Snowball, 2013; H. H. T. Prins & Okita-Ouma, 2013). Fencing can act as a deterrent to some potential local poachers but probably not to criminal syndicates.

Bushmeat hunting

Although not as high profile as poaching, the pressure from subsistence hunting in communities abutting protected areas is a major issue (Metzger, Sinclair, Hilborn, Hopcraft, & Mduma, 2010; Rist, Milner-Gulland, Cowlishaw, & Rowcliffe, 2010). Subsistence hunting is driven by the need for food, money and also for cultural reasons such as "gaining respect from other community members", and as a "traditional way of life" (Kaltenborn, Nyahongo, & Tingstad, 2005). In fact, Kaltenborn, Nyahongo and Tingstad found that the cultural and social drivers for hunting are so rooted in community life that even if social services improved and that villagers had access to better food and income, they still would be hunting. In the Serengeti, Rentsch and Packer (2015) estimate that of up to 6-10% of wildebeest population is taken annually for local bush meat consumption and in the Mara region wildlife populations have declined significantly due to hunting (Ogutu, Owen-Smith, Piepho, & Said, 2011). Hunters benefit by increasing food security and financial wealth and admit to be willing to take physical and legal risks in order to reap these benefits (Knapp, 2012).

Law Enforcement

Fences create hard boundaries that can deter and thwart the encroachment into protected areas (Hayward, 2009) and fencing acts as a physical reminder of the protected status of wildlife and plants beyond the fence. However, lax enforcement of wildlife laws exacerbates the issue. The fines for bushmeat hunting are low as is the probability of arrest and prosecution. The fines for poaching horns and tusks are greater but the enforcement of the rule of law has been weak (Rowcliffe et al., 2004). For example, in Kenya, up until recently, poachers faced maximum fines of KSH 40,000 (about C$400) for the most serious crimes (BBC, 2014). Lax enforcement of wildlife laws has lead to an increased commercialization of hunting, serving demand from urban centers and even abroad (Beyers et al., 2011; Lindsey et al., 2013; Milnergulland & Leaderwilliams, 1992). The benefits of healthy wildlife to tourism outweigh the benefits of poached wildlife. However, deterring poaching and hunting is difficult because the tourism benefits of a healthy wildlife population are not distributed evenly throughout the population (Johannesen & Skonhoft, 2005). Successful curtailing of poaching and hunting is possible when the local communities are active participants, helping authorities identify smuggling routes and poachers (Esmond Martin & Martin, 2010; Esmond Martin, Martin, & Vigne, 2013). Community members are more likely to be cooperative when their livelihood benefits directly from tourism and when depredation and crop raiding do not unduly affect their livelihood.

Habitat Loss

One of the biggest threats to wildlife diversity is the habitat loss and isolation associated with land conversion (Collinge, 1996; Fischer & Lindenmayer, 2007; Foley et al., 2005; Foley et al., 2011) and although a thorough review is beyond the scope of this introduction, I touch on a few points. Forests are under constant pressure from illegal logging (Bussmann, 1996; Gibson et al., 2011) or conversion to plantations (Brockerhoff, Jactel, Parrotta, Quine, & Sayer, 2008). The global loss of wetlands due to irrigation of agricultural lands endangers biodiversity(Lemly, Kingsford, & Thompson, 2000; Verhoeven, Arheimer, Yin, & Hefting, 2006). Runoff of nitrogen and phosphorus from agriculture into the aquatic ecosystems also creates algal blooms, loss of aquatic species and fouls water quality (Carpenter et al., 1998). Wetlands are often targeted for conversion to agriculture because of lack of coordinated protective policies (Maclean, Boar, & Lugo, 2011). As well, conversion to agriculture affects the watershed and, ultimately, lake ecosystems (OgutuOhwayo, Hecky, Cohen, & Kaufman, 1997). In addition to the direct loss of suitable habitat and the direct loss of biodiversity (Hooper et al., 2005), the remaining habitat suffers from fragmentation that renders it susceptible to edge effects, such as microclimatic shifts that can alter plant and wildlife composition, changes in ecological processes, and decline in species richness (Tilman et al., 2001). Lastly, although integrative agriculture (where food demand and conservation are integrated, such as in shade-grown coffee plantations) is sometimes touted as a potential hybrid solution, research has shown that more biodiversity is preserved by segregating land for conservation and intensely farming another portion (Phalan, Onial, Balmford, & Green, 2011). Fencing can help delimit protected areas and prevent creeping encroachment by agriculture or logging.

Livestock Competitive Pressure

As the human population grows so does the pressure on managers to allow cattle to graze within the boundaries of protected areas (H. Prins, 1992). Competitive pressure from livestock has a detrimental effect on the wildlife that depends on limited available grazing (Ogutu, Piepho, Dublin, Bhola, & Reid, 2009) as well as having negative effects on the availability of wild prey for lions (Tumenta et al., 2013). Voeten and Prins (1999) showed that wildebeest (*Connochaetes taurinus*), and zebra (*Equus quagga*) have limited overlap in their use of available resources as would be expected based on evolutionary segregation, however, zebu cattle (*Bos indicus*), an exotic domesticated species, showed considerable resource overlap with both these native herbivores depending upon the season. In Kenya, the expansion of pastoralism in areas previously only accessible to wildlife has proven detrimental to wildlife through grazing competition (Lamprey & Reid, 2004). Kinnaird and O'Brien found that species richness and endemic occupancy rates were much higher in areas with limited or no cattle suggesting that cattle ranching had also indirect detrimental effects on other species that do not compete directly with cattle for food resources (Kinnaird & O'Brien, 2012). The interactions between grazers and cattle is complex depending on seasons (Odadi, Karachi, Abdulrazak, & Young, 2011) and the presence of elephant (Young, Palmer, & Gadd, 2005). Also, because numbers of wild ungulates is historically low in many parts of sub-Saharan Africa, the quality of the forage can also be poor due to sub-optimal grazing. Oba et al. (2000) found that excluding intensive grazers led to diminished plant cover, i.e. the vegetation has evolved to be intensively grazed and then left to regrow (Garcia et al., 2014), presumably by large herds passing through. Without these large herds of wild ungulates, the vegetation covers suffers and the grasses can become moribund. In many conservancies, the number of wild ungulates supported on the land is not sufficient to keep the vegetation at its optimal yield and burning is undesired and mowing is impractical. Many conservancies allow local community cattle (especially in times of drought) to graze on conservancy land (Butt, Shortridge, & WinklerPrins, 2009) both to keep local community relations on good standing and to help regenerate moribund vegetation. By adopting intensive holistic grazing schemes that focus and rotate cattle in certain specific blocs within the conservancies, managers limit competition between cattle and wild. The plots are thus intensively grazed, inducing faster and denser regeneration of quality grasses. Managers select the blocs of land to be grazed based on where the grasses have become moribund and unpalatable to wild grazers (but not to cattle). The cattle herders use mobile fencing to keep the cattle tightly packed together, ensuring that they graze only in selected locations. Although holistic cattle management is a relatively new tool, initial results are promising and eventually this method might be an important component of grassland management for conservancies. The effectiveness of holistic grazing depends on effective perimeter fencing to control livestock access to protected areas and mobile fencing to restrict the grazing to pre-determined blocs of land.

The Tragedy of the Commons

Wildlife and the habitat it depends upon are often unregulated common goods and as with all unregulated common goods they are susceptible to the tragedy of the commons (Hardin, 1968), i.e. where individuals overexploit the cost-free "common" good for short-term gain endangering that common good's long-term future. This concept, first expounded in the late 1880s, explained the runaway effects of unregulated grazing on common land, where the unrestrained access to the commons (a traditional English term meaning common land, often accessible to everyone in a village) leads to overexploitation and to the eventual ruin of each herder (Lloyd, 1980). The term now refers to any natural resource accessible at little or no cost by every member of a society. This concept has broad applications in other unregulated and open access systems such as ocean fisheries, forestry, and industrial manufacturing affecting air quality and extends to wildlife crimes, such as illegal live animal trade, poaching, over-fishing, or smuggling wildlife skins (Pires & Moreto, 2011). Regulation, privatization and enclosure are the prescribed tools to curtail the "tragedy of the commons" issue (Hardin, 1968) and these tools have been widely implemented.

However, these tools are far from perfect solutions and in many cases, forced privatization and apportionment of land rights have led to a breakdown of traditional societal rules that have historically protected the abuse of common grazing land (Kvist, 1991; Monbiot, 1994). Enclosing land and dividing up land rights has not led to better protection or increased the quality of the habitat and suggests flaws in the assumptions underlying the tragedy of the commons argument, at least in the case of grazing rights (Cao, Yeh, Holden, Yang, & Du, 2013; McCabe, 1990; Perkins, 1996). If cattle herders have shown difficulty managing common land for their own selfish gains, it is difficult to imagine that they could manage a larger land sharing system that strives to optimize biodiversity, long-term conservation of wild populations and grazing revenues. Nonetheless, wildlife managers are often tasked with these conflicting objectives and fencing is now regarded as an essential management tool.

Fencing as a Tool for Conservation

Population pressure, human-wildlife conflicts and habitat encroachment limit the long-term prospects for large tracts of undisturbed habitat. Increasingly likely is a second-best solution: one where smaller protected areas are fenced and possibly linked to each other by connecting structures to form a matrix of larger connected habitat. The corollary to this second-best option is that management intervention is constantly needed to rebalance and/or counter some of the side-effects of prior intervention. This adaptive management framework requires a high degree of reliable monitoring that leads to structured decision-making (Lyons, Runge, Laskowski, & Kendall, 2008). For the myriad of reasons discussed, fencing has increasingly become the go-to tool for segregating people and wildlife. However, conserving, improving or creating ecologically connected habitat is of paramount importance to ecologists. The habitat must have the ability to support wildlife movement, encouraging gene flow and allowing for range shifts in the event of climate change (Beier, Spencer, Baldwin, & McRae, 2011). Ecologists thus encourage neighboring protected areas to remove internal fences and become a larger more diverse habitat (Georgiadis, Olwero, Ojwang, & Romanach, 2007; Lindsey, Romanach, & Davies-Mostert, 2009) and link fenced protected areas together in order to offer safe passage into the remaining habitat matrix (Bartlam-Brooks, Bonyongo, & Harris, 2011). Given this trend, it is crucial to evaluate how wildlife responds to these fences and to the controlled entry and exit points (Cozzi, Broekhuis, McNutt, & Schmid, 2013; Weise, Wessels, Munro, & Solberg, 2014). Much of the literature already discussed dealing with fencing concerns itself with solving human-wildlife conflict issues, but very little has been written about how wildlife might use these connecting structures, such as fence-gaps. In a way, I am testing if fencing, as one aspect of human-wildlife conflict management, is attracting an equal and opposite (or at least unintended) re-action by wildlife, what I will call Newton's third law of wildlife management conservation (with apologies to Sir Isaac Newton).

The community conservation model

The study site I chose to work at is the Lewa Wildlife Conservancy, in Kenya. This conservancy is at the forefront of conservation management science and is trying to optimize the requirements of wildlife, the protection of critically endangered species (Black rhino and Grevy's zebra) and protecting and engaging the surrounding communities. The community conservation model was introduced in Africa in the early 1990s (Songorwa, 1999) and is in use at Lewa. This model of conservation has a stated goal to improve the livelihood of communities that border protected areas, by investing donor funds and profits back into the community to better education, healthcare and long-term sustainability. The tangible benefits to these communities in turn motivate these communities to become better stewards of the land and the wildlife. At Lewa, millions of dollars are re-invested into the communities every year in support of 21 local schools, hundreds of educational bursaries, four health clinics, dozens of water projects, and hundreds of micro-credit schemes for small enterprises. Electrical fences surround the conservancy and keep the local residents safe from predators and elephants. Management also has compensation schemes to reimburse farmers and pastoralists from losses due to wildlife escaping the confines of the conservancy. Lewa operates a mixed system of access to its habitat, excluding agriculture but permitting cattle to intensely graze some sections of the conservancy therefore allowing some concessions to pastoralists. Without these schemes, farmers and herders might be less tolerant of predators or fence breaking elephants, and may turn to poaching or retaliatory killing. A fundamental aspect of this conservation model is to incentivize local communities to tolerate wildlife and help them build capacity in order to benefit from wildlife through tourism (Gillingham & Lee, 1999; Lindsey et al., 2009; Metcalfe & Kepe, 2008; Weladji & Tchamba, 2003).

Dissertation Structure

The research that follows is an exploration of how to best measure and examine the effectiveness of these connecting structures. I begin in Chapter 1 by setting the stage and reviewing the various drivers of animal movement. I briefly review how the requirements of foraging, competition, mating, migration, and climate change can shape the daily and seasonal movement patterns of animals. I also review the importance of certain primary consumers and a keystone species moving through the landscape, specifically elephant (*Loxodonta africana)*.

In Chapter 2, I review landscape ecology and how habitat fragmentation and barriers to movement negatively affect species that depend upon open landscapes for long-term survival. I start by reviewing the importance of connectivity to sustaining populations by reviewing the Island Biogeography Theory and the concepts of Minimum Viable Population and Metapopulation. This discussion then leads to a review of movement corridors as vectors of connectivity and to corridor design. I then review how barriers to movement, such as roads and fences can affect population survival directly through mortality, but also indirectly through restricting genetic diversity, restricting access to resources, changing behavioral patterns and edge effects.

In Chapter 3 and 4, I examine the effectiveness of creating gaps in fences to permit the movement of animals otherwise restricted to a fenced-in conservancy. Chapter 3 is focused on the methodology to best measure the movement in and out of a conservancy, given the sometimes-contradictory demands of timely, cost effective and accurate information for conservation management, and community early-warning systems of potential human-wildlife conflicts. I specifically examine the effectiveness of camera-trapping versus reading of tracks by trained individuals. This is an effective starting point for any further discussion on mammal movement by going back to first principles and ensuring that what I set out to measure is a realistic sample of reality. Comparing these two widely used methods leads to some important conclusions.

In Chapter 4, I examine the specific design of the fence-gaps and test if these fence-gaps permit the free movement of mammals in and out of the conservancy while restricting the movement of rhino. This chapter focuses on an applied solution to a difficult problem: balancing the needs for protecting a critically endangered, highly poached species versus the needs for habitat connectivity and access to migratory routes of highly mobile mega-herbivores. A successful fence-gap design has long-reaching management implications, as fencing and habitat connectivity will continue to be hot-button topics in wildlife conservation in the future. This chapter focuses on access to fence-gaps, and the different species using each fence-gap.

In Chapter 5, I address the possibility that the funneling of animal traffic through the fence-gaps might be creating prey-traps, i.e. areas where predators might be exploiting the spatial and temporal regularity of prey movement? I use a GIS analysis to examine if predation events are more frequently represented at the fence-gaps than they are elsewhere on the conservancy.

In Chapter 6, I expand the analysis used in Chapter 5 to investigate predation patterns near perimeter fencing as well as elephant exclusion zones. Certain predators have been known to increase their success near fences by cutting off escapes routes by directing prey into fences. Given anecdotal evidence of prey caught in the electrical fence, I also test if any edge effects have developed with regards to predation patterns, specifically if predation success rates differ near the perimeter fence. Lastly, I discuss the predation patterns within elephant exclusion zones. These electrically fenced areas exclude both elephant and giraffe and were created to protect woody vegetation for Black rhinos and Grevy's zebra. The denser vegetation should attract browsers, but does it also attract predators? Thus, in this chapter, I investigate predator success inside and near both perimeter and exclusionary fencing.

All of the empirical studies in this dissertation, chapters 3,4,5, and 6, have been accepted for publication as manuscripts in various peer-reviewed journals (noted at the beginning of each chapter). In an effort to give the reviewers of this dissertation the exact version of what has been accepted in peer-reviewed journals, I have not altered the contents of these manuscripts, although I have modified the formatting to comply with the requirements of the university. Consequently, there is some overlap with regards to the introductions and methods sections of these chapters.

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CHAPTER 1- Animal Movement

Animal dispersal falls on a continuous spectrum ranging from individuals accidently leaving their home range to full seasonal round-trip migrations taken by all members of a population (Lidicker Jr & Caldwell, 1982). I will use the definitions supplied by these authors to confine the meanings of dispersal and migration. Dispersal essentially means leaving the initial home range. There is no implied return journey in dispersal. Paleontologists use “migration” to describe permanent movement from one area to another (i.e. colonization of new ranges). Biologists occasionally use the term to describe temporary nomadic movements following food resources (e.g. irruptive migration), and for regular seasonal patterns of latitudinal and longitudinal displacement (seasonal migration) or seasonal altitudinal movement (altitudinal migration). Again, I will refer to Lidicker and Caldwell (1982) and apply a seasonality component to the movement and an implied return journey to the term migration.

Why leave an area? This is the question at the base of dispersal. Dispersal is fundamental to the life of most species (Nathan et al., 2008), but what is the evolutionary advantage to moving from one area to another? Animals move for a variety of reasons, including foraging, predator and competitor avoidance and mating.

Foraging

Optimal foraging theory (MacArthur & Pianka, 1966) predicts how individuals forage and move within the habitat matrix. According to their theory, individuals disperse when the benefits inherent in moving to a new patch of habitat outweigh the costs. Costs and benefits can be viewed in terms of energy budgets derived from food intake and the goal for individuals is to optimize energy gain and maximize reproductive fitness (Pyke, 1984; Swingland & Greenwood, 1983). Optimal foraging theory predicts that organisms have evolved to optimize resources and this theory applies at all size scale, from large mammals(Courant & Fortin, 2012), to birds (Alerstam, 2011; Wilson, Quintana, & Hobson, 2012) down to microbes in the water column(Stocker, 2012). Charnov (1976) developed the marginal value theorem and predicted that individuals would stay longer in patches when the distance between patches is greater and when the habitat is less energy rich.

The home range is defined as the area an individual occupies and uses for its daily activities (Mace, Harvey, & Clutton-Brock, 1983). The size of the home range correlates with the resources available to that individual within that area (Brown, 1975; Wilson et al., 2012) and many individual home-ranges will overlap. Territories are defined as non-overlapping areas within the home range where individuals seek to exclude other individuals or groups in order to secure access to resources, such as food, mating areas or nesting sites (Mace et al., 1983). Resources within a territory must be stable, both in time and in place, in order to be defensible. For example, species that feed on seeds can defend territories, while species that feed on aerial insects are less able to do so (Brown, 1975). Optimal foraging theory has evolved over the years, spawning more complex models encompassing minimizing predator risks (Bernstein, Kacelnik, & Krebs, 1988), and incorporating the costs of defending a territory against competitors (Kacelnik, Houston, & Krebs, 1981) as well as incorporating group dynamics and competition from within (Wilson et al., 2012). Defending a territory protects renewable resources against depletion by a competitor and makes individual defenders able to optimize time between return visits (Charnov, 1976). Even within territorial species, temporary or seasonal territory resource richness will sometimes lead to relaxation of territoriality (e.g. bears at a salmon run)(Ben-David, Titus, & Beier, 2004; Miller et al., 1997) and affect dispersal patterns.

Competition

Competition for reproduction-limiting resources is also a major driver of dispersal (Waser, 1985). Competition can come from individuals of the same species (intraspecific competition) or from other species using the same resources (interspecific competition). Interspecific competition can take the form of competitive exclusion (Hardin, 1960) and niche differentiation, in which the stronger local competitor pushes the weaker into a different ecological niche or towards extirpation. Both of these types of competition can lead to dispersal (Amarasekare & Nisbet, 2001). Intraspecific competition is a major factor limiting the carrying capacity of a population. The carrying capacity of a population refers to the population size that a particular environment can sustain in the long-term. Intraspecific competition can come from exploitation competition (for example, competition for food resources) or interference competition (such as excluding conspecifics from nesting sites or male-male competition for females) (Moore & Ali, 1984; Perrin & Mazalov, 2000).

Mating

Dispersal has also evolved as possible mechanism to avoid inbreeding depression (Charlesworth & Charlesworth, 1987). In many species, one sex will remain more philopatric and a sex-biased dispersal occurs before mating which reduces the chance of inbreeding. Some species of the same genus show diverse patterns of dispersal. For example, squirrel monkeys (genus *Saimiri)* have a wide range of dispersal patterns where in some species both the male and female disperse, in others the males are philopatric and only the females emigrate and, in a third species, only the males emigrate (Boinski, Kauffman, Ehmke, Schet, & Vreedzaam, 2005). Sex-based dispersal is often described as a mechanism of inbreeding avoidance (Greenwood, 1980; Perrin & Mazalov, 1999). However, some authors have argued that intrasexual competition and territory choice are more the likely drivers of dispersal (Moore & Ali, 1984). The current state of dispersal theory views it as a consequence of dynamic interactions that vary amongst species, habitat, social groups, sex, age and individuals (Dobson & Jones, 1985; Holekamp & Smale, 1998; Lehmann & Perrin, 2003; Perrin & Mazalov, 1999).

Migration

Some paleoecologists suggest long distance terrestrial migration may have evolved over the Pleistocene epoch as a response to shifting resource abundance, predators, weather changes (and glaciations) and competition (Barnosky, Koch, Feranec, Wing, & Shabel, 2004). Some evidence exists that Alaskan hadrosaurs in the Cretaceous period and possibly mammoths during the late Pleistocene (Guthrie, 1985) might have also migrated (Hotton, 1980) although this remains controversial (Fiorillo & Gangloff, 2001). However, the most convincing evidence for the earliest mammalian seasonal migration is from tooth wear analysis of *Bison antiquus* specimens found in the late Pleistocene (between 38,000 and 12,000 yr. B.P.) fossils of Rancho La Brea, California (Jefferson & Goldin, 1989). Recent analysis of C_4 isotopes in the tooth enamel of these specimens also supports seasonal migration (Feranec, Hadly, & Paytan, 2009).

At the heart of these movement patterns lies the question of why animals migrate. Why is returning important? Why has seasonal migration been selected from an evolutionary standpoint over residency or a nomadic existence? Migration must confer certain evolutionary advantages. Researchers initially thought that animals migrated to avoid a resource bottleneck in temperate climes (Baker, 1978). This view suggested that species were initially non-migratory and that selective pressure favored those who left the harsh winter environments for gentler tropical climate. Sinclair (1983) argued that this hypothesis was flawed; why would the animals be in the temperate latitudes in the first place? As an alternative, many studies have reported a correlation between body mass and reproductive success (Festa-Bianchet, Jorgenson, & Réale, 2000; Keech et al., 2000; Perrins, 1970; Rogers, 1987; Sinclair, 1978; Wiehn & Korpimäki, 1997). This correlation suggests a strong selection bias for individuals that place themselves in areas of superabundant food supply before breeding. Sinclair (1983) argued that organisms have always been able to breed and remain in tropical climates. He also noted that the food abundance in the summer temperate zones is greater that in the tropics, giving the advantage to migrants. Migration offers both the advantages of nomadic exploitation of habitat outside the usual home range and the security of returning to a known habitat at times when the spike in resources is depleted. Migration strategies have evolved when the advantages of travel outweigh the costs of that travel. For example, ungulate migrants tend to outnumber residents as they make better use of resources and suffer less depredation (Fryxell, Greever, & Sinclair, 1988).

Seasonal migration is evident in all taxa, on land and sea, yet not all species of each taxon migrate. Birds are the long-distance champions: Manx shearwaters (*Puffinus puffinus*) migrate 28,000 km on a yearly basis and bar-tailed godwits (*Limosa lapponica*) make the longest non-stop flight of any migrant, clocking 11,000 km between stops (Kovar, Brabec, Vita, & Bocek, 2009). A particular sooty shearwater (*Puffinus griseus*) held the record for longest measured annual migration at 64,000 km (Shaffer et al., 2006) until the use of geolocators on arctic terns (*Sterna paradisaea)* revealed an annual migration of over 70,000 km (Egevang et al., 2010). However, not all birds migrate. Some tropical raptors are endemic (i.e. do not migrate), others range from complete, partial or irruptive migrants (Bildstein, Schelsky, Zalles, & Ellis, 1998). The members of the nuthatch family (*Sitta spp.*) do not migrate except for the red-breasted variety (*Sitta canadensis*) that migrates widely.

Another member, wallcreepers (*Tichodroma muraria)*, prefers migrating only in altitude (Saniga, 1995). In some bird species, the predictability of resources in time and space will dictate if individuals behave as regular seasonal migrants or as irruptive migrants (Newton, 2006).

The longest known mammal migration belongs to the Eastern Pacific gray whale (*Eschrichtius robustus)* and covers 20,000km (Killingley, 1980). Terrestrial mammalian migration champions include various caribou herds (*Rangifer tarandus spp.)* that travel upward of 2,500 km in their seasonal migration. A range of animals, from bears (*Ursus arctos)* (Ciarniello, Boyce, Seip, & Heard, 2007; White Jr, Kendall, & Picton, 1998), ungulates (Albon & Langvatn, 1992; Mysterud, 1999; Rice, 2008), birds (Burgess & Mlingwa, 2000) to worms (Didden, 1993) also migrate in the vertical plane (altitudinal migrants). Amphibians display very short (less than 200 m) yet regular seasonal migratory patterns (Kovar et al., 2009). The most spectacular seasonal migrations involve all members of a population (complete migration) such as the wildebeests (*Connochaetes taurinus*) of the Serengeti**.** Certain migrations take multi-generations to complete, for example the four-generation migration of the monarch butterfly (Brower & Malcolm, 1991). However, long distance migration worldwide as a phenomenon is disappearing because of anthropogenic impediments to migration (Berger, Cain, & Berger, 2006; Wilcove & Wikelski, 2008). For example, springbok (*Antidorcas marsupialis*) (Roche, 2008) and wildebeest (*Connochaetes taurinus*) (Spinage, 1992) migration has ceased in southern Africa, mostly due to fencing of cattle ranches across their migration routes. Some researchers argue that the phenomenon of migration itself is so spectacular that it needs to be preserved, whether the species is in peril or not (Brower & Malcolm, 1991). Careful conservation planning can help preserve migration (Berger, Young, & Berger, 2008).

Climate change considerations

Changing climate patterns may also have serious consequences on patterns of dispersal and migration. Potential global warming is one of the most serious threats to biodiversity (Malcolm, Liu, Neilson, Hansen, & Hannah, 2006). Ecologists predict that a warming of the planet can cause various effects including drastic changes in local temperature, weather patterns, rainfall, sea level, and temperatures. In turn, these effects can cause havoc with fire regimes (Weber & Flannigan, 1997), changes in forest composition (Condit, Hubbell, & Foster, 1996), coral bleaching (N. A. J. Graham et al., 2006; Knowlton, 2001), surges in diseases (Harvell et al., 2002; Kiesecker, Blaustein, & Belden, 2001), and changes in sex ratios (Janzen, 1994). In summation, global warming could change the value of the ecological services provided to humanity (Hooper et al., 2005). Species faced with a changing environmental envelope have few choices: adapt, migrate, or perish.

There is compelling evidence that climate change has already led to extinction of certain species of trees (Condit et al., 1996), butterflies (McLaughlin, Hellmann, Boggs, & Ehrlich, 2002) and amphibians (Pounds et al., 2006). There is also evidence that climate change is leading towards the extirpation (Root et al., 2003), extinction (Pörtner & Knust, 2007; C. D. Thomas et al., 2004), or migration (Doyle, Krauss, Conner, & From, 2010) of a large number of species of plants and animals. Current models predict that by 2050, 15 to 35% of all species in certain habitat will be “committed to extinction” (C. D. Thomas et al., 2004). There is already evidence of climate change affecting the migratory populations by causing mistimed migration (Carey, 2009; Robinson et al., 2009), poleward shifts in spatial distribution (Parmesan et al., 1999) and changes in species composition (Lemoine, Bauer, Peintinger, & Bohning-Gaese, 2007).

The effects that climate change will have at a local level are difficult to predict but ecologists agree that changes in the local conditions will change the ability of sessile organisms to persist (Thuiller et al., 2008; Vitt, Havens, Kramer, Sollenberger, & Yates, 2010). These changes will lead to alterations in local ecosystems forcing mobile organisms to seek better habitat through migration (Araujo, Cabeza, Thuiller, Hannah, & Williams, 2004). Modeling various climate scenarios helps conservationists anticipate the effects on sessile organisms in particular habitats and see if their rate of colonization can keep up with predicted climate change (Collingham, Hill, & Huntley, 1996). New predictive species distribution models shed light on where future climate-change induced migration might happen and predict future species distribution (Collingham & Huntley, 2000; Dell, Pawar, & Savage, 2014; Guisan & Thuiller, 2005). Recent evidence points to certain herbaceous plants and trees being able to show evolutionary adaptations at the same pace as predicted climate change (Davis, Shaw, & Etterson, 2005). However, others argue that climate change will overwhelm the adaptive capabilities of primary producers located in fragmented landscapes (Jump & Penuelas, 2005).

Researchers also question if current reserve design can accommodate future species survival in the face of global warming (Li, Kruchi, & Gao, 2006). Ecologists debate what kinds of actions are appropriate including developing new altitudinal habitat corridors (Chapin III, Danell, Elmqvist, Folke, & Fresco, 2007) and assisted migration schemes (McLachlan, Hellmann, & Schwartz, 2007). Researchers are trying to model climate change indicators for individual species but the task ahead is daunting (Newson et al., 2009). Conservation planning suffers from the uncertainty surrounding the location of past migration corridors and by the limited options for the placement of future corridors. Migration to suitable habitat will hold the key to the long-term survival of mobile species.

Keystone species movement through the landscape

Conservationists are forced to make monitoring choices of which species are representative at the ecosystem level. When examining long-term ecosystem resilience, researchers (Simberloff, 1998; Soulé & Simberloff, 1986) have argued the importance of monitoring keystone species. The keystone species concept, i.e. a species that affects its environment in a disproportionately outsized manner (Paine, 1969, 1974), underpinned the hypothesis that not all species were equally important to the persistence of an ecosystem (Mills, Soulé, & Doaks, 1993). Determining keystone species is a challenge, as conservationists still do not fully understand the complex web of inter-relationships among the different species in different ecosystems, yet Simberloff et al. (1998) argued that engaging in this endeavor will only enhance our understanding of ecosystem function. Keystone species can be classed into five broad categories (Mills et al., 1993): top predators (Paine, 1974), prey (Holt, 1977), mutualists (Christian, 2001), hosts (Watson, 2001) and ecosystem engineers (Jones, Lawton, & Shachak, 1994).

Protecting keystone species, theoretically gives protection to the species in that particular food web. Removal of keystone species may cause trophic cascades (Carpenter & Kitchell, 1993) or even counterintuitive results due to behavioral modification (Peacor, 2002) or mesopredator release (Crooks & Soulé, 1999; Rayner, Hauber, Imber, Stamp, & Clout, 2007). For example, a long-term study of herbivory exclosure in Kenya found a negative effect on tree health due to a displacement of a symbiotic ant by a more parasitic species (Palmer et al., 2008).

The ability of a keystone species, such as the elephant, an ecosystem engineer (Hatton & Smart, 1984; Haynes, 2011; Mosepele, Moyle, Merron, Purkey, & Mosepele, 2009; Naiman, 1988; Nasseri, McBrayer, & Schulte, 2011; Pringle, 2008; Valeix et al., 2011), to migrate to suitable habitat is of utmost importance to preserving the ecosystem services and the ecological integrity of the landscape (Kerr & Packer, 1998; Noss, 2001). In Africa, climate change predictions point to increases in severe drought incidents in semi-arid and arid ecosystems. Elephants are particularly sensitive to climate variability (Chamaillé-Jammes, Fritz, Valeix, Murindagomo, & Clobert, 2008) and humans are an important factor influencing the distribution and movement of elephants (Blom, Van Zalinge, Heitkönig, & Prins, 2005; Buij & al., 2007; Dolmia, Calenge, Maillard, & Planton, 2007). The two major anthropogenic factors restricting migration appear to be water availability and fences (Loarie, Aarde, & Pimm, 2009). First, the availability of year-round water (boreholes and dams) in reserves and ranches limits the distance elephants need to move. Loarie et al. (2009a) found that dry-season home ranges become larger and the ecological footprint of the elephant becomes more significant as they can now reach areas that were once only available in the wet season. O'Connor et al. (2007) also suggest reducing water availability to increase elephant density and density-dependent effects such as foraging distance, nutritional stress, calf mortality and predation. Severe drought events are especially damaging to young males that have left the matriarchal family group and to calves of less experienced mothers (Foley, Pettorelli, & Foley, 2008). Elephant reserves are often not large enough to protect herds during droughts. Foley et al. (2008) reported that family groups that stayed within a national park suffered more calf loss than those that migrated. Foley et al. (2008) suggest that climatic change events act as a selection driver, favoring individuals that display the appropriate migratory behavior. However, with the availability of more permanent watering holes, this selection mechanism is diminished (O'Connor et al., 2007). Vanak (2010) also found that fencing created edge-effects as elephants avoided the periphery and increased the tortuosity of their foraging movements in the central areas of fenced-in reserves.

Elephant social organization revolves around a dominant matriarch and her family (Charif et al., 2005; Moss, 1988), typically consisting of a few related females and offspring (10-15 individuals) (Thouless, 1996). Females are more philopatric than males and gene flow through the population is male-mediated (Okello et al., 2008). Matriarchal groups have dynamic complex social dominance structures (Wittemyer & Getz, 2007). Elephants can recognize both maternal and paternal kin and do not need to disperse to avoid inbreeding (Archie et al., 2007; Moore, 2007). Elephants show a varied tolerance to different ecosystems, from deserts (Viljoen, 1989) to rainforest (Blake et al., 2008; Parren, De Leede, & Bongers, 2002) and have a varied diet (Hansen, Mugambi, & Dauni, 1985; Landman, Kerley, & Schoeman, 2008). In general, elephants forage on woody plants in the dry season and incorporate more grasses in the wet season (Kalemera, 1989; O'Connor et al., 2007). Elephants also raid agricultural crops for nutritional variety, salt and minerals (Rode, Chiyo, Chapman, & McDowell, 2006).

Water availability and foliage quality largely dictate the seasonal movement of elephant herds (Cerling, Wittemyer, Ehleringer, Remien, & Douglas-Hamilton, 2009; Loarie, Van Aarde, & Pimm, 2009; Shannon, Page, Slotow, & Duffy, 2006; Western & Lindsay, 1984; Young, Ferreira, & Van Aarde, 2009). Some studies found that male and female elephants had significantly different sizes of home ranges (De Villiers & Kok, 1997), while others did not (Loarie, Aarde, et al., 2009). Dominant bulls in musth show a high degree of home range fidelity while younger, less dominant bulls (also in musth) travel far to initiate contact with distant breeding herds (Hall-Martin, 1987). Males can come into musth at anytime, but do so predominantly after a long rainy season (Poole, 1987).

Elephant concentrate near water in the dry season and disperse in the wet season (Loarie, Aarde, et al., 2009), therefore establishing distinct dry and wet season home ranges (Lindeque & Lindeque, 1991) up to 200 km away (Verlinden & Gavor, 1998). In the dry season, several family groups will aggregate to form clans of 5-10 families and will share a home range and use it independently (Charif et al., 2005). Charif et al. also find that other families within clans coordinate their movement by using ultra-low frequency acoustic signaling as well as other clues (Bates et al., 2008). Travel corridors link the different seasonal home ranges (Douglas-Hamilton, Krink, & Vollrath, 2005; B. Thomas, Holland, & Minot, 2008). Elephants move at significantly greater speeds in the travel corridors than once they reach their home ranges (Douglas-Hamilton et al., 2005; M. D. Graham, Douglas-Hamilton, Adams, & Lee, 2009). Travel routes also tend to feature more vegetation cover (forested areas) (Galanti, Preatoni, Martinoli, Wauters, & Tosi, 2006) and elephants use these routes more during the night (M. D. Graham et al., 2009). Travel corridors for elephants are of utmost importance to the persistence of elephants (Hanks, 2001).

Elephants are more nomadic in the wet season, showing less site fidelity than in the dry season (Loarie, Aarde, et al., 2009; Wittemyer, Polansky, Douglas-Hamilton, & Getz, 2008). Elephant seasonal home ranges vary greatly in size and tend to be smaller in wet savannas and larger in dry savannas. Home ranges vary from 169 km^2 in areas of Mozambique where poaching is high (Ntumi, van Aarde, Fairall, & de Boer, 2005), to 300 km^2 for forest elephants (*Loxodonta africana cyclotisi)* in Sierra Leone (Merz, 1986) to almost 3,000 km^2 for desert elephants in Namibia (Viljoen, 1989). The largest home ranges occur in parts of Tanzania (over 5,000 km^2 for Tarangire NP in Tanzania (Galanti et al., 2006)) and Namibia (over 8,000 km^2 in northwest Namibia (Lindeque & Lindeque, 1991)).

Other important mammal movements

Although elephant are the largest ecosystem engineers in Eastern Africa, other mammals, specifically wildebeest (*Connochaetes taurinus*), giraffe (*Giraffa camelopardalis*) and plains zebra (*Equus burchelli*) have a direct effect on the savannah ecosystem (Holdo, Holt, & Fryxell, 2009; O'Kane, Duffy, Page, & Macdonald, 2011). Understanding the movement patterns of these mammals is important for conservation management. Kenya hosts wildebeest, three of the eight recognized species of giraffe: the Reticulated (*G. c. reticulata*), the Maasai (*G .c. tippleskirchi*) and the endangered (IUCN, 2011) Rothschild's (*G. c. rothschildi*) and both plains zebra and the endangered (IUCN, 2011) Grevy's zebra (*Equus grevii*). Only elephant, reticulated giraffe, and both zebra species roam the Laikipia plateau[1]. Giraffe are browsers (Hansen et al., 1985) that alter the savannah ecosystem by modifying certain strata of the canopy. A long-term exclosure study in Laikipia found that giraffe (and elephant) adversely affect bird populations by foraging subdominant woody vegetation in the canopy (Ogada, Gadd, Ostfeld, Young, & Keesing, 2008). The reduction in canopy density decreases the available food supply for granivorous bird species and reduces both their numbers and diversity. In a similar way, the smaller canopy size also negatively affects herbivorous arthropods. In turn, the reduction in arthropod biomass reduces the size of the insectivorous bird community. Giraffe have a diverse diet consisting of up to 45 different species of plants (Ciofolo & Le Pendu, 2002). Giraffe browse between 7

[1] I will restrict my review of important mammal movements to the three major herbivores present at my research site at Lewa (Kenya), i.e. the elephant, giraffe, and zebra.

kg and 50 kg of woody vegetation daily. In areas of high-density giraffe population, they limit canopy regeneration and alter the species composition of woody plant ecosystems (Birkett, 2002; Birkett & Stevens-Wood, 2005; Bond & Loffell, 2001). Giraffe historically migrate between wet and dry season ranges in search of woody vegetation (Bigalke, 1962; Le Pendu & Ciofolo, 1999; Leuthold, 1978). Some free ranging giraffe can migrate up to 300km between seasonal ranges (Le Pendu & Ciofolo, 1999). However, other giraffe populations in the Namib desert show no seasonal migration (Fennessy, 2009) although undertook long distance movement (> 50 km) within their large home ranges at various times. Giraffe home range sizes can vary greatly depending on climatic conditions, rainfall being the main factor (Ogutu, Piepho, Dublin, Bhola, & Reid, 2008). Larger home ranges up to 1950 km^2 exist in the drier and less vegetated ecosystems such as Namibia (Fennessy, 2009), while in the wetter savannahs of Kruger National Park giraffe hold smaller home ranges of up to 282 km^2 (du Toit, 1990).

Both zebra species are also important ungulates in Laikipia. Both species are highly dependent on water and access to water dictates their migratory behavior (Estes, 1991) in the dry acacia-commiphora bushland of Laikipia (White, 1983). Although they have many differences in behavior (Ginsberg & Rubenstein, 1990; Sundaresan, Fischhoff, & Rubenstein, 2007) and foraging preferences (Becker & Ginsberg, 1990; Sundaresan, Fischhoff, Hartung, Akilong, & Rubenstein, 2008), both species are grazers that affect the ecosystems they pass through in a similar way. Zebra foraging reduces small rodent populations by limiting the available grass supply (Keesing, 1998) and regulate savannah fire regimes by reducing the grass cover (Hobbs, 1996).

Ecosystems worldwide are under constant anthropogenic pressure, from population growth and habitat encroachment to land-use changes and resource exploitation. Unlike the great historical migration of bison (*Bison bison*) in north America, the vast savannah ecosystems of the Serengeti and the north of Kenya are still host to some of the largest terrestrial migrations on Earth (Fryxell et al., 1988). Landscapes shape mammal behavior and in turn are shaped by community dynamics, animal movement, and foraging behavior (Hobbs, 1996). Herbivores regulate fire regimes (Johnson & Matchett, 2001; Van Langevelde et al., 2003), reduce non-native species invasions (Foxcroft, Richardson, Rejmanek, & Pysek, 2010), influence plant success (Augustine & McNaughton, 2004; Hobbs, 1996), and even change edaphic qualities (Denyer, Hartley, & John, 2010; Fine, Mesones, & Coley, 2004; Frank, Depriest, McLauchlan, & Risch, 2011; Kielland & Bryant, 1998; Porensky & Veblen, 2011). Our understanding of the ecology of keystone species and important primary consumers is an integral part of our desire to preserve complete ecosystem functioning in an increasingly fragmented landscape. It is critical to understand the movement of large herbivores through the landscape in order to preserve the ecosystem services they provide.

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CHAPTER 2- Landscape Ecology

Introduction

Landscape ecology is an interdisciplinary science based on a systems approach to ecology and concerns itself with landscape level patterns and scale (Levin, 1992) and examines how ecosystems function together (Hansson & Angelstam, 1991). Landscape ecology integrates both theoretical and applied ecology as it strives to explicitly examine the importance of heterogeneity of the landscape in both space and time (Pickett & Cadenasso, 1995; Sanderson & Harris, 2000). It also accounts specifically for relevant anthropogenic history, disturbances, barriers, and effects, on ecosystem patterns and processes (Foster et al., 2003; Turner, 2005). Understanding landscape interaction, connectivity, and ecosystem functioning as well as how landscape factors influence genetic dispersal, migration and persistence of species is at the core of this discipline (Manel, Schwartz, Luikart, & Taberlet, 2003; Ricketts, 2001).

Landscape ecology is a tool in the arsenal of the conservation biologist to better understand the impacts and interactions of fragmented and disturbed biomes (Fischer & Lindenmayer, 2007; Wiens, 2009). Conservation biology is the science-based approach to protecting wildlife and habitat to ensure long-term biodiversity survival (Soulé, 1985). Landscape ecology addresses some of main conservation issues dealing with anthropogenic impacts that cause habitat loss and fragmentation (Collinge, 1996; Spellerberg, 1998; Wilcox & Murphy, 1985). Landscape ecology concerns itself with the processes (biotic and abiotic) and organisms that preserve proper ecosystem functioning and ecological integrity. Anthropogenic effects leading to fragmentation and loss of connectivity can decouple mobile organisms and processes from their ecosystem role and lead to an impoverished and unstable habitat structure that changes species dynamics and composition.

Habitat Fragmentation

Habitat fragmentation leads to alterations in species composition, richness, and abundance (Crooks, 2002; Debinski & Holt, 2000; Fahrig, 2003; Soule, Alberts, & Bolger, 1992; Young, Boyle, & Brown, 1996). Habitat fragmentation also leads to changes in patterns of animal movement, including migration patterns and home range utilization (Baguette & Van Dyck, 2007; Lima & Zollner, 1996; Van Dyck & Baguette, 2005). Habitat fragmentation can also lead to devastating edge effects that cause a wide range of issues for species that depend on large tracts of pristine habitat (Hooftman & Bullock, 2012; Laurance, 2008; Laurance et al., 2011; Laurance & Bierregaard, 1997; With, 2002). For example, long-term studies of edge effects in the Amazonian rainforest found an incredible range of ecosystem disturbances including: wind disturbance, elevated tree mortality, invasion of disturbance-adapted fauna and flora, altered species composition and trophic dynamics, increased air temperature, decreased humidity, reduced canopy height and density, lower leaf water content, lower soil moisture content, increased leaf phosphorous and carbon-13 content slowing litter decomposition and reduced density of fungal fruiting bodies (Laurance, Lovejoy, & al., 2002). Because anthropogenic habitat fragmentation is ubiquitous, it is important to understand the effects at different scales and on different species (Markovchick-Nicholls et al., 2008; Nathan et al., 2008; Sinclair et al., 2007; Trombulak & Frissell, 2000). For certain generalist species, edge specialists, or invasive species, fragmentation can lead to higher densities (Debinski & Holt, 2000; Gascon et al., 1999; Swihart, Feng, Slade, Mason, & Gehring, 2001) which in turn puts further pressure on native species that require untouched landscapes.

Conservation biologists are taking a more active role in protecting, restoring, and linking fragmented habitat (P. Beier, D. R. Majka, & W. D. Spencer, 2008a; Meffe & Carroll, 1994). Understanding the movement patterns of species between fragments is important for the conservation of critical migration stopover sites (Hobson, 1999; Myers, 1987). There is also evidence that certain species have successfully re-established migration through a series of inter-connected reserves and corridors (Bartlam-Brooks, Bonyongo, & Harris, 2011; Beier & Noss, 1998). The importance of re-establishing migratory corridors is at the forefront of landscape ecology since it is apparent that isolating populations within a protected area often undermines their long-term survival (Brown, 1971) although landscape connectivity is a difficult notion to measure (Bélisle, 2005; Goodwin & Fahrig, 2002; Schumaker, 1996; Tischendorf & Fahrig, 2000). Habitat efforts should seek to optimize connectivity to larger less disturbed landscape patches (Halme et al., 2013; Hanski, 2000).

Biogeography and Population Studies

An appropriate starting point to understand the importance of connectivity and the usefulness of corridors is the Island Biogeography Theory (IBGT) (MacArthur & Wilson, 1967). In this seminal work, the authors developed a model to explain species richness on oceanic islands, proposing that smaller, more isolated islands contain fewer species and are more prone to extinction. Research on arthropods (Simberloff and Wilson, 1969) and birds (Diamond, 1970, 1973, 1974; Terborgh, 1974) supported their theory. Researchers found that immigration and emigration relate to the distance to the mainland source population (colonists) and extinction rates correlate inversely to island size (i.e. the larger the island, the smaller the probability of extinction due to stochastic events). Eventually, the island populations/communities stabilize at equilibrium. The power of the IBGT model was its predictive capacity to estimate the number of species on a particular island.

Biologists drew parallels between real islands and isolated ecosystems on continental mainland. When biologists applied the IBGT models to empirically test virtual "islands" such as land-locked reserves and isolated mountaintops they found that extinction (and emigration) rates surpassed colonization rates and that no equilibrium was reached (Brown, 1971). Using ideas from IBGT as well as other ecological principles, Diamond (1975) coined the "island dilemma": where species counts on islands (or reserves) are initially at over capacity but then move towards extinction patterns correlated with their area size. He proposed conservation planning prescriptions based on his findings that large connected natural areas would offer better long-term species diversity. Others also found a correlation between extant diversity of species and the quality of the habitat, i.e. both the gross area and heterogeneity of the landscape (Collingham & Huntley, 2000; Newmark, 1986). Early applications of IBGT also drew criticism as researchers found that under heterogeneous habitat conditions, smaller refuges could harbor a larger total number of species (J. G. Blake & Karr, 1986; Quinn & Harrison, 1988; Simberloff & Abele, 1976) and that subdivided populations were more likely to persist (Quinn & Hastings, 1987). The key finding was that heterogeneous landscapes provided more opportunity for species diversity. The complexities of animal movement through a heterogeneous landscape matrix are difficult to reduce to permit easy modeling (Bowler & Benton, 2005; Gustafson & Gardner, 1996; With, Gardner, & Turner, 1997) but with phylogenetic data combined with known dispersal drivers, predicting patterns of dispersal has become more rigorous and successful (Brace, Turvey, Weksler, Hoogland, & Barnes, 2015; K. M. Donald, Winter, Ashcroft, & Spencer, 2015; Fraser, Nikula, & Waters, 2011; Jonsson, Fabre, Ricklefs, & Fjeldsa, 2011; J. T. Li et al., 2015). Population size was also one of the key determinants of long-term survival for many species (Brown, 1971; Newmark, 1987). Ecologists calculated the lower population limits necessary for long-term species survival, i.e. the concept of the MVP, minimum viable population (Soulé, 1980). Three types of dangers threaten small populations: genetic degradation, demographic imbalance and random environmental disaster (Shaffer, 1981). Demographic research led to estimates of between 50 (to stem inbreeding depression) and 500 individuals (to stem genetic drift) as key minimum values. These numbers represent the effective population sizes (i.e. breeding individuals) and these estimates were applied widely as rules of thumb by practitioners even as researchers were still debating them (Simberloff, 1988). Newer estimates of MVP, derived from models that also account for environmental and demographic stochasticity, range in the thousands of individuals for a wide variety of vertebrate species (Reed, O'Grady, Brook, Ballou, & Frankham, 2003; Traill, Bradshaw, & Brook, 2007) while other studies reject the idea of an effective estimate of MVP (Flather, Hayward, Beissinger, & Stephens, 2011; Frankham, Bradshaw, & Brook, 2014). Demographic imbalance considers key ratios such as birth/death, immigration/emigration and sexes and can further reduce the effective population size. Many demographic models suggest that extinction can occurs quickly once the population crosses a certain threshold whereas there can be long-term population persistence above this threshold (Reddingius & den Boer, 1970; Richter-Dyn & Goel, 1972).

Environmental stochasticity such as changes in predator/prey ratios, external competition and physical environmental dangers (disease, fire, weather) (Simberloff, 1988) also can lead to extinction. This random element is difficult to model and depends heavily on the variance of the population growth rate and the frequency and severity of catastrophes (Russell Lande, 1993). Long-term survival in stochastic models depends on very large single populations or on an array of smaller, distinct but connected populations to re-seed depleted areas (Goodman, 1987). Diamond (1984) examined historical extinctions and concluded that risk of extinction decreases as the size of habitat and population density increase. Diamond (1989) examined oceanic islands and determined that recent (<300 years) extinctions coincided with the arrival of humans. The colonization by humans caused mass extinction of the biota due to overhunting, introduction of invasive species and habitat destruction. Isolation can have some benefits as isolation acts as a buffer against the spread of disease and stochastic events (Simberloff & Abele, 1982).

Closely related to MVP is the concept of metapopulation: a group of spatially separated populations that have some regular yet infrequent interactions (Levins, 1970). Metapopulation studies, by definition, examine the effect of connectivity on long-term species persistence in partially isolated populations. Sub populations can either occupy a habitat patch or colonize an empty one. Metapopulation studies model the effects when a local population patch is locally extirpated from that habitat patch, and the vacated habitat patch is re-colonized by a neighboring population. The metapopulation can survive long-term even when many local populations fail as long as new seed population can reach the vacated habitat. Increasing movement among populations increases probability of long-term survival (Roff, 1974). The metapopulation concept first described the interactions of spatially separated populations of insects (Levins, 1969) and then was applied widely by others in studies of single-species metapopulation dynamics (Gilpin, 1987; Hanski, 1985; R. Lande, 1987; Quinn & Hastings, 1987). The metapopulation assumptions differed from the IBGT in one important aspect, i.e. no population was large enough to be immune from possible extinction (Hanski & Gilpin, 1991). Metapopulation studies produce reliable results for small species that turn over on a relatively short time span and do not migrate, or for very small populations (Lehmkuhl, 1984). For larger migrating mammals (Elmhagen & Angerbjörn, 2001), birds (Esler, 2000) or long lived species such as turtles (Shoemaker, Breisch, Jaycox, & Gibbs, 2013) metapopulation analysis becomes more problematic. Brook et al. (2006) argued that MVP is a poor predictor of extinction compared to anthropogenic factors. Because large scale empirical metapopulation studies are often likely to take inordinate amounts of time, population viability models are necessarily often theoretical (Shaffer, 1981). Models tend to be either analytical or simulation based and authors have pointed out limitations to theoretical modeling and dangers arising from drawing conservation management decisions based upon these models (Beissinger & Westphal, 1998).

Minimum viable metapopulation (MVM) size studies attempt to describe the minimum number of interacting population nodes to prevent extinction. The alarming conclusion of MVM analysis is that without reversing habitat loss and fragmentation, many rare species are considered "living dead" as their population equilibrium eventually relaxes to zero due to a lack of connectivity and declining minimum amount of suitable habitat (MASH) (Hanski, Moilanen, & Gyllenberg, 1996). Some researchers found that protected natural areas were never large enough to ward off eventual extinction because of the effects from the surrounding fragmented landscape matrix (Brashares, Arcese, & Sam, 2001; Gurd & Nudds, 1999; Newmark, 1987; Nicholls, Viljoen, Knight, & Van Jaarsveld, 1996; A.S.L. Rodrigues & Gaston, 2001). These papers and others (Berger, 2004; Newmark, 1996) stressed the importance of linkages between conservation areas and the importance of proper ecological networks designed especially for terrestrial migration. Long-term survival of species depends on genetic connectivity (Scribner, Blanchong, Bruggeman, & al., 2005; Soulé & Simberloff, 1986). Genetic disadvantages of isolated populations can potentially be managed through translocation and captive breeding (Thomas, 1990), however, these solutions are suboptimal to connected populations (Reed & Bryant, 2000; Snyder et al., 1996).

The most important aspect for long-term species survival is safety from human activity and habitat encroachment (Brook, Traill, & Bradshaw, 2006; Diamond, 1984; Harcourt, 1994) as anthropogenic activity is the prime agent of deleterious habitat fragmentation (Fahrig, 2003; Fischer & Lindenmayer, 2007; Kruess & Tscharntke, 1994). Anthropogenic modifications to habitat can also lead to changes in behavior and migration patterns that can affect long-term survival (Hebblewhite et al., 2006; Loarie, Aarde, & Pimm, 2009). Agriculture, urbanization, rural development, and roads all contribute to increased fragmentation. Wilcox and Murphy (1985) argue that fragmentation results in a reduction of total area habitat, increased edge to area ratio, isolation, and division of habitat into smaller patches. Most biologists agree that a decrease in total habitat area is harmful to biodiversity (Simberloff, 1988) and that preserving biodiversity and ecosystem functioning is of paramount importance (Hooper et al., 2005; McCann, 2000).

Movement Corridors as Connectivity Vectors

Corridors have various objectives and definitions (G. R. Hess & Fischer, 2001) and here, I focus on corridors used to facilitate movement of wildlife in order to promote population connectivity. A common definition is a linear feature of vegetation that differs from the surrounding habitat matrix and connects at least two patches that were connected in historical time (Saunders & Hobbs, 1991). In this section, I examine corridors that allow for movement of species from one place to another and that are not intended as linear habitat for long-term residency. This definition is species specific, i.e. a movement corridor for a large mammal may very well be suitable linear habitat for small mammals or insects. Movement corridors facilitate dispersal and migration of species from one suitable patch of habitat to another and are also referred to as dispersal corridors or landscape linkages (Beier & Loe, 1992).

Intuitively, the idea of corridors re-connecting patches of land that were formerly connected is almost self-evident and that may be the best argument for the re-establishment of corridors (Noss, 1987). Preserving and re-establishing connectivity is a key element of conservation efforts worldwide and organizations allocate considerable resources towards their establishment (Wilson, McBride, Bode, & Possingham, 2006). Wildlife linkages can alleviate the impacts of habitat fragmentation (Beier & Noss, 1998; Merriam, 1991), however connectedness does not equate connectivity (Debinski & Holt, 2000; Horskins, Mather, & Wilson, 2006; Tischendorf & Fahrig, 2000). Poorly designed corridors are ineffective and expensive (Nichols & Margules, 1991; Simberloff, Farr, Cox, & D.W., 1992; Soulé & Gilpin, 1991; Soulé & Simberloff, 1986). They can also be vectors of disease, invasive species, wildfires, poaching and genetic sinks (Simberloff & Cox, 1987) although no ecological catastrophes due to corridors have been documented (Beier & Loe, 1992). Some corridors become population sinks and are ineffective even though considered high quality habitat, i.e. the higher quality habitat can impede the movement by becoming a de facto extension of the home range and encouraging residency (Horskins et al., 2006). On the other hand, softening of hard agricultural boundaries offers corridor-like potential (P. F. Donald & Evans, 2006). The call to reconnect safe pockets of habitat for migrating animals has been growing for many years (Hobbs, 1992) and has never been higher. Habitat loss to larger ecosystems results in fragmented and isolated wildlife populations that are more vulnerable to stochastic events (Russell Lande, 1993; Liu & Wang, 2014; Sinclair & Pech, 1996; Winterbach, Winterbach, Somers, & Hayward, 2013). However, keeping some populations distinct and isolated might be a wise strategy against fast spreading diseases. Hess (1994) showed that while most metapopulation survived better under connected landscapes, under certain scenarios a highly communicable disease dramatically increases the probability of extinction of the whole population in connected populations unless quarantine population pockets are established (G. Hess, 1996). The recent devastation of more than 62% the entire worldwide saiga population (*Saiga tatarica*) by a relatively common and opportunistic bacterium is a case in point where a whole population was afflicted and perished in under three weeks (Milner-Gulland, 2015). The future of this species now lies with geographically isolated populations distal to the area where this mass die-off just happened.

Corridor design

Designing a randomized and replicable large-scale study to test if corridors serve their intended purpose of enhancing genetic stock and favoring re-colonization has been described as almost impossible and certainly questionable on ethical grounds (Nichols & Margules, 1991). Researchers theoretically would need to randomly apply the two essential treatments of the experiment, i.e. the creation and destruction of corridors and the extirpation of local population to see if the habitats are re-colonized. However, Nichols and Margules (1991) argue such experimental design is unnecessary, as most conservationists would argue that any habitat design that promotes migration among protected blocks would enhance population viability. Recent reviews of the effectiveness of corridors support the intuitive notion that corridors have been mostly positive at mitigating habitat fragmentation (Beier & Noss, 1998; Haddad et al., 2003).

The design of a corridor usually involves the following steps (P. Beier, D.R. Majka, & W.D. Spencer, 2008b). First, stakeholders in the corridor define the ecological goals of a corridor (e.g., the focal ecosystem and related focal species). Species using the corridor fall in two categories: passage species and corridor dwellers (Beier & Loe, 1992). Passage species can move through the corridor in a few hours to a few weeks; corridor dwellers persist more than one generation. A conservation team develops a model of the landscape using expert information concerning landscape elements that will influence the movement of the focal species such as topography, roads and human disturbance. The information is transformed into a GIS model using a least-cost analysis or some other type of algorithm (Possingham, Ball, & Andelman, 2000), but there are many variants, including some recent models based on dynamic optimization (Martin et al., 2007) and on electrical circuitry (McRae, Dickson, Keitt, & Shah, 2008; Proctor et al., 2015). The chosen model yields various suggested linkages depending upon the weight assigned to each landscape element. Beier et al. (2008b) argued that once a least-cost corridor is proposed, it must be analyzed to see if it will likely serve the chosen focal species better than existing conditions or alternative corridor designs. They also discuss how to account for the change in vegetation within corridors in an age of climate change. Williams et al. (2005) developed a quantitative method that incorporates many corridors and offers different pathways that will likely accommodate climate change for a selected South African habitat. However, linkage corridors are unlikely to be sufficient to assure the persistence of tropical species under various climate change scenarios (J. W. Williams, Jackson, & Kutzbach, 2007).

Roads: Barriers to movement and agents of habitat fragmentation

Roads influence the survival of animals differently, depending on the species and individual propensity to avoid roads, either because of noise, road surface, road size or traffic volume (Dickson, Jenness, & Beier, 2005; Jaeger et al., 2005). For example, roads fragment habitat by creating barriers to dispersal, especially for small species (Alexander & Waters, 2000; Keller & Largiadèr, 2003; Mader, 1984; McGregor, Bender, & Fahrig, 2008). However, large mammals are not immune to this effect. Research shows that black bear (*Ursus americanus*) (Brody & Pelton, 1989), grizzly bear (*Ursus arctos horribilis)* (McLellan & Shackleton, 1988), wolf (*Canis lupus)* (Kaartinen, Kojola, & Colpaert, 2005; Thurber, Peterson, Drummer, & Thomasma, 1994; Whittington, St. Clair, & Mercer, 2005), cougar (*Puma concolor*) (Dickson et al., 2005) and elephant (*Loxodonta africana)* (Barnes, Barnes, Alers, & Blom, 1991; S. Blake et al., 2008; Blom, Van Zalinge, Heitkönig, & Prins, 2005) also suffer**.** Roads also act as vectors for poaching (Blom et al., 2005; Wright & Duber, 2001) and as agents of dispersion for invasive species (Hansen & Clevenger, 2005; Jules, Kauffman, Ritts, & Carroll, 2002; Pauchard & Alaback, 2004; Von Der Lippe & Kowarik, 2007). Roads also interrupt seasonal migration, thus reducing genetic diversity (Clark, Brown, Stechert, & Zamudio, 2010). In the case of anuran species richness, roads can be as devastating as deforestation (Eigenbrod, Hecnar, & Fahrig, 2008).

The growing importance of road ecology stems from studies that explore the effect of roads on ecological processes and animal populations. Research on bird presence and breeding suggests that road disturbances affect species as far as 1200m away (Forman, Reineking, & Hersperger, 2002). Using the most conservative estimates that roads disturb animal population at 100m, Forman (2000) estimates that one fifth of the US land area is directly affected by roads. For bird species, indirect effects of roads (noise, light, edge effects) can have a greater influence on population than direct effects (vehicular mortality, pollution, habitat loss)(Kociolek, Clevenger, Clair, & Proppe, 2011; Mammides, Kadis, & Coulson, 2015).

Crossing roads and highways is a major source of mortality for animals (Barthelmess & Brooks, 2010; Baruch-Mordo, Breck, Wilson, & Theobald, 2008; Grilo, Bissonette, & Santos-Reis, 2009; Kramer-Schadt, Revilla, Wiegand, & Breitenmoser, 2004; McCall et al., 2010) and a major cause of human-animal conflict (Smith-Patten & Patten, 2008; Trombulak & Frissell, 2000). Although most research has focused on major roads and highways, others (Clevenger, Chruszcz, & Gunson, 2002; Garcia-Gonzalez, Campo, Pola,

& Garcia-Vazquez, 2012; van Langevelde, van Dooremalen, & Jaarsma, 2009) found that lower volume roads and minor roads are also responsible for high mammalian, anuran, and bird mortality. Small mammals use roadside habitat regardless of the high risk of mortality (Bissonette & Rosa, 2009). Species specific scaling of crossing structures and vegetation cover are important (McDonald & St. Clair, 2004) as well as construction materials and design (Martinig & Smith, 2016). Measures implemented to reduce vehicle speed are also a possible solution (Bullock, Malan, & Pretorius, 2011; Jaarsma, van Langevelde, & Botma, 2006; van Langevelde & Jaarsma, 2009) although Bullock et al. (2011) found that road signs had no decreasing effect on vehicular traffic speeds.

When mammal size increases and collision damage to people is more severe, ecologists have gone to great lengths to devise safe and efficient road crossing structures that promote connectivity (Glista, DeVault, & DeWoody, 2009; McCollister & Van Manen, 2010; Ng, Dole, Sauvajot, Riley, & Valone, 2004). Research shows that to be connective, road crossings need to vary in keeping with how specific species move through the landscape (Clevenger, 2005; A. P. Clevenger, B. Chruszcz, & K. Gunson, 2001; Mata, Hervés, Herranz, Suàrez, & Malo, 2008; McDonald & St. Clair, 2004). Road ecology integrates animal movement patterns, road mortality, animal behavior, invasive species, traffic management, and population genetics (Shepard, Kuhns, Dreslik, & Phillips, 2008). Because of these complexities, road ecology is becoming a specialty field of landscape ecology (Y. Li, Hu, Li, & Xiao, 2003; Lugo & Gucinski, 2000; van der Ree, Jaeger, van der Grift, & Clevenger, 2011). Population genetics is increasingly important in evaluating the success of road crossing structures at the population level (Simmons, Sunnucks, Taylor, & van der Ree, 2010; van der Ree, Heinze, McCarthy, & Mansergh, 2009). Genetic information can be gathered from trapping or road kill but there are also non-invasive genetic sampling techniques such as collecting DNA information passively, i.e. through hair traps, fecal samples, egg shells, etc.…

(Morden et al., 2011; Poole, Reynolds, Mowat, & Paetkau, 2011; Schmaltz, Somers, Sharma, & Quinn, 2006). Clevenger and Sawaya (2010) used barbed wire hair traps at two underpasses to collect samples from a wide variety of mammals using two crossing structures without altering crossing behavior.

Fencing: segregation of wildlife and people

In order to direct animal movement to safe crossing structures, conservationists rely heavily on the use of fencing. Fences are used along side the road to block random crossing points and funnel animal traffic towards overpasses, underpasses and culverts (A. P. Clevenger, B. Chruszcz, & K. E. Gunson, 2001; Reidy, Campbell, & Hewitt, 2008; VerCauteren, Lavelle, & Hygnstrom, 2006). Conservationists use fences regularly to protect wildlife and segregate it from the surrounding habitat matrix (Bode & Wintle, 2010; Hayward & Kerley, 2009; Lagrange, Hansen, Andrews, Hancock, & Kienzler, 1995; O'Connell-Rodwell, Rodwell, Rice, & Hart, 2000). Fences are hard barriers that can stop or direct migrating species (Fox, Dhondup, & Dorji, 2009), from frogs (Bouchard, Ford, Eigenbrod, & Fahrig, 2009) to elephants (Loarie et al., 2009) and are often used in order to mitigate road mortality. Fences have many benefits including protecting wildlife and habitat (Harvey et al., 2005) and reducing human-wildlife conflict (Hayward & Kerley, 2009; Packer et al., 2013) and understanding the role played by fences is crucial (Mata, Hervàs, Herranz, Suàrez, & Malo, 2005).

However, fences also cause substantial animal mortality. Hard fences tangle and kill thousands of animals yearly including mammals (Harrington & Conover, 2006; Mbaiwa & Mbaiwa, 2006) and birds (Baines & Summers, 1997; Martinez, Martinez, Manosa, Zuberogoitia, & Calvo, 2006). Fences also come with more subtle long-term costs such as reduced gene flow (Atwood et al., 2011; Flesch et al., 2010; Nikolov, Gum, Markov, & Kuehn, 2009), reduced access to resources (Olsson & Widen, 2008), edge effects (Vanak, Thaker, & Slotow, 2010) and local community displacement (Hoole & Berkes, 2010). Fences can also lead to behavioral changes in predation (Beschta & Ripple, 2007; Lindsey, du Toit, & Mills, 2004; Rhodes & Rhodes, 2004).

Wildlife managers are aware of many of the drawbacks of fencing-in wildlife (Jaeger & Fahrig, 2004; Olsson & Widen, 2008) and are encouraged to mitigate these shortcomings by designing better fences (Bode & Wintle, 2010) and creating effective gaps in the fences to enhance connectivity between protected habitat (Newmark, 2008). Conservation biologists have mixed feelings in their effort to protect wildlife and pristine ecosystems by fencing them and the need for effective landscape connectivity. Knowing that no single park is large enough to safeguard species in the long-term, biologists are looking to the largest landscape scale to systems of linked-up refuges, on private and public lands, to ensure long-term persistence of biodiversity (Chester, 2003; Plumptre, Kujirakwinja, Treves, Owiunji, & Rainer, 2007; A. S. L. Rodrigues & Gaston, 2002; Wikramanayake et al., 1998; Wolmer, 2003).

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CHAPTER 3: COMPARING MOTION-CAPTURE CAMERAS VERSUS HUMAN OBSERVER MONITORING OF MAMMAL MOVEMENT THROUGH FENCE-GAPS: A CASE STUDY FROM KENYA

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Author Contributions

Marc Dupuis-Désormeaux conceived and designed the experiments, performed the experiments, analyzed the data, contributed materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Zeke Davidson performed the experiments, contributed materials/analysis tools, wrote the paper, prepared figures and/or tables, and reviewed drafts of the paper.

Edwin Kisio and Mary Mwololo performed the experiments, contributed materials/analysis tools, and reviewed drafts of the paper.

Suzanne E. MacDonald conceived and designed the experiments, performed the experiments, contributed materials/analysis tools, wrote the paper, prepared figures and/or tables, and reviewed drafts of the paper.

COMPARING MOTION-CAPTURE CAMERAS VERSUS HUMAN OBSERVER MONITORING OF MAMMAL MOVEMENT THROUGH FENCE-GAPS: A CASE STUDY FROM KENYA

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Abstract

Monitoring the movement and distribution of wildlife is a critical tool of an adaptive management framework for wildlife conservation. We installed motion-triggered cameras to capture the movement of mammals through two purpose-built migration gaps in an otherwise fenced conservancy in northern Kenya. We compared the results to data gathered over the same time period (Jan 1, 2011 – Dec 31, 2012) by the human observers monitoring mammal tracks left at the same fence-gaps in a sandy loam detection strip. The camera-traps detected more crossing events, more species and more individuals of each species per crossing event than did the human track observers. We tested for volume detection differences between methods for the five most common species crossing each gap and found that all detection rates were heavily weighted towards the camera-trap method. We review some of the discrepancies between the methods and conclude that although the camera-traps record more data, the management of that data can be time consuming and ill-suited to some time-sensitive decision-making. We also discuss the importance of daily track monitoring for adaptive management conservation and community security.

KEY WORDS camera traps, tracking, wildlife monitoring.

Introduction

The importance of reliable wildlife monitoring is critical to wildlife conservation management (Gibbs et al., 1999, Lyons et al., 2008). At semi-porous conservancies, monitoring the points of ingress and egress into the surrounding communities is vitally important to reduce human-wildlife conflicts with elephant (*Loxodonta africana*) and lion (*Panthera leo*). Using community-based track observers can produce reliable results (Elbroch et al., 2011, Stander et al., 1997, Liebenberg, 1990) and can be a valuable monitoring tool (Balme et al., 2009, Gusset and Burgener, 2005, Stander, 1998) although it is not without drawbacks (Burton, 2012). Camera-traps have proven to be useful to detect the presence of rare or cryptic species and to monitor crossing-structures (Ahumada et al., 2011, Balme et al., 2009, Clevenger, 2005, Gagnon et al., 2011, Rovero and Marshall, 2009), and to be a cost-effective and reliable alternative to track-based monitoring at crossing structures (Ford et al., 2009, Wolf et al., 2003, Guzvica et al., 2014).

At our study site, managers use daily reports by track observers to monitor the movement of mammals in or out of the conservancy through purpose-built fence-gaps as part of a multitude of other monitoring tools within their adaptive management model. Managers use the movement data collected at the fence-gaps to monitor migratory patterns and predator movement into the conservancy and out to the neighboring communities. At our study site, observers from the local communities are employed to identify mammal species by the tracks left behind and count the number of individuals that have passed through the fence-gaps. The track observers report their findings on a daily basis. Camera-traps were first installed at our study site in 2010 to document and monitor the movement of endangered Grevy's zebra (*Equus grevyi*) as part of a national effort.

The objective of this study was to examine the effectiveness, reliability and advantages of both methods in the specific context of a semi-porous conservancy. We had no pre-conceived bias towards one method or the other and, based on previous findings, generally expected to see a close correlation between the observer and camera data.

Material And Methods

Study Area

Our study was conducted at the Lewa Wildlife Conservancy (Lewa) in Isiolo, Kenya. The habitat at Lewa consists of northern acacia-commiphora bushlands and thickets (White, 1983) with an afromontane section and areas of savannah. The conservancy supports over 70 species of mammals. A 142 km long, two-meter high fence, consisting of twelve-strand of alternating electrified and grounded wires surrounds the 25,000 ha conservancy. The fence is continuous except for a few manned gates permitting vehicle traffic and three migratory fence-gaps (see Figure1). The Northern gap leads to community pastoral lands and towards traditional elephant migratory routes. The Western gap leads to an adjoining wildlife conservancy (Borana) that also has fence-gaps connecting it to the outside landscape matrix. Finally, the Southern gap leads into an elephant corridor that leads towards Mount Kenya. Camera-trap and observer comparative data were available at two of these fence-gaps, the Northern and Western gaps.

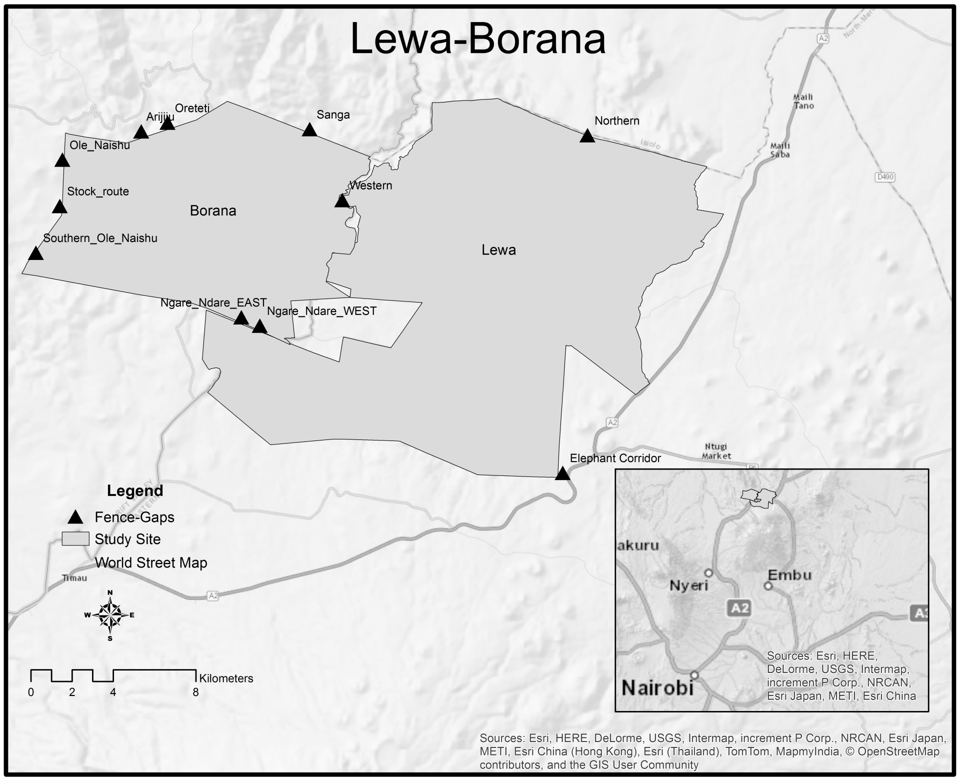

Figure 1- Map of the study site with fence-gaps. (Note: data from the Northern and Western fence-gaps were used in the comparative analysis.)

Data Collection

We collected data between Jan 1, 2011 and Dec 31, 2012. We only compared the data from the days where we had both human observer and camera-trap data. We had 560 days of comparable data from the observers and the cameras at the Northern fence-gap and 474 days at the Western fence-gap.

The track observers were selected from a large pool of local applicants through a competitive process that tested each candidate's proficiency at track interpretation. The successful candidates had a thorough knowledge of track identification. Each track observer monitored one fence-gap, by reading the tracks left in a strip of sandy loam soil on the Lewa (conservancy) side of each fence-gap. These observers monitored their respective fence-gap sand traps in the mornings (approx. 8am-9am). The track traps consisted of a three-meter wide strip of sandy loam soil that spanned the length of the fence-gaps and were kept free of vegetation, debris and other obstructions by daily sweeping, immediately after reading the tracks, thus refreshing the detection surface every 24 hours. The observers transmitted the information via VHF radio to the central operations manager on duty.

We installed three infrared motion-triggered cameras (Reconyx RC60HO Hyperfire, Holmen, WI) at the same fence-gaps monitored by the trackers. Two cameras (Camera-1 and Camera-2) were installed at the wider (30m) Northern gap, facing one another across the gap, in order to cover the whole span. Camera-2 data was used to confirm the species, count or direction of ambiguous crossing events captured by Camera-1. We installed one camera at the narrower (20m) Western gap, also oriented across the gap. All cameras field of view were perpendicular to the directions of wildlife travel. We mounted cameras in "elephant-proof" custom built steel housings that set the height of the camera at roughly 1.5 meters above the ground. Cameras were configured for a three exposure burst upon being triggered by their inbuilt motion detectors and set for rapid-fire to ensure continuous shooting for as long as their sensors detected motion. Images were stored on Secure Digital (SD) memory cards. Staff collected data roughly every two weeks from the cameras. Trained observers, one of the authors (MDD) or a research assistant, catalogued the images.

Inter-observer reliability of the two photo data observers was calculated from a sample that was catalogued by both observers and is reported with the results.

Testing agreement between the detection methods

We compared both methods first by testing inter-observer agreement between methods at the most general level by comparing the daily species detection. We defined a "species crossing event" as the record, either by photographs or by tracks, of the passage of one or more individuals of a species going in the same direction (inbound or outbound) through a particular fence-gap. For every crossing event, both methods recorded: date, species detected, direction of travel and number of individuals of that species crossing in the same direction (count). In the first analysis, we looked at the occurrences where one method recorded the passage of a species and compared if the other method managed to record the passage of the same species. For this general comparison, we did not account for the number of individuals crossing or the direction of travel, we looked to see if the methods would agree as to which species were moving through the fence-gaps. We tested the data at various levels of granularity. We first examined if the two methods were in agreement with regards to species detection, using the pooled data from both gaps, then tested each gap separately. We tested if the two detection methods agreed with regards to direction as well at different traffic volumes. Finally, we tested for agreement between the detection methods for the most common individual species at both fence-gaps.

Testing for volume detection differences

We tested for differences in the number of individuals detected between the methods by using a paired difference test. We tested the ratio of reported counts as:

$$\frac{no.of\ individuals\ detected\ by\ tracker\ at\ event\ i - no.of\ individuals\ detected\ by\ camera\ at\ event\ i}{no.of\ individuals\ detected\ by\ tracker\ at\ event\ i + no.of\ individuals\ detected\ by\ camera\ at\ event\ i}$$

A ratio near zero indicated no difference between the methods. A positive ratio indicated that the trackers detected more individuals per crossing for that particular species and a negative ratio indicated that the camera-traps detected more individuals per crossing event. We tested the data sets for normality of distribution of total detected individuals by performing a Shapiro-Wilks test and found that neither the camera nor the tracker data sets were normally distributed (camera-traps W_{2457}=0.525, p<0.001; tracker W_{2457}=0.370, p<0.001). Because of the non-normal distribution of the data sets, we calculated the paired difference test using a non-parametric Wilcoxon signed-ranks tests.

We tested pooled data as well as data from each gap separately. We tested for the effect of volume, using the mean number of individuals per crossing events as the cutoff between low and high volume days. We tested down to very low traffic volumes (less than three individuals per day) to see if we could find a level where the methods might report more similar activity. We tested for the effect of direction on detection. We tested each common species to each gap separately in order to examine if any of the species were equally detected. Lastly, we also aggregated the data and tested both the agreement and the paired differences with regards to the detection of lion and leopard (*Panthera pardus*) as these species are of specific concern to the management of human-wildlife conflicts. All statistics were calculated using SPSS statistical software (IBM SPSS Statistics version 22).

Results

We tested the paired data using Cohen's Kappa coefficient ("Kappa") to test individual inter-observer reliability between the methods. A Kappa of 0 is approximately equivalent to a reliability of 50%, a negative Kappa is less reliable and a positive Kappa indicates higher inter-observer reliability. Kappa scores are divided into broad categories of agreement, with Kappa scores below zero representing poor agreement, scores of 0.00-0.20 as slight agreement, 0.21-0.40 as fair, 0.41-0.60 as moderate, 0.61-0.80 as substantial and 0.81-1.00 as almost perfect strength of agreement (Landis and Koch, 1977).

Inter-observer reliability between the camera-trap photo observers was classified as very high with agreement on species identification (n=118, Kappa= 0.899, almost perfect), individual counts (n=118, Kappa=0.725, substantial) and on direction (n=118, Kappa= 0.879, almost perfect). We also tested a sample of the camera data from the Northern fence-gap's Camera-1 and Camera-2. We found that both cameras were in fair agreement with regards to species detection (n=64, Kappa=0.333, or fair agreement) as well as detection of volume count and direction of travel (Wilcoxon's signed ranked test, In: $Z=-1.735$, $p<0.083$; Out: $Z=-0.121$, $p<0.904$).)

Agreement results between the detection methods are presented at the more general level in Table 1, and then by individual species in Table 2. We tested the detection of crossing events with respect to the identification of daily species detected, irrespective of the number of individuals detected or the direction of travel. The camera-trap method detected more crossing events (2,112 vs. 1,159), more species (29 vs. 11) as well as detecting twice the number of animals using the gaps (16,403 vs. 7,857) than were detected by the track observers. At this most general level, using pooled data from both the Northern fence-gap (NG) and the Western fence-gap (WG), we found agreement in 845 out of 2426 events (NG: 756/1865, WG: 87/561). Cameras detected 1267 (NG: 897, WG: 370) crossing events that were not detected by the track observers, conversely, the track observers detected 316 (NG: 212, WG: 104) crossing events that were not detected by the cameras. These raw results translated into negative Kappa scores representing poor agreement between the two methods as detailed in the inter-observer reliability section of Table 1. We found poor agreement between methods at all levels of inquiry.

Table 1. Estimation of Inter-observer reliability between detection methods based on daily species detection and detection difference based on total number of individuals detected per crossing for aggregated gap data (01 Jan 2011 to 31 Dec 2012).

						Paired Difference Test				
		Inter-observer Reliability				Ranks (n)			Wilcoxon	
All Species	n	Kappa	*Strength of agreement*			Negative	Positive	Ties	Z	p level
Both gaps	2426	-0.263	Poor			1685	560	181	-19.929	p<0.001
Northern fence-gap	1865	-0.225	Poor			1311	440	114	-19.417	p<0.001
Western fence-gap	561	-0.407	Poor			374	120	67	-10.854	p<0.001
Inbound	1788	-0.224	Poor			1235	435	108	-19.582	p<0.001
Outbound	1823	-0.208	Poor			1326	410	87	-15.309	p<0.001
Below Mean Volume (*n*<6)	2169	-0.304	Poor			1511	495	163	-20.804	p<0.001
Above Mean Volume (*n*>=6)	859	-0.130	Poor			640	201	18	-15.721	p<0.001
Lion/leopard	54	-0.598	Poor			33*	14	7	-2.792	p<0.005

***31 of the 33 negative ranks were calculated by cameras detecting one or more lion or leopard crossing events where the track observers did not detect any crossing, the remaining two were disagreement between methods in the count.**

The results of the paired differences tests are presented at the more general level in Table 1, and then presented by species in Table 2. Using the combined data from both gaps, the paired differences were significantly skewed towards the camera-trap method with negative ranks (1685) outpacing positive ranks (560) by a ratio of 3:1 ($Z=-19.929$, $p<0.001$). Both fence-gaps, taken separately, also showed significant detection volume differences in favor of the camera-traps. Significantly large detection differences in favor of the camera-traps were also apparent irrespective of which direction the animals were travelling or for days that had above or below average traffic volume. Finally, significant detection differences in favor of the camera-traps were also apparent at all of the individual species level, including when we pooled lion and leopard data, except for the case of the detection of giraffe (*Giraffa camelopardalis*) at the Western fence-gap (Table 2).

Table 2: Inter-observer Reliability and Paired Difference Test for individual gaps and most commonly found species at those gaps (Jan 1, 2011 to Dec 31, 2012).

	Northern Gap					Western Gap				
	Inter-observer Reliability			Paired Difference Test		Inter-observer Reliability			Paired Difference Test	
				Wilcoxon					Wilcoxon	
	n crossings	Kappa	*Strength of agreement*	*Z*	*p<*	n crossings	Kappa	*Strength of agreement*	Z	*p<*
Elephant	301	-0.229	Poor	-7.830	0.001	162	-0.401	Poor	-4.459	0.001
Hyena	224	-0.357	Poor	-8.042	0.001	126	-0.355	Poor	-7.218	0.001
Giraffe	451	-0.137	Poor	-9.875	0.001	69	-0.592	Poor	-0.381	0.703
Common Zebra	377	-0.216	Poor	-10.682	0.001	0	n.a.	n.a.	n.a.	n.a.
Grevy's Zebra	359	-0.3	Poor	-4.933	0.001	0	n.a.	n.a.	n.a.	n.a.
Waterbuck	1	n.a.	n.a.	n.a.	n.a.	71	-0.119	Poor	-6.909	0.001
Lion	2	n.a.	n.a.	n.a.	n.a.	37	-0.456	Poor	-2.537	0.011

Discussion And Management Implications

Camera-trap monitoring reported a broader range of species and more individuals crossing the gaps than the human observers monitoring the same gaps by observing tracks left in a sandy strip of soil. The camera-trap data are rich with information concerning time of travel, group size and predator-prey interaction (prey potentially being followed) that could not be compared with the simple reporting scheme of the daily morning observation of tracks. We thus had to simplify the information from the camera-traps in this study to make it directly comparable with the daily reporting schedule of the observers. We found that, contrary to our prediction, the agreement between detection methods was poor and the detection was heavily skewed towards the camera-trap method. In similar analyses (camera-traps versus track-pads) used at crossing structures in North America, Ford et al. (2009) reported some species detection differences between methods, as did Guzvica et al. (2014) in Croatia, although both reported general agreement between methods. Ford et al. (2009) found that camera-traps more readily detected some ungulate species and that some carnivore species were more often detected by track-pads, whereas Guzvica et al. found the opposite. In our study, the detection differences were all heavily skewed towards the cameras, regardless of species.

Tracking is dependent on two factors – the skill of the observer and the suitability of the substrate (Stander et al., 1997, Funston et al., 2010, Liebenberg, 1990). The observers at our study site were highly trained, but their judgments were, by necessity, based on incomplete physical evidence. All human judgments are subject to some degree of error (Diefenbach et al., 2003, Harris, 1915), even in skilled observers (Stocks et al., 2013, Taylor et al., 2012). However, it is unlikely that the disagreement or detection differences were due entirely to human error. Both Ford et al. (2009) and Guzvica et al. (2014) found that the composition and quality of the track pads affected detection rate. Guzvica et al. as well also found that a higher proportion of sand in the soil composition was detrimental to detection. The composition of the soil at our site was sandy loam, which may have been a contributing factor to the lower track detection rates. There was also a diel pattern in the usage of the Northern fence-gap, where outbound traffic is heavier in the evening and inbound traffic is heavier in the morning (data from camera-traps). This movement pattern might make it more difficult for the track observers to detect the outbound traffic as it may have been trampled over by inbound traffic.

We discovered that even at the very lowest traffic volumes the disagreement was still high. The fence-gap locations were chosen along historic migration routes that crossed the fence line at a perpendicular angle. The wildlife using these routes have established permanent game trails at both gaps and tend to travel along it directly, as opposed to walking in flanked groups spread out across the landscape. Migrating animals, walking in file behind one another thus naturally obliterate the tracks of those travelling ahead of them, even at low traffic volumes. It is likely that this phenomenon is also partly responsible for the lower detection rates of the track observers.

It is possible that certain animals approached the gaps at night but did not cross, thus not triggering the cameras but left spoor behind for the track readers to see the next morning. In addition, the fence-gaps attract almost daily human traffic. The gaps permit access to the conservancy at points where there is no road access for several kilometers on either side. The camera traps have documented herders with their cattle, security personnel, curious tourists, community members as well as poachers using the gaps. One incident of poaching for bush meat was captured on camera when a member of the community was photographed entering the conservancy and leaving a few hours later with bird in hand. However, we have had camera-traps destroyed at another study site because the community suspected that these would be used to monitor hunters. Thus, we hesitate to promote the use of camera-traps to prosecute poachers unless the cameras are safely housed and out of reach of people. Further, people often linger at the gaps and wander across the track pads, potentially obliterating tracks which further reduces the probability of track detection.

We found it curious that the track observers detected 316 crossing events that were not detected by camera. Out of those 316 events, 71 involved predators, 14 of these were lions (9) or leopards (5), which are vitally important species to the human-wildlife conflict reduction aims of the wildlife managers. Although the cameras potentially missed 14 lion or leopard crossing events, the tracker observers definitely missed 31 crossing events. We investigated those 14 incidents in more detail and found that 4 of those incidents could be attributed to species misidentification where the cameras in these cases captured hyena crossing, and we suspect that these tracks were misread by the track observers and reported as lion or leopard tracks (as the track observers had not reported any hyena on those days). Regarding the other 10 incidents, the cameras were functional and had detected the passage of other species during that day, however did not detect these predators. This potential camera deficiency is somewhat worrying given the importance of monitoring these predators.

Motion activated sensors used in camera-traps sometimes fail to detect the movement or heat differential required to trigger the camera, especially as the ambient temperature approaches the body temperature (Meek and Pittet, 2012, Rovero et al., 2013, TrailcamPro, 2014). Further, different cameras, even cameras of the same make and model, can produce significantly different photographic data (Hughson et al., 2010). It is possible that some of the differences between the detection methods are attributable to the camera-traps not firing properly. Our comparative test of Cameras 1 and 2 yielded only a fair agreement level. Even though the detection statistics between the cameras were adequate, out of the 54 crossing events in the sample period, 12 events were recorded by only one of the two cameras. Interestingly, 11 of these 12 crossing events involved leopard, spotted hyena (*Crocuta crocuta*) or striped hyena (*Hyaena hyaena*). We found that although the cameras were set for 3 rapid bursts, often only one clear photo of a predator would be taken, as predators would move mostly in the dead of night, and move quickly or low to the ground when passing over the exposed rock wall at the fence-gaps. We found that the infrared flash units on the cameras were not always powerful enough to throw the infrared light in a wide enough beam to consistently give a clear picture, which has been reported before (Meek, 2012).

Although the cameras collected large amounts of data, there were issues associated with the camera maintenance and management of the data that are common to many other camera-trap studies (Swann et al., 2011, Barrueto et al., 2013). We lost a large number of study days due to cameras that were not functioning properly. Cameras were maintained every two weeks to collect SD memory cards and test batteries. During weeks of heavy traffic, the memory cards were quickly filled. In addition, because the bulk of crossing traffic was nocturnal, the infrared flash units were in constant use, draining the batteries quickly. We found that the management of the camera data was often given lower priority in daily management decisions than daily track reports, due to the immediate availability of the reports. This is a potential drawback to using camera traps for adaptive management goals since the time, effort and expense commitments can be unsuitable for supporting the timeframe in which critical decisions are made.

However, given the advantages of the richness of the camera-trap data it is important to find a way to use these data for more immediate managerial decision-making. We thus recommend combining both methods by training the track observers to examine the camera data in the field on a daily basis and report the findings through their usual channels, effectively harnessing the best of each method.

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CHAPTER 4: USAGE OF SPECIALIZED FENCE-GAPS IN A RHINO CONSERVANCY IN KENYA.

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Author Contributions

Marc Dupuis-Désormeaux conceived and designed the experiments, performed the experiments, analyzed the data, contributed materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Zeke Davidson performed the experiments, contributed materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Edwin Kisio and Mary Mwololo performed the experiments, contributed materials/analysis tools, and reviewed drafts of the paper.

Suzanne E. MacDonald conceived and designed the experiments, performed the experiments, contributed materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

USAGE OF SPECIALIZED FENCE-GAPS IN A RHINO CONSERVANCY IN KENYA.

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Abstract

Fencing is increasingly used in wildlife conservation. Keeping wildlife segregated from local communities while permitting wildlife access to the greater landscape matrix is a complex task. We investigated the effectiveness of specially designed fence-gaps on animal movement at a Kenyan rhino conservancy, using camera-traps over a four-year period. The fence-gap design restricted the movement of black and white rhino (*Diceris bicornis* and *Ceratotherium simum simum*) but permitted the movement of other species. We documented over 6,000 crossing events comprising over 50,000 individuals using the fence-gaps to enter or leave the conservancy. We recorded 37 mammal species and two species of bird using the fence-gaps. We conclude that this fence-gap design is effective at restricting rhino movement and at permitting other wildlife movement into and out of the conservancy. We recommend that fenced-in rhino conservancies that desire enhanced connectivity consider this fence-gap design to help re-connect their reserves to the outside landscape matrix while continuing to provide enhanced protection for their rhino species.

Introduction

Managers entrusted with the protection of wildlife face conflicting demands. On the one hand, managers must protect wildlife and on the other hand, they strive to keep the landscape under their management as close to possible to a natural state, with well functioning migration and predator-prey dynamics. Habitat fragmentation and connectivity concerns continue to drive conservation discussions (Beier & Noss, 1998; Debinski & Holt, 2000; Fahrig, 2007; Newmark, 2008; Packer et al., 2013; Tischendorf & Fahrig, 2000). Wildlife managers view fences as a useful tool to protect people and wildlife (Hayward & Kerley, 2009; Hoare, 1992), especially in mixed-use landscapes where communities, roads, and wildlife have to co-exist (Newmark, 2008). Keeping wildlife segregated from communities protects wildlife, by reducing the likelihood of habitat loss and poaching, and protects people and their livestock from collisions (McCollister & Van Manen, 2010), depredation (Hazzah et al., 2014), crop raiding (Kikoti, Griffin, & Pamphii, 2010), and disease (Taylor & Martin, 1987).

Fencing also has many drawbacks, ranging from direct mortality, such as when animals can entangle themselves while attempting to leave the fenced habitat, (Albertson, 1998; Harrington & Conover, 2006; Mbaiwa & Mbaiwa, 2006) to more subtle ecological changes that can affect long-term population viability by isolation (Atwood et al., 2011), reduced access to resources (Brenneman, Bagine, Brown, Ndetei, & Louis Jr, 2009; Loarie, Aarde, & Pimm, 2009; Olsson & Widen, 2008), and the creation of edge effects (Massey, King, & Foufopoulos, 2014; Newmark, 2008; Vanak, Thaker, & Slotow, 2010).

Fences are used in road ecology projects in North America and Europe to restrict access to highways and to direct movement to crossing structures (ecopassages) that are designed to permit connectivity (Aresco, 2005; Clevenger, Chruszcz, & Gunson, 2001;

Olsson & Widen, 2008). The fences are meant to guide the animals towards gaps in the fences that permit access to these crossing structures (underpasses or overpasses). Typically, in road ecology projects, the fences are installed at roadkill 'hot spots', as it would be too expensive to fence the whole road. In contrast, in the African wildlife management context, typically the entire conservancy is fenced. In ecosystems with elephants (*Loxdonta africana*), fencing can be expensive to maintain (Kioko, Muruthi, Omondi, & Chiyo, 2008) as elephant often break their way through fences (Kioko et al., 2008; Mutinda et al., 2014; Thouless & Sakwa, 1995) either for migratory purposes or to raid crops. Crop raiding by elephant is a complex problem that requires measured responses (Davies et al., 2011; Guerbois, Chapanda, & Fritz, 2012; R. Hoare, 2012) but migrating elephant tend to use regular travel corridors to link seasonal home ranges (Douglas-Hamilton, Krink, & Vollrath, 2005; Thomas, Holland, & Minot, 2008). These corridors can be accommodated by opening gaps in the fences that, in theory, can allow elephant, and other migratory species, to move in and out of protected areas. Strategically placed fence-gaps, away from agricultural communities and along historical travel routes, could therefore be a useful tool in ongoing efforts to increase connectivity by keeping natural travel corridors open (Beier & Noss, 1998; Bouché et al., 2011; Di Minin et al., 2013).

Although leaving gaps in the fences might be a practical solution to the needs of migrating elephant, for wildlife conservancies hosting endangered black rhino (*Diceros bicornis*), management must resort to extreme protection measures from poachers by erecting electrical fencing, deploying active surveillance (Walpole & Leader-Williams, 2002), conducting armed patrols, and implementing shoot-on-sight policies (Messer, 2010). The demands of rhino protection often trump the need for ecological connectivity and for example, more than half of the rhino population in Kenya live in fenced-in conservancies (Kenya Wildlife, 2012). At our study site, management has struck a compromise between rhino protection and elephant migratory needs by designing a fence-gap that allows all the species except rhino to migrate in and out of the conservancy. These fence-gaps have been located at sites of historical damage caused by migratory elephant.

The purpose of our study was to test the effectiveness of this special fence-gap design at restricting the movement of rhinos while permitting the movement of other species in an otherwise fenced conservancy in Kenya. We analyzed which species used the fence-gaps and detailed some of differences in the usage patterns between the fence-gaps, by highlighting differences in traffic volume and species composition. We also wanted to better understand why certain species did not use the fence-gaps and so computed usage ratios based on the traffic volume and the size of the population *in situ*. Should this fence-gap design prove to be suitable, it may become a cost effective and useful tool to managers of fenced-conservancies that seek to enhance the connectivity of their protected area.

Methods

Study Site

We conducted our study at the Lewa Wildlife Conservancy (Lewa) in Isiolo, Kenya (0.20^{o} N, 37.42^{o} E). The habitat at Lewa consisted of Northern Acacia-Commiphora Bushlands and Thickets with an Afromontane section (White, 1983). Lewa was initially a cattle ranch (1920-1983) and had a perimeter fence to contain its cattle. In 1983, in response to declining black rhino population, management converted 2000 ha to a rhino sanctuary. This sanctuary grew over the subsequent years and in 1995, Lewa officially converted all of its 25000 ha and upgraded its perimeter fence to a 142 km long, two-meter high fence, consisting of twelve-strands of alternating live electrical and grounded wires. The perimeter fence at our study site was patrolled daily and meticulously maintained by teams of rangers and workmen. The primary purpose of the fence was to segregate the wildlife from the neighbouring communities, thereby reducing human wildlife conflicts. The fence also acted as a secondary anti-poaching deterrent, but the main anti-poaching efforts were through armed patrols, aerial surveillance and community intelligence. The perimeter fence was continuous except for a few manned gates permitting vehicle traffic and for the fence-gaps designed for wildlife traffic (see Figure 2).

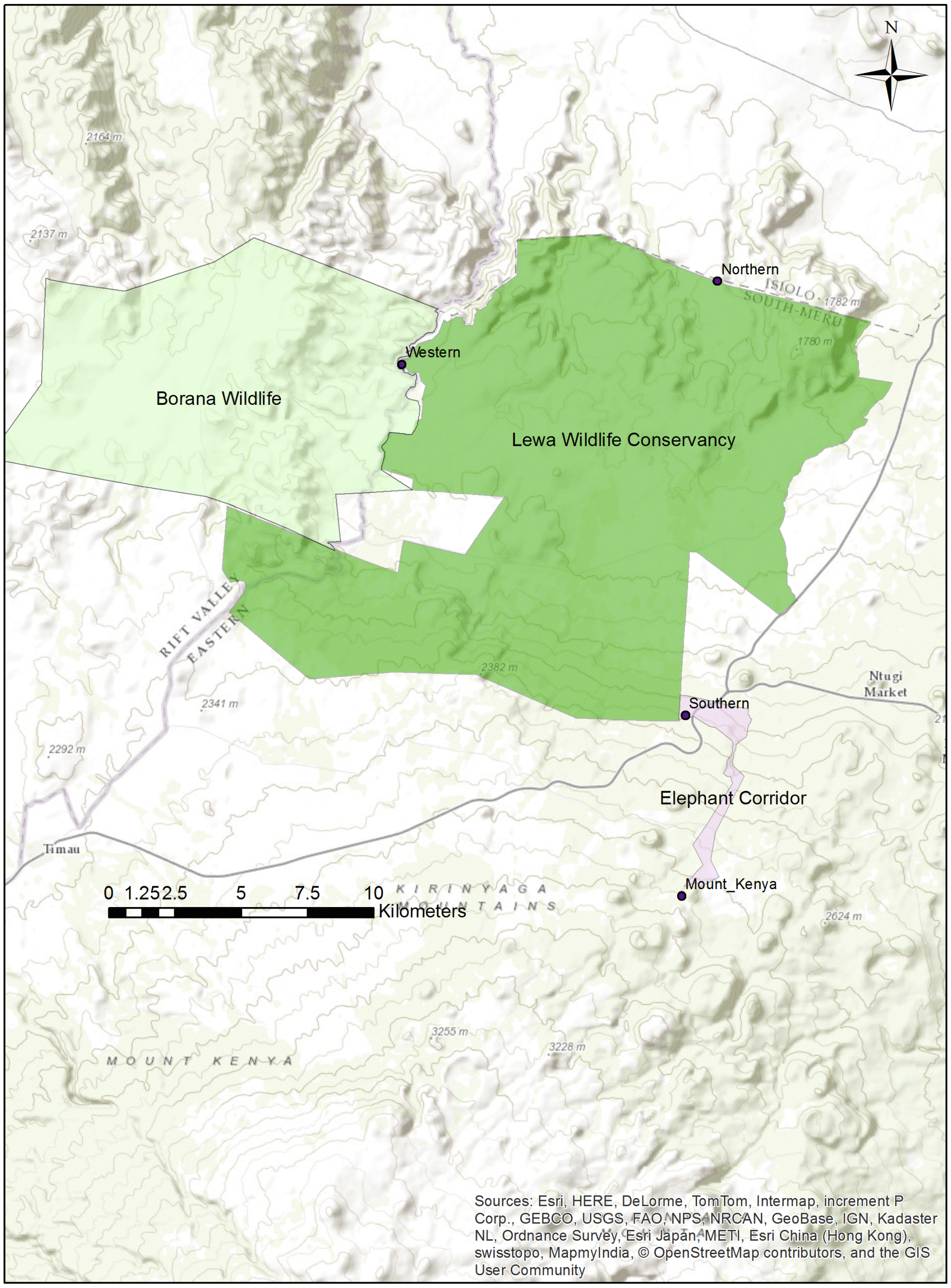

Figure 2- Map of study site with elephant corridor and fence-gaps.

Fence-gaps

The northern fence-gap was put in place in 1994, at the same time as the perimeter fencing was completed, and leads into the Leparua agro-pastoral community that has a population of approximately 3,500 people over an area of 34,000 ha with over 25,000 head of cattle, camel, sheep, and goats. Six ethnic semi-nomadic tribes share the land, and conflict over grazing pastures is common. The western fence-gap (opened in 2009) connects Lewa to the neighbouring Borana conservancy. The exact location of the western gap was chosen at the site of heavy historical elephant damage. The Borana wildlife conservancy is a 13,000 ha property that has a diverse suite of wildlife and is also a functioning cattle ranch. In late 2011, Lewa opened a southern fence-gap that leads into a 14km elephant corridor (Nyaligu & Weeks, 2013) that links Lewa to the Mount Kenya National Forest Reserve. There is also a fourth fence-gap, excluded from this study, at the Mount Kenya end of the corridor. This fence-gap is a secondary exit, distal from the conservancy by 14 km.

Fence-gap design

The fence-gap design at the study site consisted of a sloping loose rock wall built to a height of approximately one and a half meter in height and spanning the whole length of the fence-gaps (20-30m). The rock wall fence-gap design exploited the rhino's perceived poor ability to climb loose rock. However, in 2012, after two rhinos managed to climb out of Lewa, management modified the fence-gap design by adding low bollards in an attempt to make it more difficult for rhino to squeeze through (see Figure 3). This specialized fence-gap design, because of its elevated wall-like feature, is not necessarily easily discoverable or easily scalable and thus we wanted to test its suitability for other species by recoding usage patterns.

Figure 3-Elephant returning through the northern fence-gap. Note new bollards to restrict rhino movement. Lewa February 2013.

Suitability of Fence-Gap Design

We tested if this specialized fence-gap design was suitable (discoverable and accessible) to permit the movement of all species except for rhino by monitoring the movement of wildlife at each gap. We monitored the three fence-gaps using infrared motion-triggered cameras (Reconyx RC60HO Hyperfire, Holmen, WI) from 2010-13. We started monitoring the northern fence-gap with camera-traps in 2010 and the western fence-gap in mid-2012 and then the southern fence-gap in late 2012. We positioned the cameras to maximize the field of view in each particular camera trap set-up. We mounted cameras in "elephant-proof" custom built steel housings. There was one camera at the western fence-gap, one camera at the southern gap inside a narrow highway underpass approximately 500m south of the southern fence-gap, and two cameras facing each other at the wider northern fence-gap. At the northern fence-gap, the second camera data was used mainly as a back up, when one camera failed, or for difficult species identification or counting large groups. We configured all of the cameras for a three-exposure burst upon trigger by their inbuilt motion detectors and set for rapid-fire to ensure continuous shooting for as long as their sensors detected motion. Camera-traps recorded many images per crossing events. Images were stored on 32GB Secure Digital (SD) memory cards. Conservancy research staff collected data roughly every two weeks from the cameras, uploaded the photographs into a central database and recorded the date, time, species, number of individuals crossing, and direction of travel into a spreadsheet. Traffic volume for each species was calculated by counting all of the individuals crossing in both directions at each respective fence-gaps. One of the challenges of monitoring the effectiveness of fence-gap usage is discriminating between individuals using the gaps. We could recognize certain individuals of well-marked species (zebra, giraffe) by their unique patterns. For example, we could identify one particular male Grevy's zebra, as a wound had left an unusual stripe pattern on one of its flanks. This territorial individual was a repeat user of the northern fence-gap. In 2010, we were able to identify this male crossing the fence-gap in excess of 80 times (out of 396 total number of individuals Grevy's captured in 2010), either alone, or with one or two females. We could also detect the regular use of the fence-gap by certain reticulated giraffes and certain collared elephants but not with the same regularity. Consequently, the reported totals of individual animals crossings per species are an overestimation of the true number of unique individuals using the fence-gaps. While we recognise this limitation, the purpose of this study was to examine the ease, the frequency of use, and the diversity of species accessing areas outside the conservancy and in this capacity, the regular use of the fence-gaps by some individuals is viewed as an indication of their ease of use and accessibility.

Proportional selection ratio

In an effort to better understand the accessibility and attractiveness of the fence-gap locations, we calculated a proportional selection ratio. For this ratio we used as the numerator the total number of crossing individuals per species divided by the total number of crossing individuals by all species; and for the denominator we used the total population number of that species divided by the total population number of all species. We used population numbers based on the annual population census numbers collected by Lewa staff using standardized aerial and ground surveys in 2013. A usage ratio greater than one indicates that a species has used the fence-gaps to a greater extent than could be expected given its population and could be seen as "preferring" the fence-gaps (i.e. more likely to use than a species with a lower ratio). We would expect that certain species, based on their life histories, would be more frequent users of migration corridors, and that a lack of movement through the gaps by these species might indicate that there were some issues with gap location or design. We reported the proportional selection ratio for the top-ten species using the fence-gaps (we selected the top-ten species based on the total numbers of individuals crossing the fence-gaps in 2013). Although we did not have 2013 census data for the spotted hyena, we used population estimates derived from a 2015 call up survey (Groom, Funston, & Mandisodza, 2014) that estimated the population size at 65 to 80 individuals (Lewa unpublished data, 2015).

Results

Suitability of Fence-Gap Design

We captured camera data for a combined 2,041 trap-days over the 2010-2013 period at the three fence-gaps (Northern: 1,128 days, Western: 550 days, Southern: 363 days). During 2010-2013, we recorded 50,444 crossing animals of 39 species (37 species of mammals and 2 species of birds) through the Lewa fence-gaps (45,826 at the northern fence-gap, 1,176 at the southern fence-gap, 3,442 at the western fence-gap). Because we had camera-traps at all gaps in 2013, only the species usage per fence-gap for the top-ten species in 2013 is shown in Table 3.

Table 3. Top ten species crossing the fence-gaps in 2013 based on the number of total individual crossings per species. The number of crossing individuals per species at each fence-gap in 2013 is also reported. The population census results are derived from 2013 aerial and ground surveys and the proportional selection ratios were calculated using 2013 population census data and 2013 individual crossing data.

Common name	***Species***	**Total individual crossings**	**Population census**	**Number of individuals crossing - northern gap**	**Number of individuals crossing - western gap**	**Number of individuals crossing - southern gap**	**Proportional selection ratio**
Elephant	*Loxodonta africana*	10234	166	8055	1513	666	8.7
Plains zebra	*Equus quagga burchellii*	9714	946	9714	0	0	1.4
Reticulated giraffe	*Giraffa camelopardalis reticulata*	2916	158	2866	50	0	2.6
Spotted hyena*	*Crocuta crocuta*	918	65	637	226	55	2.0
Grevy's zebra	*Equus grevyi*	660	316	660	0	0	0.3
Defassa waterbuck	*Kobus ellipsiprynmus defassa*	177	96	1	176	0	0.3
Lion	*Panthera leo*	113	23	101	12	0	0.7
Black-backed jackal	*Canis mesomelas*	64	3	64	0	0	3.0
Leopard	*Panthera pardus*	58	6	17	11	30	1.4
Bushbuck	*Tragelaphus scriptus*	24	20	0	2	22	0.2

*Population estimates from a 2015 call-back survey (Lewa unpublished data, 2015).

Elephant, plains zebra (*Equus quagga burchellii*) and giraffe (*Giraffa camelopardalis reticulata*) accounted for the large majority of the traffic. The major predators, spotted hyena, lion, and leopard, were also frequent users of the fence-gaps. Rhinos were not photographed trying to cross the fence-gaps since the implementation of a modification to the fence design in 2012. That year, both a black and a white rhino (*Ceratotherium simum simum*) managed to escape (but were quickly recaptured), which prompted a redesign of the fence-gaps to include a row of bollards in front of the rock wall. We have reported the aggregated fence-gap crossings for all 39 species captured by the camera-traps over 2010-2013 period, as well as the species with a population census count but without a crossing record in Appendix 1.

Proportional selection ratio

The results of the proportional selection ratio analysis are shown in Table 3 for the top-ten species in 2013 as well as in Appendix 1 for all species for 2010-2013. Elephant, plains zebra, giraffe, spotted hyena (*Crocuta crocuta*), leopard (*Panthera pardus*) and black-backed jackal (*Canis mesomelas*) showed a high propensity to use the gaps in relation to other species in the conservancy.

Discussion

Suitability of Fence-Gap Design and Fence-Gap Usage Patterns

The fence-gaps were effective at blocking the passage of rhino, especially once the gaps were modified with additional bollards. The fence-gaps were also effective at allowing elephant and many other species to move in or out of the study site given that a wide variety of species located and used one or more of the fence-gaps. Based on these data, we feel confident in asserting that this specialized fence-gap design is both discoverable and usable by most migratory species. We found that a different mix of species was present at each fence-gap but that only elephant, spotted hyena and leopard used all fence-gaps extensively.

Proportional selection ratio

The proportional selection ratio highlights which species were more likely to migrate or exploit areas outside the boundaries of the conservancy, relative to other species. A high usage ratio could indicate that the foraging or breeding needs of a particular species are not met inside the conservancy.

Conversely, Grant's gazelle (*Nanger granti*), Beisa's oryx (*Oryx gazella beisa*), buffalo (*Syncerus caffer*) and impala (*Aepyceros melampus*) stand out for having large *in situ* populations and proportional selection ratios near zero (see Appendix 1). These species are capable of long-range migrations (Du Toit, 1990; R. D. Estes, 1967; Murray, 2008; Naidoo, Du Preez, Stuart-Hill, Beytell, & Taylor, 2014; Smithers, 1983; Walther, 1972), but generally have smaller home ranges than the species represented with high ratios. Would these low selection ratio species use fence-gaps more frequently if these were located in areas more proximate to their main home ranges? Was there something in the location or the design of the fence-gaps that made them difficult to access? As structures designed to facilitate movement of wildlife across fenced boundaries, the fence-gaps do appear to have been discovered by many species and seemed to function effectively. They appeared to pose no obvious mechanical difficulties for most individuals to cross, although we did record an elephant tripping during a rainy crossing and several juvenile giraffe hesitating and turning back from the fence-gaps. The fence-gap design does not appear to impede movement, but the different levels of usage relative to population density might suggest that more fence-gaps in different locations might be useful, depending upon species-specific movement requirements and life history characteristics, among other factors.

For territorial predators, the usage of the fence-gaps could indicate a level of normal exploratory activity (VanderWaal, Mosser, & Packer, 2009) or it could be an indication that these species have reached their local carrying capacity (Hayward, O'Brien, & Kerley, 2007; Honer, Wachter, East, Runyoro, & Hofer, 2005). Intra- and/or inter-species competition, lack of prey and territoriality battles may be encouraging exploratory movements out of the conservancy by individuals relegated to sub-optimal foraging areas (Honer et al., 2005). The regular access into a pastoral community through the northern fence-gap by all predators, and most frequently by spotted hyena, also supports evidence that predators and particularly hyena readily use human-dominated landscape (Kissui, 2008; Kolowski & Holekamp, 2008; Yirga et al., 2013). Whatever the motivating factor for the predator movement through the fence-gaps, it appears that the gap design and locations permitted dispersal and/or exploratory foraging on the landscape.

Risks to the community

The success of the fence-gaps at permitting movement off the conservancy is not without its risks to the surrounding communities or to the wildlife population (Hazzah et al., 2014). Lewa has developed an active predator early-warning system that alerts neighbouring communities when predator tracks are detected at the northern fence-gap and has also implemented a compensation program for neighbouring pastoralists that suffer from depredation of their livestock and for agriculturalists that suffer from elephant crop-raiding.

Risks of the development of a prey-trap

The compromise between an open landscape and one with only a few fence-gaps is that all of the mammal traffic that moves on or off the conservancy needs to do so at a few specific locations. This spatial predictability of animal movement could potentially lead to predators exploiting the fence-gaps and eventually lead to an imbalance of the predator-prey dynamic. A recent study by Dupuis-Desormeaux et al. (2015) found that fence gaps on the Lewa and neighbouring Borana conservancies did not act as prey-traps, but managers contemplating the use of fence-gaps should monitor the dynamics of predator-prey interactions near the fence gaps for the potential emergence of prey-traps.

Conclusions

Fencing will continue to be the first line of defense against human-wildlife conflicts and poaching. Any amelioration of the isolating effects of completely fencing a wildlife habitat should be considered. Our data show that the design of the fence-gaps permits landscape connectivity, as intended, for the main migratory species present on the conservancy as well as effectively preventing the escape of rhino species. We conclude that the fence-gap design is well suited to rhino conservancies that need to manage elephant movement and want to encourage more natural animal movement and landscape connectivity.

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APPENDIX 1-List of all species captured at the gaps with their proportional selection ratios for 2013 and over the 2010-2013 period.

Common name	Species	Population census (2013)	Individual Crossings (2013)	Mean Population (2010-3)	Individual Crossings (2010-3)	Proportional Selection ratio (2013)	Proportional selection ratio (2010-3)
Elephant	*Loxodonta africana*	166	10234	214	20319	**8.7**	**8.0**
Plains zebra	*Equus quagga burchellii*	946	9714	1042	17281	**1.4**	**1.4**
Giraffe	*Giraffa camelopardalis reticulata*	158	2916	224	7774	**2.6**	**2.9**
Spotted hyena*	*Crocuta crocuta*	65	918	65	2066	**2.0**	**2.7**
Grevy's zebra	*Equus grevyi*	316	660	352	1890	0.3	0.5
Waterbuck	*Kobus ellipsiprynmus defassa*	96	177	116	272	0.3	0.2
Lion	*Panthera leo*	23	113	20	188	0.7	0.8
Baboon	*Papio cynocephalus*	no data	0	no data	155	n.a.	n.a.
Wild dog	*Lycaon pictus*	no data	0	no data	73	n.a.	n.a.
Leopard	*Panthera pardus*	6	58	9	69	**1.4**	0.6
Black-backed jackal	*Canis mesomelas*	3	64	10	64	**3.0**	0.5
Eland	*Tragelaphus (Taurotragus) oryx*	162	29	136	50	0.0	0.0
Bushbuck	*Tragelaphus scriptus*	20	24	20	39	0.2	0.2
Stripped Hyena	*Hyena hyena*	no data	0	no data	39	n.a.	n.a.
Aardwolf	*Proteles cristatus*	no data	0	no data	37	n.a.	n.a.
Hare	*Lepus capesis*	no data	0	no data	29	n.a	n.a
Genet	*Genetta tigrina*	no data	0	no data	13	n.a	n.a
Mongoose sp.	*Herpestes ichneumon, Ichneumon albicauda*	no data	0	no data	13	n.a	n.a
Cheetah	*Acinonyx jubatus*	12	0	10	9	0.0	0.1
Duiker	*Sylvicapra grimmia*	no data	0	no data	9	n.a.	n.a.
Impala	*Aepyceros melampus*	563	5	910	8	0.0	0.0
Ground Squirrel	*Xerus erythropus*	no data	0	no data	7	n.a.	n.a.
Grant's gazelle	*Nanger granti*	292	5	357	5	0.0	0.0
Buffalo	*Syncerus caffer*	547	0	388	4	0.0	0.0
Warthog	*Phacochoerus africanus*	31	1	89	4	0.0	0.0
Ostrich	*Struthio molybdophanes*	26	0	34	4	0.0	0.0
Caracal	*Felis caracal*	no data	0	no data	3	n.a.	n.a.
Porcupine	*Hystrix cristata*	no data	0	no data	3	n.a	n.a

Dik dik	*Madoqua kirkii*	no data	0	no data	2	n.a.	n.a.
Thomson's gazelle	*Eudorcas thomsonii*	no data	0	no data	2	n.a.	n.a.
Ratel	*Mellivora capensis*	no data	0	no data	2	n.a	n.a
Vervet monkey	*Cercopithecus aethiops*	no data	0	no data	2	n.a	n.a
Beisa oryx	*Oryx gazella beisa*	74	0	75	1	0.0	0.0
Rhino, black	*Diceros bicornis*	69	0	67	1	0.0	0.0
Rhino, white	*Ceratotherium simun*	56	0	53	1	0.0	0.0
Serval cat	*Felis serval*	no data	0	no data	1	n.a.	n.a.
Spurfowl	*Pternistis leucoscepus*	no data	0	no data	1	n.a.	n.a.
Zorilla	*Ictonyx striatus*	no data	0	no data	1	n.a.	n.a.
Jackson's Hartebeest	*Bubalis buselaphus lelwel*	10	0	7	0	0.0	0.0
Greater Kudu	*Tragelaphus strepsiceros*	8	0	18	0	0.0	0.0
Gerenuk	*Litocranius walleri*	6	0	8	0	0.0	0.0
Klipspringer	*Oreotragus oreotragus*	6	0	7	0	0.0	0.0
Hippopotamus	*Hippopotamus amphibius*	2	0	2	0	0.0	0.0

*Based on 2015 population estimates. Proportional selection ratios above 1 in bold

SPECIAL APPENDIX: Estimating Species Richness Using Camera-Traps at the Fence-Gaps

We investigated whether camera-traps at the gaps could be used to monitor biodiversity. We estimated how many more camera-trap days we would need to detect most of the detectable species on the conservancy, i.e. whether a similar camera-trap arrangement could be used to monitor species richness at other study sites. We used a non-parametric estimator based on incidence data, the Chao2 estimator (Chao et al., 2009) to calculate sufficient sampling in order to detect a certain percentage of detectable species. The Chao2 estimator calculates a valid *lower bound* of species richness, which under certain conditions (randomness, large sample size) can approach the true asymptotic richness curve. The Chao2 estimator assumes that all the detectable species might eventually encounter the camera-traps, a condition we suspect our set-up of camera-traps at the edges of the habitat would violate as certain species present are limited in their annual movement patterns to areas distal to any of the fence-gaps. Nonetheless, the estimation might prove useful to give an approximation of how much more sampling would be needed to capture most of the species in situ.

The Chao2 estimator projected that an additional 1,513 sample days (approximately one year of continuous data at each of the four gaps) would be needed to detect 90% of detectable species and a further 12,324 sample days (or 8.4 years of sampling) to detect 100%. The Chao2 estimator projected that approximately 48 species were detectable on the conservancy; this is in comparison with the known 52 species of detectable mammals.

We attribute the discrepancy between the Chao2 estimate of mammal biodiversity (48 species) and the known number of detectable species (52) as an indication that the habitat at the locations of our camera-traps failed to adequately represent the diverse habitat within the conservancy and thus skews the estimator. Interestingly, in 2014, we collected a further 2,729 fence-gap crossing incidents and capturing 22 different species and detected only one previously undetected species (steenbok), bringing the total detected species to 38. Based on the Chao2, we would have expected to detect four previously undetected species for that amount of additional sampling. In a mixed habitat study site with a large area to cover, it is unsurprising that four camera-traps at the edges of the 25,000 ha habitat fail to completely capture all of the detectable species.

CHAO, A., COLWELL, R. K., LIN, C.-W. & GOTELLI, N. J. 2009. Sufficient sampling for asymptotic minimum species richness estimators. *Ecology,* 90, 1125-1133.

CHAPTER 5: TESTING THE PREY-TRAP HYPOTHESIS AT TWO WILDLIFE CONSERVANCIES IN KENYA

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Author Contributions

Marc Dupuis-Désormeaux conceived and designed the experiments, performed the experiments, analyzed the data, contributed materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Zeke Davidson performed the experiments, contributed materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Sam Taylor, Edwin Kisio and Mary Mwololo performed the experiments, contributed materials/analysis tools, and reviewed drafts of the paper.

Suzanne E. MacDonald conceived and designed the experiments, performed the experiments, contributed materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

TESTING THE PREY-TRAP HYPOTHESIS AT TWO WILDLIFE CONSERVANCIES IN KENYA

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Abstract

Protecting an endangered and highly poached species can conflict with providing an open and ecologically connected landscape for coexisting species. In Kenya, about half of the black rhino (*Diceros bicornis)* live in electrically fenced private conservancies. Purpose-built fence-gaps permit some landscape connectivity for elephant while restricting rhino from escaping. We monitored the usage patterns at these gaps by motion-triggered cameras and found high traffic volumes and predictable patterns of prey movement. The prey-trap hypothesis (PTH) proposes that predators exploit this predictable prey movement. We tested the PTH at two semi-porous reserves using two different methods: a spatial analysis and a temporal analysis. Using spatial analysis, we mapped the location of predation events with GPS and looked for concentration of kill sites near the gaps as well as conducting clustering and hot spot analysis to determine areas of statistically significant predation clustering. Using temporal analysis, we examined the time lapse between the passage of prey and predator and searched for evidence of active prey seeking and/or predator avoidance. We found no support for the PTH and conclude that the design of the fence-gaps is well suited to promoting connectivity in these types of conservancies.

Introduction

In many parts of Africa, including in Kenya, there is an increased reliance on electrical fencing to protect wildlife and reduce human-wildlife conflicts (J. Kioko, Muruthi, Omondi, & Chiyo, 2008; O'Connell-Rodwell, Rodwell, Rice, & Hart, 2000; Sitienei, Jiwen, & Ngene, 2014; Thouless & Sakwa, 1995), including in very large protected areas such as the Abedare Conservation Area (Massey, King, & Foufopoulos, 2014; Mungai et al., 2011) and an ambitious project to enclose the Mount Kenya Forest Reserve with a 500 km electrified fence (Kenya Wildlife & Service, 2008). Lion (*Panthera leo*) and other predators can thrive within small fenced reserves (Miller & Funston, 2014). Population numbers can be close to their estimated carrying capacity and prey abundance regulates space use and density (Hayward, Hayward, Druce, & Kerley, 2009; Packer et al., 2013). Although fencing is viewed as the most effective way to protect wildlife and reduce human-wildlife conflicts (Hayward & Kerley, 2009), fences come with a long list of drawbacks. Fencing wildlife causes mortality as animals can get entangled and killed while attempting to leave the fenced habitat(Albertson, 1998; Harrington & Conover, 2006; Mbaiwa & Mbaiwa, 2006). Fencing also has many secondary drawbacks that can affect long-term population viability, including reduced access to resources (Brenneman, Bagine, Brown, Ndetei, & Louis Jr, 2009; Loarie, Van Aarde, & Pimm, 2009; Olsson & Widen, 2008), and the creation of edge effects (Massey et al., 2014; Newmark, 2008; Vanak, Thaker, & Slotow, 2010). Further, fencing is expensive to install and maintain as elephant often break their way through fencing (J. Kioko et al., 2008; Mutinda et al., 2014; Thouless & Sakwa, 1995) leading to costly repairs and potential human-wildlife conflict.

Wildlife managers attempt to mitigate these shortcomings by designing better fences (Bode & Wintle, 2010), creating effective linkages between protected habitat (Chetkiewicz, St. Clair, & Boyce, 2006; Newmark, 2008), reconnecting habitat by removing certain portions of fencing (Bartlam-Brooks, Bonyongo, & Harris, 2011) and ensuring minimal encroachment from agriculture, urban development or roads (Berger, Cain, & Murray Berger, 2006; J. M. Kioko & Seno, 2011; Nyaligu & Weeks, 2013; Osborn & Parker, 2003). Biologists emphasize creating connected landscape systems, on private and public lands, to ensure long-term persistence of highly mobile species (Chester, 2003; Plumptre, Kujirakwinja, Treves, Owiunji, & Rainer, 2007; Wikramanayake et al., 1998; Wolmer, 2003). Purpose-built fence-gaps permit some landscape connectivity for migration and dispersal. However, linkages and other connecting structures necessarily funnel animal movement into narrow areas that predators could learn to exploit due to the spatial predictability of prey passage. Due to this funnelling of movement, there is a concentration of spoor near the fence-gaps, which creates depositional odour trails that can be detected and followed by predators (Conover, 2007). Predators do not necessarily have to kill at the fence-gaps but could use these cues to track prey further away from the crossing structures. For example, spotted hyena (*Crocuta crocuta*) use olfaction for hunting and will follow migrating prey for long distances (Trinkel, Fleischmann, Steindorfer, & Kastberger, 2004) and can run down prey in an active chase for up to 4km (Holekamp, Smale, Berg, & Cooper, 1997).

The prey-trap hypothesis (PTH) has been advanced as a possible negative consequence of highway crossing structures by suggesting that predators can improve their predation success by hunting in and around these high prey traffic areas (Ford & Clevenger, 2010; Foster & Humphrey, 1995; Hunt, Dickens, & Whelan, 1987). Although the empirical evidence is weak (Little, Harcourt, & Clevenger, 2002), anecdotal (Barichivich & Dodd Jr, 2002; Pagnucco, Paszkowski, & Scrimgeour, 2011) or unsupportive (Aresco, 2005; Dickson, Jenness, & Beier, 2005; Ford & Clevenger, 2010), there is evidence that fencing can lead to behavioural changes in some predators. For example, wild dog (*Lycaon pictus*) will incorporate fences into their hunting strategy to significantly increase their ability to take down large prey (Davies-Mostert, Mills, & Macdonald, 2013; Rhodes & Rhodes, 2004; Romañach & Lindsey, 2008). These studies raise fundamentally interesting questions that have yet to be fully tested in different ecosystems although the possibility of prey-traps developing at passageways has been raised (Weise, Wessels, Munro, & Solberg, 2014). Our research is the first to examine and formally test the PTH in a fenced conservancy equipped with fence-gaps to allow the passage of wildlife and is the first to test the PTH in an African savannah ecosystem.

The objective of this study was to test if predation events clustered near the fence-gaps and if we could detect active hunting or tracking at the fence-gaps. Successful management of migratory species within fenced conservancies depends on wildlife crossing structures acting as safe passageways in and out of suitable habitat, enhancing connectivity and long-term survival. Therefore, it is critical to verify that the connecting structures do not have any unforeseen negative consequences.

Study Site

We tested the PTH at ten fence-gaps on the Lewa Wildlife Conservancy (25,000ha UTM 37 N 326024 25124, www.lewa.org), and at the adjacent Borana Conservancy (12,000ha, UTM 37 N 309280 24777, www.borana.co.ke) near Isiolo, Kenya. The properties comprise approximately 37,000 ha of electrically fenced wildlife refuge within a larger mixed habitat matrix that includes many small plot agricultural and pastoral communities, roads, towns, farms, and other conservancies. Both conservancies support the full breadth of the Eastern African savannah wildlife.

The vegetation of Lewa and Borana is classified as a mix of Northern Acacia-Commiphora bushlands and thicket (White, 1983) with significant areas of savannah. A 142 km long, two-meter high fence, consisting of twelve-strand of alternating electrified and grounded wires surrounds Lewa. The Northern fence-gaps measures approximately 30 m and leads to an unfenced pastoral area (Leparua community). The Western fence-gap measures approximately 20 m and joins the Borana Conservancy. The fence-gaps serve primarily to let elephant (and other migratory species) move through the fence and in and out of the conservancy. Lewa also has a fence-gap to the South that leads to a 14 km long elephant corridor linking Mt-Kenya and Lewa (Nyaligu & Weeks, 2013). Borana has nine fence-gaps, including the shared fence-gap with Lewa (see Fig 4). Borana's fence-gaps lead into different pastoral and agricultural community lands. Borana maintains 54 km of electric fence line that varies including 42 km of the same type of two-meter high twelve-strand variety, 4km of shorter elephant fencing (with electric "ticklers"- stinging wires protruding approximately one meter at a perpendicular angle to the fence- designed to discourage fence-breaking) and 8 km of double fencing, i.e. where both types of fences are used together. Borana's fence-gaps measure between 5 m and 1000 m (Ngare Ndare gap) in width.

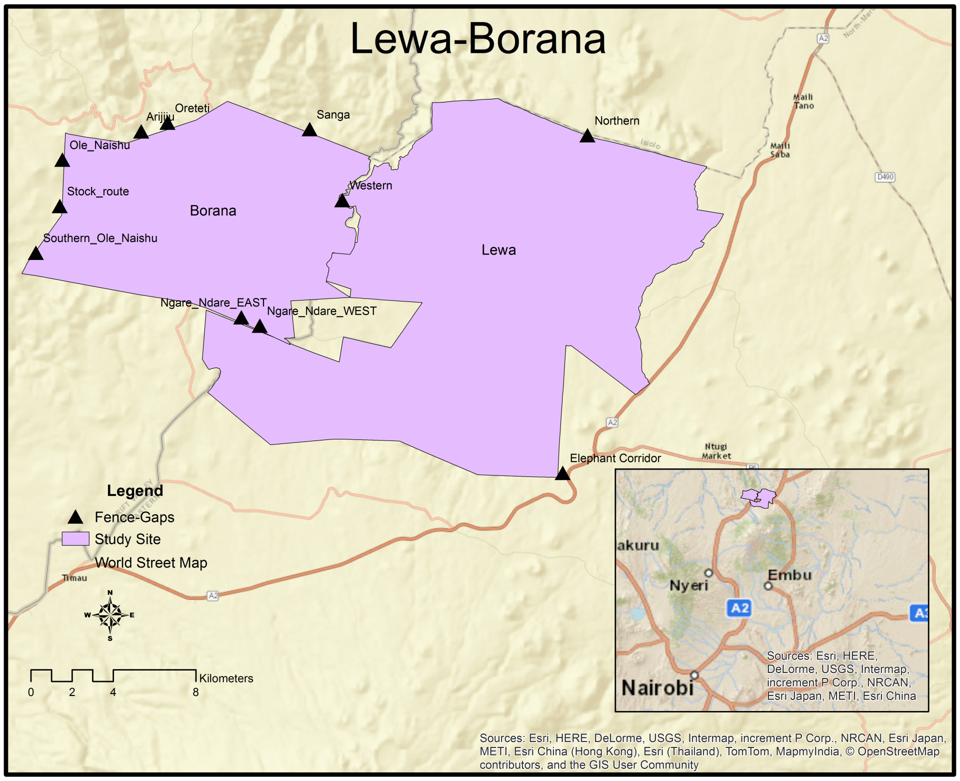

Figure 4 Lewa and Borana fence-gaps locations

The design of the fence-gaps varies considerably between conservancies. Borana's fence-gaps were designed primarily to permit easy access to community cattle, whereas Lewa's fence-gaps were specifically designed to restrict rhino but permit other wildlife passage. As such, the Lewa design exploits a few of the unique anatomical features of the rhino, (i.e. short legs and wide body) by using a low wall constructed out of loose stones paired with a series of low bollards (see Fig 5). The placement of the bollards makes it very difficult for an adult rhino to squeeze through and the rock wall acts as a further obstacle should a smaller individual make it past the bollards. Species using the Lewa fence-gaps usually slow their pace and cross the fence-gap cautiously, but without much difficulty.

Figure 5- Photo of a lion crossing one of Lewa's fence-gaps. The combination of the rock wall with the bollards is used to restrict rhino escaping from the conservancies into non-protected areas.

Methodology

In order to test if predators learned to exploit the passage of prey at the fence-gaps, we captured baseline data measuring the volume of traffic through the fence-gaps using camera-traps. We then performed spatial analyses of predation events as well as a temporal analysis of predator and prey movements at the gaps.

Baseline movement data

We used remotely triggered cameras (Reconyx RC60HO Hyperfire, Holmen, WI) to capture movement data at the fence-gaps in order to verify that there was regular prey traffic volume. Each fence-gap had at least one camera; all camera fields of view were perpendicular to the direction of wildlife travel. We mounted cameras in "elephant-proof" custom built steel housings. Cameras were configured for a three exposure burst upon being triggered by their inbuilt motion detectors and set for rapid-fire to ensure continuous shooting for as long as their sensors detected motion. Images were stored on 32GB Secure Digital (SD) memory cards. From time to time photographs were uploaded into a central database for later analysis.

Spatial Analysis

We collected predation data from Lewa dating back to 2004 (702 kills) and from Borana since 2010 (115 kills). The collection of carcass data is a strategic imperative for all 283 field staff at the study site and, as of 2015 included anti-poaching patrollers, rhino rangers, safari guides, fencers, trackers, herders, and research personnel. Anti-poaching patrols (n=62, as of 2015) are armed and can travel by foot or by vehicle. These patrollers are deployed 24-hours a day, seven days a week and patrol mostly near the access points, roads, fence-line and fence-gaps but can access all of the study site, including by vehicle, plane and helicopter. They also patrol the entire fence-line searching for security breaches and elephant damage to the electrical fence on a regular basis. On Lewa, rhino rangers (n=81) track on foot each individual black rhino, 24-hours a day and report position on a daily basis via radio. These rangers follow the rhino everywhere they go on the conservancy. Safari guides (n=32) work mostly out of vehicles, but also on foot and sometimes on horseback and report kills to the main office. Further, it is important to note that the safari guides are highly incentivized to locate fresh kills for the tourists. There are also fencers (n=38) that patrol the 150km perimeter and 98 km exclusion fences for damage. Trackers (n=2) read the spoor of mammals that have used the fence-gaps on a daily basis and would report any carcasses found near the fence-gaps. As the study site supports local cattle herds at various times of the year, herders (n>55) also come across carcasses when tending their cattle. Finally, researchers (n=13) at the study site are actively monitoring rhino, elephant, ungulates and predators by road vehicle or by plane. It is also noteworthy that the study site has an extensive road network (in excess of 800 km of internal tracks and roads) and that no point is more than 1 km away from a track or road. The study area is thus well monitored and mortality data are considered representative.

We established the exact location of the predation events by assigning a set of GPS coordinates to the descriptive physical locations of each reported carcasses. We used only verified predator kills in our data set. We assigned a cause of death to every carcass found and animals that had died of other causes (unverified as predator kills, drought, electrocution, etc.) were not included in our analysis.

Starting in April 2014, Lewa began using a cluster point method (nearest neighbour) as described by Davidson et al. (Davidson et al., 2013) as an additional search method focused on certain lion prides. Researchers collared five lion groups with GPS radio collars and monitored potential kill sites by identifying locations where the lion activity clustered in excess of four hours.

The detection of carcasses in the field is sensitive to prey size, as larger carcasses are easier to detect and last longer increasing the probability of discovery, therefore smaller prey is likely under-represented in our sample (Davidson et al., 2013).

Proximity Analysis

Using the Pearson's chi-squared test statistic, we tested the hypothesis that the level of kills at or near the fence-gaps was not significantly different than what could be expected elsewhere on the conservancies by comparing the actual density of kills near the gaps with the expected density of kills in the rest of the conservancy.

We created concentric ring buffers around the fence-gaps at various radii (500, 1000 and 2000 m) and intersected those buffers with the shape of the conservancy to calculate the captured areas. We then measured the number of kills recorded in each buffer and compared that number to the expected number of kills on each conservancy for an area of equal size. The total buffer area at each radius distance represents the sum of the areas captured within the defined radius at all the gaps on each respective conservancy.

Stander (Stander, 1992) reported that the majority of lion kills (73%) were recorded after short chase distances (less than 20m) and the rest (27%) were between 20m and 150m. Scheel (Scheel, 1993a) observed hunting distances of up to 200m. Although Holekamp et al. (Holekamp et al., 1997) reported that hyena chased down their prey over distances ranging from 75 m up to 4 km. For our analysis, given that ambush predators dominate our predation data set, (lions, cheetah and leopards representing approximately 81%, 8% and 6%, resp. of the kills in our data) we report the search radius analysis up to 2000m.

Clustering

We tested for clustering of the predation locations at the conservancy level by calculating separate global measures of clustering, the Getis-Ord General G statistic, and Global Moran's I. For the clustering analyses, we aggregated individual incident data points by selecting locations that were within a 100m radius of each other, to match with the precision tolerances of the data collection methods, approximately +/- 50m of each data point.

The Getis-Ord General G measures the degree of clustering of the locations with high/low predation counts over the whole landscape. The General G returns a global z-score, if it is significantly positive then the areas of high predation tend to cluster with other areas of high predation. If the z-score is significantly negative then areas of low predation are clustered with other areas of low predation. The null hypothesis is complete spatial randomness.

Global Moran's I measures spatial autocorrelation based on the location and the weight of each data point (weight based on the number of reported kills for that location) and compares it against randomness. If the z-score is significantly positive then the spatial distribution is more spatially clustered than would be expected under a random spatial process. If the z-score is significantly negative, then the spatial distribution is more dispersed than would be expected under a random scenario. We calculated the spatial autocorrelation for a number of incremental neighborhood sizes. We selected the smallest distance needed to ensure that all weighted predation locations had at least one neighbor as our starting point. We created a table of z-scores from which we selected the neighborhood distance that corresponded to the first peak in significant z-scores (i.e. where the next incrementally larger neighborhood had a smaller z-score). The selected neighborhood size represents the smallest neighborhood distance where significant spatial autocorrelation is occurring, i.e. the smallest distance where the spatial processes promoting clustering are most pronounced.

Hot Spot Analysis (Getis-Ord Gi)*

In addition to calculating a global clustering measure as above, we also tested if any of the individual predation locations were significantly different from the others by performing a hot spot analysis using a local statistic, the Getis-Ord Gi*.

The Gi* statistic returns a z-score for each location in the data set. Significantly positive scores indicate statistically significant clustering of locations with high predation counts (i.e. the hot spots) and significantly negative scores indicate statistically significant clustering of locations with low predation counts (i.e. cold spots). We performed the hot spot analysis (Getis-Ord Gi*, zone of indifference conceptualization) on the aggregated incident data (used in the incremental spatial autocorrelation) and identified the statistically significant hot and cold spots. We used the first peak in significant autocorrelation values, as computed with Global Moran's I above, as the distance input factor in the Hot Spot Analysis, since the first peak is at the spatial scale representing the smallest distance with the most pronounced clustering.

All spatial analysis was done in ArcMap 10.1, (ESRI, USA).

Temporal Analysis

For the temporal analysis we used a different data set based on the time stamp from each photo. The camera-trap data was collected at the busiest fence-gap, at Lewa's Northern gap, between January 1, 2010 and December 31, 2011. We defined a "species crossing event" as the photographic record of the passage of one or more individuals of a species going in the same direction (inbound or outbound) through the fence-gap. For every crossing event, we recorded date, time, species detected, direction of travel and number of individuals of that species crossing in the same direction. We selected a subset of these data where the crossing of a prey species was followed by the crossing in the same direction of a predator species. We calculated the time differential of these paired crossing events and designated this time differential as the HUNT variable. We also paired the crossing of the predator to the next prey crossing. We calculated the time differential between these paired crossings and designated this time differential as the AVOID variable.

We tested for normality and performed a paired difference test to compare the means of HUNT and AVOID. To test whether prey passage modified predator behavior, we followed Ford and Clevenger (Ford & Clevenger, 2010), where we compared the mean time lapse between the passage of prey followed by predator (HUNT) versus the inverse, the passage of predator followed by prey (AVOID). We expected that if predators were actively using the gaps to pick-up scent tracks and if prey species were actively avoiding using the gaps after predator passage the HUNT time interval should be shorter than the AVOID time interval. We tested the HUNT and AVOID variables for normality and performed a paired differences test on the means.

Results

Baseline Camera-trapping data

We monitored wildlife movements through the various fence-gaps using camera-traps. During 2010-13, we recorded in excess of 50,000 mammals of 34 species crossing through the Lewa fence-gaps (46,065 crossings at the Northern fence-gap, 1,176 at the Southern fence-gap, 3,427 at the Western fence-gap joining Lewa and Borana). The most frequent prey species using the fence-gaps were elephant (n=20,335), plains zebra (*Equus quagga*) (n=17,292), reticulated giraffe (*Giraffa camelopardalis reticulata*) (n=7,879), and Grevy's zebra (*Equus grevyi*) (n=1,930). The most common predators using the fence-gaps were spotted hyena (n=2,055), lion (n=167), and leopard (*Panthera pardus*) (n=68). Temporal analysis of the movement data showed strong predictability of prey through the busiest fence-gaps (see Fig 6). We also conducted a brief survey of Borana's other fence-gaps and found in excess of 800 mammal passages in a few months of camera-trapping.

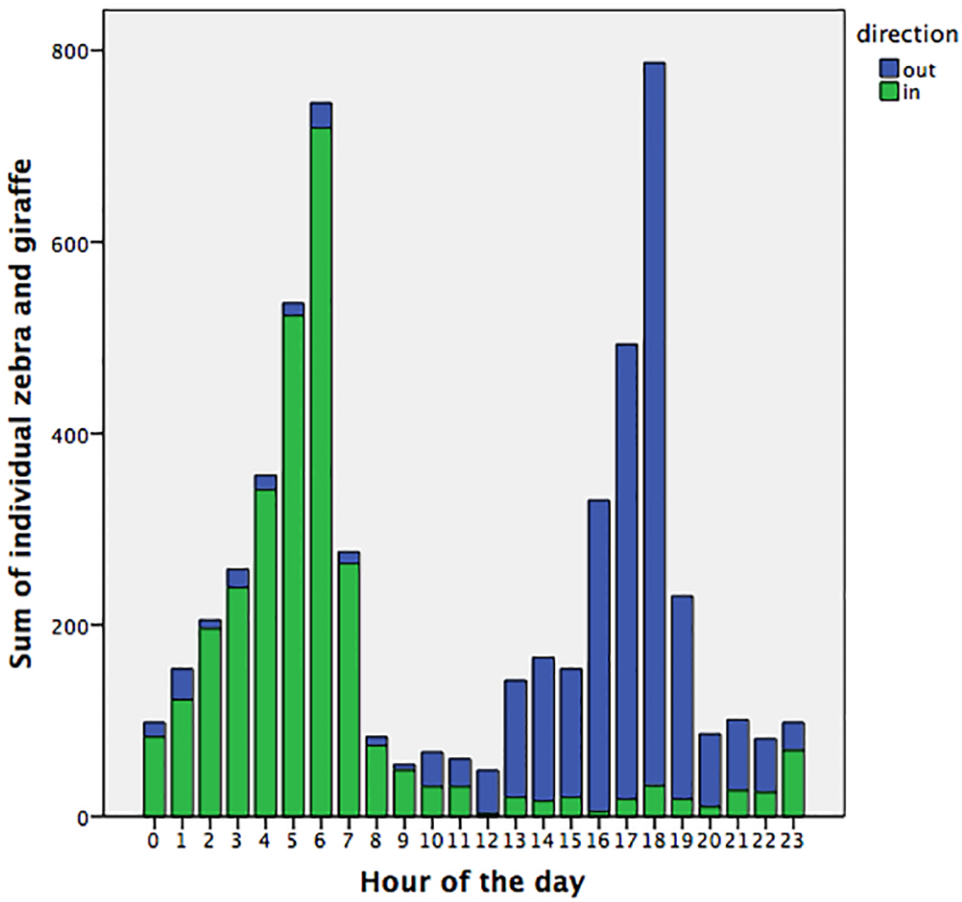

Figure 6. Predictability of prey passage through Lewa's Northern fence-gap (2010-2011). *Equus quagga* (n=2773, into Lewa=1488, out of Lewa=1285), *Equus grevyi* (n=422, into Lewa=245, out of Lewa=177), *Giraffa camelopardalis reticulata* (n=2413, into Lewa=1201, out of Lewa=1212)

Spatial Analysis

Proximity Analysis

We recorded two kills within 500m of the crossing gaps, nine kills within 1000m and 46 kills within 2000m over both conservancies. We calculated the chi-squared statistic for the probability of the kills being over or under represented in the sampled area near the gaps. As shown in Table 4, predation events were significantly under-represented near the gaps.

Table 4- Proximity Analysis (2004-2014) of the predation events by conservancy.

	Total Kills	Kills in buffer area	Buffer radius (m)	Total buffer area (km^2)	Expected kills in buffer area	Pearson's Chi-squared	p-value (df 1) <
Lewa	702	15	2000	19.40	53	26.87	0.0001 *
		2	1000	5.07	14	10.43	0.001*
		1	500	0.98	3	1.11	0.292
Borana	115	22	2000	43.10	33	3.89	0.048*
		5	1000	12.75	12	3.90	0.048*
		1	500	3.11	3	1.31	0.252

*Pearson's chi-squared values where the recorded kills in the buffer zones around the fence-gaps differed significantly from the expected values ($p<0.05$).

Clustering

We tested the data at each conservancy for High/Low Clustering by calculating the Getis-Ord General G statistic. We found that predation locations were significantly clustered on both conservancies (see Table 5).

Table 5-Overall Clustering Analysis-using collected predation events at 100m tolerances.

	Observed mean distance between kill locations (m)	Maximum distance between kill locations (m)	Getis-Ord General G statistic	z-score	p-value>
Lewa	495	2052.2	0.07	3.10	0.002
Borana	614	2472.2	0.21	3.08	0.002

We performed an incremental spatial autocorrelation (ISA) analysis using Global Moran's I statistic (zone of indifference conceptualization). We aggregated the data points that fell within the precision tolerance of 100m resulting in the 702 individual predation locations to aggregate into 304 weighted data points (weighted by incident count ranging from 1-15 individual predation events) on Lewa. Similarly, the 115 individual kill locations on Borana aggregated into a set of 89 weighted data points (ranging from 1-4 individual predation events).

We found that the first distance at which significant spatial autocorrelation occurred was at 3538 m on Lewa (z-score= 3.035, $p<0.01$) and at 4315 m on Borana (z-score= 2.576, $p<0.01$).

Hot Spot Analysis

We calculated the Getis-Ord Gi* statistic for each point of aggregated data and mapped these points in Fig 7. Hot spots are represented in red, cold spots in blue. No hot spots were detected near the gaps.

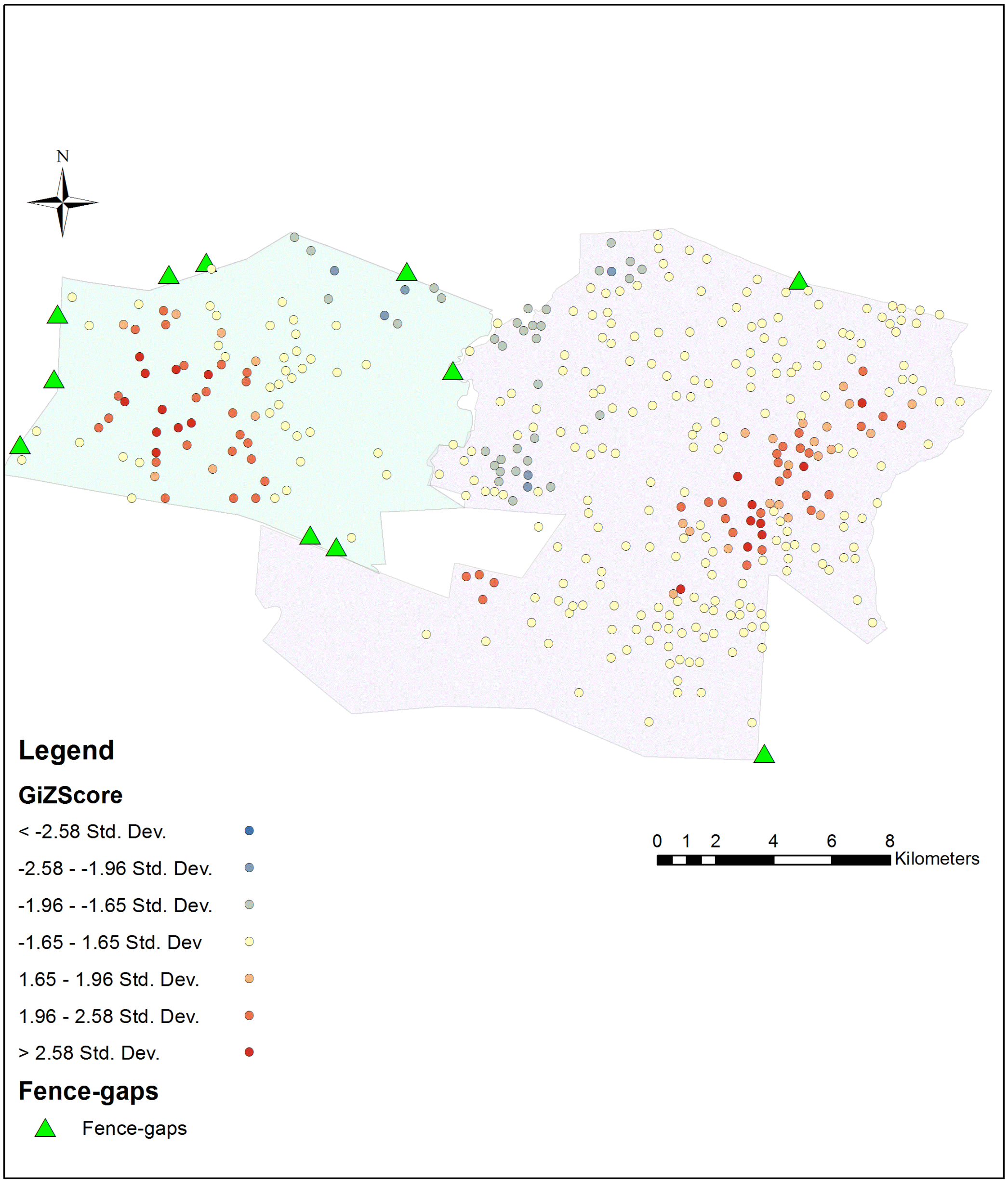

Figure 7- Hot Spot Analysis. Lewa and Borana calculated separately but shown on the same map. Predation events (2004-2014). Each predation location (collected to 100m tolerance) has its Getis-Ord Gi* statistical Z-score reported as a color ranging from blue (cold) to red (hot).

Temporal Analysis

For the temporal analysis we used a different data set based on the time stamp from each photo. The camera-trap data was collected at the busiest fence-gap, at Lewa's Northern gap, between January 1, 2010 and December 31, 2011. During that time interval, we captured 4546 crossing events (14,194 individuals) including 444 crossing events that involved a predator species. Out of those 444, we recorded 217 HUNT and AVOID events. The range of HUNT was from 1 minute to almost 24 hours (mean=3.77 hrs, median= 1.8 hrs, STD=5.23 hrs, n=217). The range of AVOID was from 1 minute to in excess of 22 hours (mean=3.29 hrs, median= 1.3 hrs, STD=4.54 hours, n=217).

We tested both HUNT and AVOID for normality by performing a Shapiro-Wilk (SW) test and found that both variables were not normally distributed (HUNT: SW=0.680, $p<0.001$, AVOID: SW=0.689, $p<0.001$). We compared the means of HUNT and AVOID by performing a non-parametric paired difference test and found that the means of both variables were equal (Wilcoxon signed ranked test $z=-0.652$, $p<0.514$).

Discussion

Using spatial analysis, we found no support for the prey-trap hypothesis as it related to fence-gaps at our study site. On the contrary, our data show significant under-representation of predation locations near the gaps. We found that predation events did cluster, but not near the fence-gaps. Cluster analysis found that the kill locations were focused near denser vegetation and watering holes (Pratt, 2014). We also identified many hot spots of predation activity, but none were near any of the fence-gaps.

Temporal analysis found no discernible difference between time intervals between the passage of predator followed by prey or prey followed by predator, i.e. showed no active hunting by predators or avoidance of predators by prey at the busiest fence-gap. However, this finding does not rule out that predators pick up scent trails just outside of camera range and start tracking the prey.

Based on general behavioural theory for large carnivores, we suggest that the lack of predation at the fence-gaps may be due to the risk of encountering humans (Cotterill, Valeix, Laurence, Riginos, & Macdonald, 2015), the condition of the prey using the fence-gaps and the potential hyper-vigilance of the prey due to the open nature of habitat at the gaps. Lion movement near the borders of protected areas is heavily influenced by the risk of encounters with humans. Lion will tend to avoid areas of high human traffic and times of high human activity (Hayward & Hayward, 2009; Valeix, Hemson, Loveridge, Mills, & Macdonald, 2012). It is possible that the threat of encountering humans discourages hunting at the fence-gap locations. Human activity near the fence-gaps includes daily anti-poaching patrols, conservancy vehicle traffic, daily track observers, bi-weekly researchers checking camera traps, and occasionally tourists and curious community members. Poachers have also been detected passing through the fence-gaps. In addition, nomadic pastoral people frequently occupy homestead sites within 2 km of the fence-gaps. Their herding, wood and water gathering activities provide a constant flow of human and livestock traffic near these conservancy boundaries.

Lion and other predators suffer constant persecution outside of protected areas (Hazzah, Mulder, & Frank, 2009; Hoare & Williamson, 2001; Kissui, 2008; Maclennan, Groom, Macdonald, & Frank, 2009), in retaliation for livestock depredation, especially in areas of subsistence pastoralism (Romanach, Lindsey, & Woodroffe, 2007). Such evidence suggests that lion with home ranges spanning both protected areas and communal lands will not follow migrating wildlife herds out of the protected areas, but prefer to hunt inside the borders of the protected area. This combined with the regular presence of nomadic pastoralists adjacent to both conservancies' boundaries may partly explain why predators avoid hunting near the fence-gaps and hunt in more central locations on the conservancies.

Lion discriminate for substandard (older, sick, infirm) individuals when selecting prey (Schaller, 1972). Substandard prey might not be able or willing to travel off the conservancies and thus might not encounter the fence-gaps. Given that our study sites have permanent water and forage resources, weaker animals do not have to travel outside the conservancies in order to survive. Work by Pratt (Pratt, 2014) at our study site supports the findings of Valeix et al. (Valeix et al., 2010) and Davidson et al. (Davidson et al., 2012) respectively, that lion intensify their search for prey within 2km of watering holes and use these areas where prey congregate as hunting grounds and focus their searches in bushed grasslands and near watering holes, but that their kill success is highest in dense vegetation.

We also suspect that frequent traffic of elephant and giraffe might be a deterrent to hunting. Although lion will occasionally kill an elephant or a giraffe, they prefer prey species between 32 and 632 kg (Clements, Tambling, Hayward, & Kerley, 2014). Prey in their preferred weight range abounds on both Lewa and Borana, making the gap sites less desirable as they attract constant traffic of mega herbivore species. Landscape features also affect where lion hunt, as lion prefer to hunt where prey is easier to catch versus areas where prey is more abundant (Hopcraft, Sinclair, & Packer, 2005). Elephant feeding behaviour significantly modifies the landscape by transforming woody vegetation into grasslands (Haynes, 2011; Nasseri, McBrayer, & Schulte, 2011) and this phenomenon is extensive at our study site (Lewa Wildlife Conservancy Research Department, 2014). Areas where herds of elephant regularly pass through are often devoid of large trees and offer better visibility (Valeix et al., 2011). Many herbivores tend to use these more open habitats to reduce the risk of ambush (Valeix et al., 2009). Prey species have developed behaviours that protect against predation risks (Brown, 1999; Périquet et al., 2012) including hyper vigilance in the presence of lion (Periquet et al., 2010; Scheel, 1993b). The vegetation at our study site varies from forest, to thick bushland, to grassland. The vegetation cover at the various fence-gaps varies according to their location, but open grasslands dominate at the two most highly used fence-gaps, the Northern and Western gaps. We suspect that the open nature of the immediate area near these fence-gaps might deter lion predation.

Thus, in conclusion, our findings do not support the argument for prey traps developing at fence-gaps. Our study site provides useful dynamics of robust predator and prey populations, and strong prey trap potential. It appears, that despite prey availability, predatory behaviour is not focused at these fence-gaps. Habitat structure, landscape topography, water availability elsewhere, density of vegetation, prey condition, and human activity appear to make the costs outweigh the benefits of expending predation effort at these locations at this time. However, management should remain vigilant for the development of prey-traps as predation dynamics may change over time. Given the trend towards fencing for conservation throughout Africa and the need to establish safe connecting routes between protected areas, we conclude that fence-gaps are a feasible wildlife management tool.

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CHAPTER 6: Testing the effects of perimeter fencing and elephant exclosures on lion predation patterns in a Kenyan wildlife conservancy.

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Marc Dupuis-Désormeaux conceived and designed the experiments, performed the experiments, analyzed the data, contributed materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Zeke Davidson performed the experiments, contributed materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

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TESTING THE EFFECTS OF PERIMETER FENCING AND ELEPHANT EXCLOSURES ON LION PREDATION PATTERNS IN A KENYAN WILDLIFE CONSERVANCY.

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Abstract

The use of fences to segregate wildlife can change predator and prey behaviour. Predators can learn to incorporate fencing into their hunting strategies and prey can learn to avoid foraging near fences. A twelve strand electric predator-proof fence surrounds our study site. There are also porous one-strand electric fences used to create exclosures where elephant (and giraffe) cannot enter in order to protect blocs of browse vegetation for two critically endangered species, the black rhinoceros (*Diceros bicornis*) and the Grevy's zebra (*Equus grevyi*). The denser vegetation in these exclosures attracts both browsing prey and ambush predators.

In this study we examined if lion predation patterns differed near the perimeter fencing and inside the elephant exclosures by mapping the location of kills. We used a spatial analysis to compare the predation patterns near the perimeter fencing and inside the exclosures to predation in the rest of the conservancy. Predation was not over-represented near the perimeter fence but the pattern of predation near the fence suggests that fences may be a contributing factor to predation success. Overall, we found that predation was over-represented inside and within 50 m of the exclosures. However, by examining individual exclosures in greater detail using a hot spot analysis, we found that only a few exclosures contained lion predation hot spots. Although some exclosures provide good hunting grounds for lions, we concluded that exclosures did not necessarily create prey-traps per-se and that managers could continue to use this type of exclusionary fencing to protect stands of dense vegetation.

Introduction

Conservancies that host endangered species, such as black rhinoceros (*Disceros bicornis*) and Grevy's zebra (*Equus grevyii*), go to great lengths to provide adequate habitat, food resources and security for their wildlife to ensure long-term viability. These conservancies protect rhinoceros by erecting multi-strand electrical perimeter fences as well as using a multitude of other security measures, including armed anti-poaching patrols and aerial surveillance. These perimeter fences are also effective at segregating wildlife from the surrounding agricultural and pastoral lands. In many parts of Africa, including Kenya, there is an increased reliance on fencing to protect wildlife and reduce human-wildlife conflicts (Kioko et al. 2008; O'Connell-Rodwell et al. 2000; Sitienei et al. 2014; Thouless & Sakwa 1995).

Fencing wildlife can cause direct mortality if animals become entangled and killed while attempting to cross the fence (Albertson 1998; Harrington & Conover 2006; Mbaiwa & Mbaiwa 2006) or can cause indirect mortality, when predators, such as wild dog (*Lycaon pictus*), hunt near fences, as escape routes are limited (Davies-Mostert et al. 2013; Romañach & Lindsey 2008). Further, fenced reserves are essentially closed systems, which can provide advantages to predators that can quickly deplete prey populations. For example, Tambling and Du Toit (2005) found that the ratio of lion to prey population could be three times higher inside a fenced reserve.

Fencing also has secondary drawbacks that can affect long-term herbivore population viability, including reduced access to resources (Brenneman et al. 2009; Loarie et al. 2009; Olsson & Widen 2008), and the creation of edge effects (Massey et al. 2014;

Newmark 2008; Vanak et al. 2010). Vanak et al. (2010) found that perimeter fences in a completely fenced reserve affected elephant foraging movement up to 3.8 km inside the fencing irrespective of habitat composition. Effective protection of species is usually highest deeper inside a protected reserve, where human encroachment is less likely. Human wildlife conflict near reserve edges are the principal cause of mortality and border areas can become population sinks and therefore reduce the density of wildlife populations near the edges (Woodroffe & Ginsberg 1998).

Our study site displays characteristics of both an open and a closed system as it has a semi-porous perimeter fence where three migratory gaps (20-30m wide) have been created in the perimeter fence to allow wildlife to move freely between the protected area and neighboring multi-use landscape (Dupuis-Desormeaux et al. 2015). The first objective of this study was to investigate the effect of perimeter fencing on predation patterns in a semi-porous reserve, testing whether predators have learned to take advantage of perimeter fencing to increase hunting success. Anecdotal evidence of preyed upon carcasses near the perimeter fence suggested that predators might be finding success hunting at the boundary of the conservancy. We tested the hypothesis that prey were killed in proportionally higher numbers near the perimeter fence than elsewhere in the conservancy.

We also investigated the role of elephant exclosures in predation. The presence of mega herbivores, such as elephant (*Loxodonta africana*) and giraffe (*Giraffa camelopardalis reticulata*) can substantially change the availability of browse vegetation accessible to browsers. The elephant's ability to change woody areas into grasslands by felling trees, breaking branches, and debarking trunks is well documented (Hatton & Smart 1984; Haynes 2011; Mosepele et al. 2009; Naiman 1988; Nasseri et al. 2011; Pringle 2008; Valeix et al. 2011). In arid savannas, and in fenced habitat, elephant browsing can have severe negative effects on woody vegetation (Guldemond & Van Aarde 2008). Giraffe are heavy browsers of tree canopies that result in the suppression of growth, and in combination with elephant and black rhino can have long-term detrimental effects on woody vegetation regeneration (Birkett 2002; Bond & Loffell 2001; Smart et al. 1985). This risk of depleting woody resources to the detriment of the protected browsers can cause management to take proactive measures by creating exclosures, areas that allow free movement of some species while keeping others out. The use of elephant exclosures by managers seeking to protect critical vegetation has been effective and has become more widespread throughout the continent (Lagendijk et al. 2011; Lombard et al. 2001; Slotow 2012).

However, the success of exclosures at protecting vegetation can attract both browsers and grazers as vegetation outside the exclosures can become more depleted by the foraging habits of the excluded mega herbivore population. Lions prefer hunting where prey is easier to catch rather than where prey is more abundant (Hopcraft et al. 2005) and so lion intensify their prey search in bushed grasslands and near water (Davidson et al. 2012; Valeix et al. 2010). At our study site, previous work by Pratt (2014) found that the location of Grevy's zebra carcasses killed by lions were clustered in denser vegetation and near watering holes. Given the enhanced nutritional characteristics of the vegetation, it is probable that prey might be preferentially attracted to forage within these exclosures, which may then act as prey-traps. Thus, the second objective of this study was to test if predation events were over-represented either near or inside the exclosures, i.e. do elephant exclosures become prey-traps. This question is important to managers invested in the care of critically endangered species (such as rhinoceros and Grevy's zebras) that are attracted by the browse quality inside exclosures. Thus determining if exclosures are functioning as prey-traps for these species is crucial.

Materials and Methods

Study Site

We conducted our study at the Lewa Wildlife Conservancy (Lewa) in Isiolo, Kenya (0.20° N, 37.42° E). The habitat at Lewa consisted of Northern Acacia-Commiphora Bushlands and Thickets with an Afromontane section (White, 1983) with significant areas of savannah. Lewa was initially a cattle ranch (1920-1983) and in 1983, in response to declining black rhinoceros population, management converted 2000 ha to a rhino sanctuary. This sanctuary grew over the subsequent years and in 1995, Lewa officially converted all of its 25000 ha and upgraded its perimeter fence to a 142 km long, two-meter high electric fence, consisting of twelve-strands of alternating live electrical and grounded wires. The primary purpose of the fence was to segregate the wildlife from the neighbouring communities, thereby reducing human wildlife conflicts. The perimeter fence was continuous except for a few manned gates for vehicle traffic and three purpose-built wildlife gaps created to permit the safe movement of migratory species in and out of the conservancy. There was one 30m-wide fence gap to the north leading to a pastoralist community, one 20m-wide fence gap to the west leading to a neighbouring reserve and one 20m-wide fence gap to the south (20m wide) leading to a 14 km long elephant corridor connecting to Mount Kenya. The perimeter fence was patrolled daily and maintained by teams of rangers and workmen.

There were 23 exclosures at the study site consisting of areas where single or double-strand electrical wires were set at a height of approximately 1.7-2m, permitting rhino, zebra and other wildlife to pass underneath, but excluding elephant and giraffe. Both the perimeter fence and the exclusionary fencing had voltage maintained at between 5.0-9.0

kV, levels suitable to keep large animals away without causing permanent injury. The locations of the exclosures were chosen based on a combination of factors, including the protecting the remaining stands of woody vegetation from elephant (and giraffe) damage, to promote the recovery of woody vegetation, to maintain the aesthetic value of some areas and, to protect residential areas. Given that exclosures were not randomly placed on the study site but were targeted to areas that already had vegetation to protect, vegetation cover and the presence of exclosures are confounded variables.

These exclosures have been in place between 4 and 22 years (mean= 14.3±4.4 years) and cover approximately 12% of the conservancy. The creation of these exclosures has allowed a different and a denser woody vegetation mix to develop (Baker del Aguila 2010; Giesen et al. 2007) and the recruitment of tree saplings was significantly higher inside exclosures (Baker del Aguila 2010). In exclosures protecting riverine habitat, tree cover has become significantly denser over the years, increasing from under 10% in 1979, to 25% in 2000 and to more than 50% in 2006 (Giesen et al. 2007). However, the creation of exclosures at our study site has deflected browsing pressure to the unprotected habitat and has led to severe decline of unprotected woody vegetation (Giesen et al. 2007). To this point, fixed-point photography used at the study site has revealed stark visual changes in vegetation density (see Figures 8 and 9).

Figure 8-View from Craig House (Lewa 1990)

Figure 9-View from Craig House (2014)

In 2014, Lewa reported approximately 500 elephants in the conservancy (Mutinda et al. 2014) and approximately 225 giraffe (*Giraffa camelopardalis reticulata*). All necessary permits were obtained for the described field study from the appropriate agencies (Kenya Wildlife Service Affiliation, KWS/BRM/5001, and Kenyan National Council for Science and Technology, NCST/RRA112/I/NIASI).

Mortality data

We collected predation data from Lewa dating back to 2004. The collection of carcass data is a strategic imperative for all 283 field staff at the study site and, as of 2015, included anti-poaching patrollers, rhinoceros rangers, safari guides, fencers, trackers, herders, and research personnel. Anti-poaching patrols (n=62, as of 2015) are armed and can travel by foot or by vehicle. These patrollers are deployed 24-hours a day, seven days a week and patrol mostly near the access points, roads, fence-line and fence-gaps but can access all of the study site, including by vehicle, plane and helicopter. They also patrol the entire fence-line searching for security breaches and elephant damage to the electrical fence on a regular basis. On Lewa, rhinoceros rangers (n=81) track on foot each individual black rhinoceros, 24 hours a day and report position on a daily basis via radio. These rangers follow the rhinoceros continuously throughout the conservancy. Safari guides (n=32) work mostly out of vehicles but also on foot and horseback and report kills when they discover them. It is important to note that the safari guides are highly incentivized to locate fresh kills for visiting tourists. There are also fencers (n=38) that patrol the 150km perimeter and 98 km exclusion fences for damage. Trackers (n=2) read the spoor of mammals that have used the fence-gaps on a daily basis and report any carcasses found near the fence-gaps. Because the study site supports local cattle herds at various times of the year, herders (n>55) also come across carcasses when tending their cattle. Finally, researchers (n=13) at the study site actively monitor rhinoceros, elephant, ungulates and predators by road vehicle or by plane. It is also noteworthy that the study site has an extensive road network (in excess of 800 km of internal tracks and roads) and that no point is more than 1 km away from a track or road. The study area is thus well monitored and mortality data are considered representative. Despite these efforts, the detection of carcasses in the field is sensitive to prey size and habitat type, given that larger carcasses in more open habitat are easier to detect and last longer, increasing the probability of their discovery. Therefore, smaller prey and prey in very dense habitat was likely under-represented in our sample (Davidson et al. 2013).

We established the location of the predation events by assigning a set of GPS coordinates to the descriptive physical locations of each reported carcasses (with a tolerance of +/- 50m). We used only verified predator kills in our data set. We assigned a cause of death to every carcass found and animals that had died of other causes (unverified as predator kills, drought, electrocution, etc.) were not included in our analysis.

Starting in April 2014, Lewa began using an additional technique to locate carcasses of prey killed by lion. The search method is based on the nearest neighbour cluster point method, as described in Davidson et al. (2013) where researchers collared five lion groups with GPS radio collars and monitored potential kill sites by identifying locations where the lion activity clustered in excess of four hours. Because of the predominance of lion kills in our data set, we limit the analysis to lion kills (lions, cheetah and leopards representing approximately 81%, 8% and 6%, resp. of the kills in our data).

Proximity Analysis

We performed a proximity analysis to investigate the spatial distribution at the conservancy level. We tested the hypotheses that the level of kills near the perimeter fencing and inside the exclosures were not significantly different than what could be expected elsewhere on the conservancy by comparing the actual density of kills inside the selected zones with the expected density of kills in the rest of the conservancy (using Pearson's chi-squared test).

We created buffers of 100m and 500m inside the perimeter fence and intersected those buffers with the shape of the conservancy to calculate the area captured. We then measured the number of kills recorded in each buffer and compared that number to the expected number of kills based on area. With regards to exclosures, we measured both the number of kills inside the exclosures and also the area including a 50m buffer and compared to the expected number of kills based on the calculated area of the exclosure. Stander (1992) reported that the majority of lion kills (73%) were recorded after short chase distances (less than 20m) and the rest (27%) were between 20m and 150m. Scheel (1993) observed hunting distances of up to 200m. We chose to include a buffer distance of 50m, to allow for a lion ambush somewhere inside the exclosure but where the actual kill might have terminated just outside the exclosures.

We also calculated a prey selectivity index following Hayward and Kerley (2005) using the Jacob's selectivity index (Jacobs 1974) of the prey killed inside the exclosures versus available prey (based on the mean annual census numbers collected from 2004-2014 by Lewa staff using standardized aerial and ground surveys), and we compared it to the selectivity index for lion kills outside of the exclosures. Jacobs' selectivity index is calculated as follows:

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

where r is the proportion of the total kills for a particular species at the study site and p is the proportional availability of this prey species. The index ranges from -1 to +1, where negative values represent relative avoidance (-1 being complete avoidance) and positive values represent relative preference (+1 being complete preference).

Hot Spot Analysis

In order to investigate the spatial processes at a local level, we performed a hot spot analysis on the aggregated lion predation data using a local statistic (Getis-Ord Gi*). First, we aggregated predation locations that were within a 100m radius of each other in order to create a set of weighted features necessary for the analysis. We then calculated a global measure of spatial autocorrelation (using a Global Moran's I statistic) between the aggregated predation locations where the Global Moran's I returned a Z-score, positive if the spatial distribution was more spatially clustered than would be expected under a random spatial process, negative if more dispersed. We calculated the spatial autocorrelation for a number of incremental neighbourhood sizes, starting with the minimum neighbourhood where every location has at least one neighbour. We selected the neighbourhood size that corresponded to the first peak in significant Z-scores (i.e. where the next incrementally larger neighbourhood had a smaller Z-score), thus selecting a neighbourhood size that corresponded to the smallest distance where significant spatial autocorrelation was occurring, i.e. the first distance where the spatial processes promoting clustering were more pronounced. We used this neighbourhood size as the distance input factor of the hot spot analysis.

The hot spot analysis is sensitive to which conceptualization of spatial relationship is used when searching for neighbouring points of influence. We used a zone of indifference conceptualization, a hybrid of fixed distance and inverse distance conceptualizations, where the influence of locations inside a fixed neighbourhood distance are weighed equally and where the influence of locations that fall outside that distance are reduced in proportion to the distance away from the neighbourhood boundary. The hot spot analysis returned a local Z-score (Getis-Ord Gi* statistic) for each aggregated location where significantly positive scores indicated locations that were clustering with other locations of high predation (hot spots) whereas negative scores indicated clustering of locations with low predation counts (cold spots). We then examined if any of the hot spots fell within the perimeter buffers and exclosures. Spatial analysis was done in ArcMap 10.3 (ESRI, Redlands, CA, USA) and statistical analysis was performed in SPSS (IBM Corp., Armonk, NY, USA).

Vegetation Survey

In order to better understand the role of vegetation within the exclosures, we performed a supervised classification of the vegetation cover using imagery gathered from Landsat 8 satellite images with a 30m resolution. We matched the supervised classification with on the ground plot survey data collected by Giesen et al. (2007) and created five bands of vegetation cover, ranging from grasslands (tree cover less than 2%) to forests (tree cover larger than 40%). We then tabulated the number of kills that fell within each zone and compared the actual kills versus expected kills given the area covered by each zone in order to get a better understanding of lion hunting habitat preferences.

Results

We recorded 772 kills that could be attributed to a specific predator species over a ten-year period, including 628 identifiable lion kills. The top ten preyed upon species within the study site, and their representation within the perimeter buffers and the exclosures (including a 50m buffer), are shown in Table 6.

Table 6-Top ten preyed-upon species by lion (Lewa 2005-2014)

Common Name	**Species**	**Lion kills at study site**	**Lion kills inside exclosures**	**Lion kills inside exclosure +buffer (+50m)**	**Lion kills inside 100m of perimeter fence**	**Lion kills inside 500m of perimeter fence**
Plains zebra	*Equus quagga*	253	43	49	13	42
Grevy's zebra	*Equus grevyi*	127	26	28	4	14
Reticulated Giraffe	*Giraffa camelopardalis reticulata*	60	6	9	5	9
Eland	*Tragelaphus (Taurotragus) oryx*	43	6	8	3	5
Buffalo	*Syncerus caffer*	29	4	4	0	3
Waterbuck	*Kobus ellipsiprynmus defassa*	28	10	11	1	2
Warthog	*Phacochoerus africanus*	25	12	13	1	2
Impala	*Aepyceros melampus*	23	8	8	0	0
Beisa Oryx	*Oryx gazella beisa*	11	2	2	0	1
Hartebeest	*Alcelaphus buselaphus*	6	0	0	1	1
All Others		23	4	6	1	3
TOTAL		628	121	138	29	82

Of those 628 lion kills, 29 were located within 100m of the perimeter fence, an additional 53 were inside the next 400m, 121 were located inside exclosures and an additional 27 kills were within a 50m buffer zone outside the exclosure perimeter. We mapped the individual kills in relation to the perimeter fence and exclosures in Fig 10.

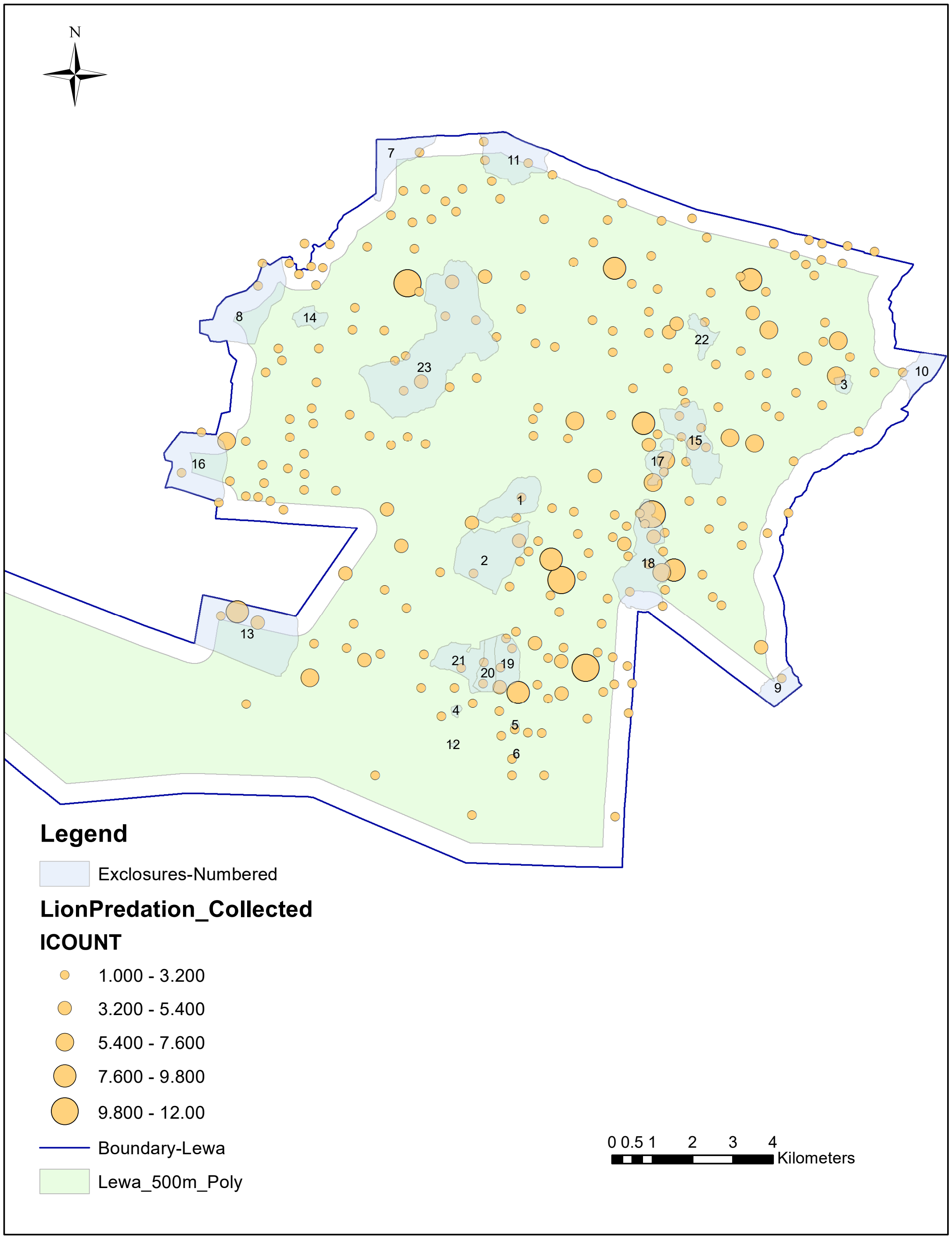

Figure 10-Map of lion kills in relation to exclosure and perimeter fencing

Predation rates near the perimeter fencing as a whole were in proportion or lower than elsewhere in the whole of the conservancy. The number of kills inside the 100 m perimeter fence was not significantly different than a random distribution given the area represented. However, within the 500m buffer zone, the number of kills was significantly lower than expected.

In aggregate, the number of kills within the combined exclosure area and within the 50m buffers is significantly larger than would otherwise be expected (see Table 7).

Table 7-Actual kills versus expected kills near perimeter and exclosure fencing (Lewa 2005-2014)

	Area (km^2)	Lion Kills	Kills per km^2	Expected Kills	Pearson's Chi-Squared	p-value (df 1)<
Total	250	628	2.51			
Within 100m of perimeter	9.52	29	3.04	23.91	1.08	0.2984
Within 500m of perimeter	46.53	82	1.76	116.88	10.41	0.0013*
Exclusion zones	27.47	121	4.40	69.00	39.18	0.0001**
+50m buffer	32.43	140	4.31	81.46	42.06	0.0001**

Although exclosures as a whole appear to attract more predation than would otherwise be expected based on the size of these zones, this phenomenon is not uniformly distributed across all exclosures. An individual assessment reveals that only a few exclosures seem to be significantly over-represented, i.e. showing a large differential of actual kills over the expected values: exclosures 15, 17 and 18 (see Table 8). Also of note, there were seven exclosures that had perimeter fencing as one border and none of these exclosures showed significantly over-represented predator kills.

Table 8-Individual exclosures actual number of kills versus expected based on area. Potentially meaningful differences in bold. (Lewa 2005-2014)

Zone ID	Area (ha)	Lion Kills	Exp. Kills	Actual-Exp.	Area +50m	Kills +50m	Exp. Kills +50m	Actual-Exp. +50m	Min tree cover %
6	1.2	0	0.03	-0.03	4.3	0	0.11	-0.11	21
12	1.3	0	0.03	-0.03	4.5	0	0.11	-0.11	40
5	3.2	1	0.08	0.92	7.6	1	0.19	0.81	21
4	5.4	0	0.14	-0.14	10.9	0	0.28	-0.28	21
3	15.9	0	0.40	-0.40	24.6	6	0.62	5.38	11
14	32.8	0	0.82	-0.82	46.1	0	1.16	-1.16	21
22	37.7	3	0.95	2.05	55.3	3	1.39	1.61	12
17	48.6	15	1.22	**13.78**	66.5	15	1.67	**13.33**	11
20	49.1	4	1.23	2.77	67.2	4	1.69	2.31	21
9	55.4	1	1.39	-0.39	71.9	1	1.81	-0.81	21
10	61.6	1	1.55	-0.55	80.3	1	2.02	-1.02	6
19	72.5	8	1.82	6.18	92.0	8	2.31	5.69	21
21	86.1	3	2.16	0.84	113.2	3	2.84	0.16	21
7	96.8	1	2.43	-1.43	125.0	1	3.14	-2.14	11
1	103.8	1	2.61	-1.61	127.2	1	3.19	-2.19	21
11	150.7	5	3.79	1.21	177.5	5	4.46	0.54	11
15	158.2	12	3.97	**8.03**	190.5	15	4.79	**10.21**	21
2	204.3	6	5.13	0.87	235.9	6	5.92	0.08	21
16	207.0	1	5.20	-4.20	236.9	5	5.95	-0.95	1
18	216.7	29	5.44	**23.56**	256.0	30	6.43	**23.57**	21
8	220.6	2	5.54	-3.54	256.8	4	6.45	-2.45	16
13	342.1	14	8.59	5.41	380.7	14	9.56	4.44	21
23	576.2	14	14.47	-0.47	643.1	15	16.15	-1.15	18
All		121	69			138	82		

Prey Selectivity Index

We calculated a prey selectivity index (PSI) to compare the proportion of prey species inside the exclosures to that outside the exclosures (see Table 9). The PSI inside the exclosures generally mirrored the PSI outside the zones although we noted some increases in the preferences for waterbuck and warthog and decreases in the proportions of plains zebra and eland (both open plains species). Unsurprisingly, the preference for giraffe was lower (due to this species generally being excluded from the exclosures unless elephant have managed to break the electrical wire). Notably, the proportion of Grevy's zebra killed remained the same inside or outside the exclosures.

Table 9-Prey Selectivity Index (PSI), inside versus outside exclosures

Top prey species	Mean pop. from census 2004-2014	Lion kills at study site	Lion kills outside exclosures (+50m)	Lion kills inside exclosures (+50m)	PSI outside exclosures	PSI inside exclosures
Plains z.	1069	253	204	49	0.26	0.13
Grevy's z.	380	127	99	28	0.37	0.37
Giraffe	207	60	51	9	0.31	0.06
Eland	181	43	35	8	0.18	0.07
Buffalo	378	29	25	4	-0.37	-0.60
Waterbuck	119	28	17	11	0.02	0.43
Warthog	132	25	12	13	-0.21	0.46
Impala	881	23	15	8	-0.83	-0.69
Oryx	79	11	9	2	-0.09	-0.21

Vegetation

Vegetation cover varied through the study site and was classified in 5 broad classes. We partitioned the vegetation cover and the number of lion kills in each cover class (see Table 10 and Fig 11). Out of the 628 lion kills, 619 could be associated with a distinctive class of vegetation. Kills were under-represented in both extreme types of cover, i.e. open grasslands and in forested areas. Kills were over-represented in mixed habitat, where tree cover ranged from 2% to 40%, i.e. in woody grassland, shrubland and in woodland.

Table 10-Vegetation cover and kill distribution using a supervised classification (LANDSAT 8 data)

Vegetation Cover	Tree cover	Percentage of Lewa	Actual Kills (619)	Percentage of kills	Expected Kills	Chi-Squared (df=4)	Prob<
Grassland	0- 2%	25.7%	123	19.7%	159	8.13	0.087
Woody grassland	2-10%	10.3%	110	17.8%	64	33.22	0.0001**
Shrubland	11-20%	33.7%	268	43.3%	209	16.84	0.002**
Woodland	21-40%	11.3%	102	16.5%	70	14.72	0.005**
Forest	41% +	19.0%	16	2.6%	117	87.69	0.0001*

*Significantly LESS than expected; ** Significantly MORE than expected

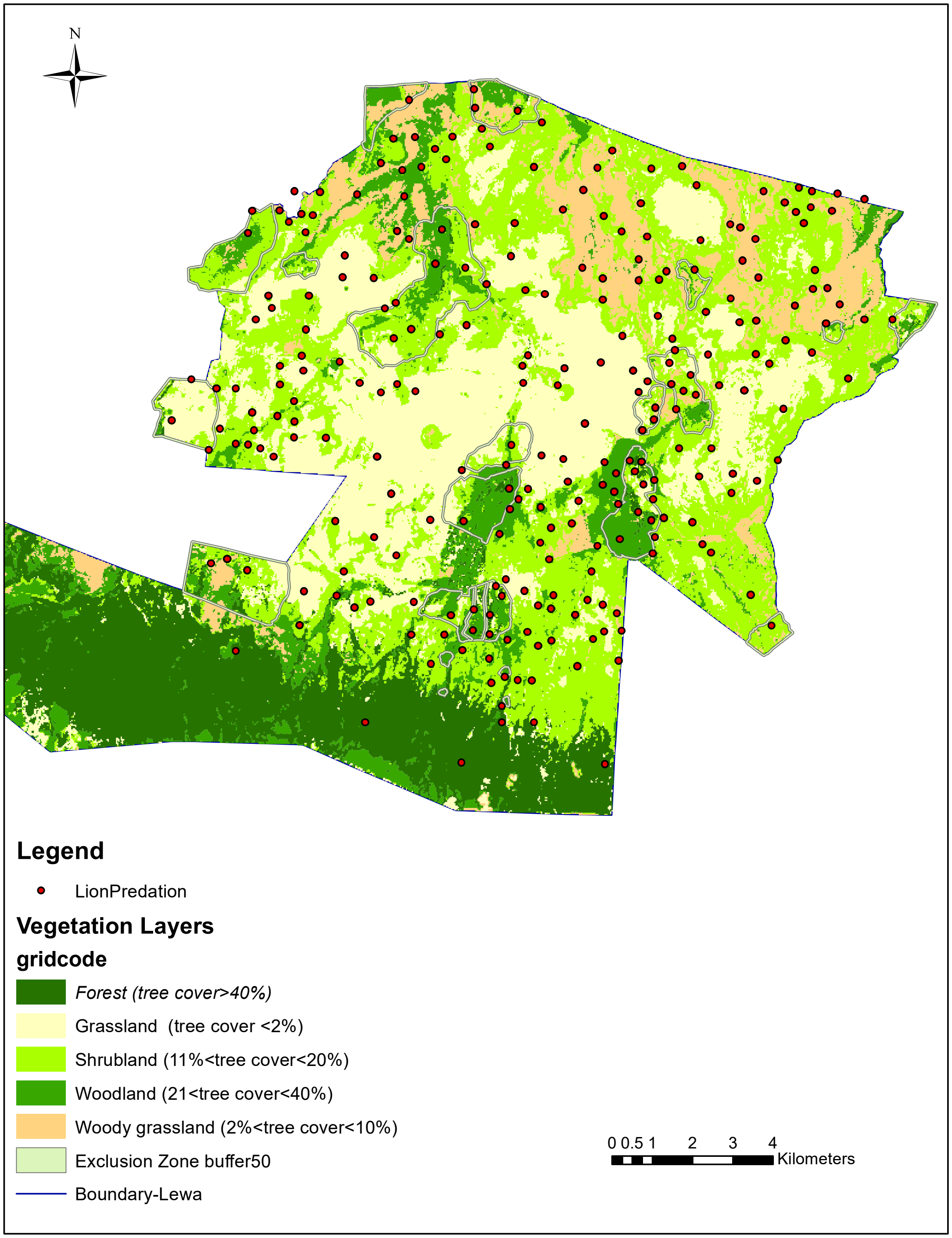

Figure 11-Lion predation and vegetation cover using a supervised classification of LANDSAT 8 imagery.

Hot Spot Analysis

We aggregated the individual lion kill sites from 628 individual locations to 263 aggregated kill sites using the 100m tolerances yielding a range from 1-12 kills at each aggregated site. We calculated the Getis-Ord Gi* statistic for each point of aggregated data using a search distance threshold of 5796m (as calculated by performing an incremental spatial autocorrelation procedure) and mapped these points in Fig 12. Each predation location had its Z-score fall within one of seven bins, representing the statistical probability of significance, reported as a color ranging from blue (cold) to red (hot). Hot spots were mainly detected deeper inside the conservancy, although a few hot spots fell within the buffer areas near the eastern perimeter fence. Statistically significant hot spots were also detected within three of the exclosures (15, 17 and 18), some of these containing multiple hot spots. However, hot spots were also detected in many other areas throughout the conservancy. Of the 263 aggregated predation locations, 51 were classified as hot spots with a Gi* score greater than 1.96 (p-value <0.05) and of these 51 hot spots, 11 were located inside the exclosures (five in exclosure 15, and three in exclosures 17 and 18), none in exclosures with perimeter fencing.

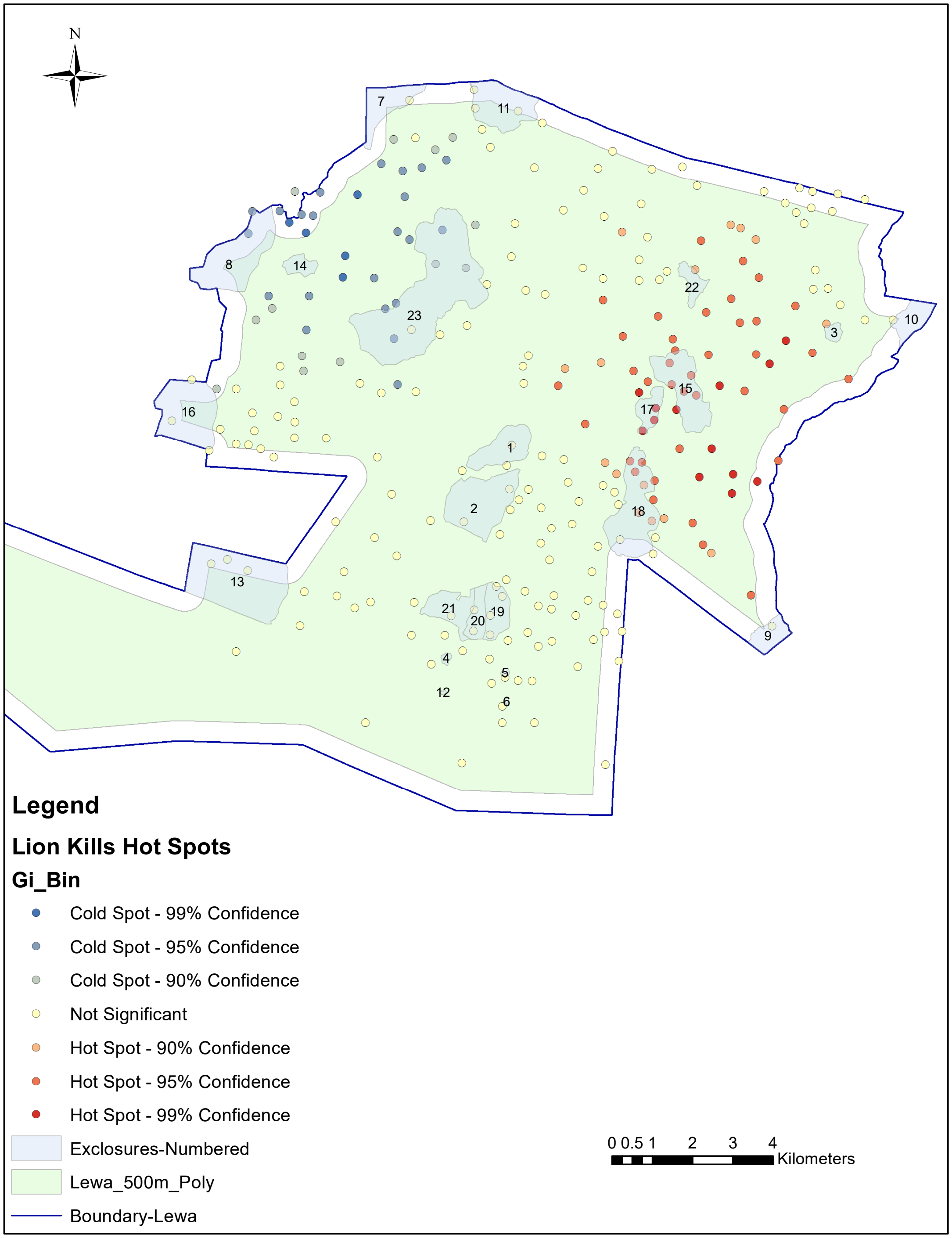

Figure 12-Hot spot analysis of lion predation using a zone of indifference conceptualization and a search distance of 5796 m.

Discussion

Predator-prey dynamics within fenced wildlife reserves can change in response to being held in a constrained habitat. Prey might avoid the fence, thereby creating an edge effect, while predators might drive prey into the direction of the fences, thereby reducing escape options. In this study we examined if predation cases were disproportionally found near perimeter fencing and found that, at the conservancy-level, predation events were not over-represented near the perimeter fence. On the contrary, our results indicated that there were fewer predation events than expected near the perimeter fencing, suggesting some edge effect. We suspect that human activity near the perimeter fence and the risk of human wildlife conflict discouraged herbivory near the boundary.

However, if edge effects were solely responsible for the predation pattern near the boundary fence then we would expect predation success to increase proportionally farther away from the perimeter fence. Our results showed that predation was proportionally lower within the 500m buffer zone than it was within the 100m buffer zone suggesting greater hunting success nearest the perimeter fence. The results of the hot spot analysis also showed a few locations near the perimeter fence where predation was overrepresented. Taken together, these results suggest that predators might have higher hunting success in certain specific locations near the boundary fence although not at sufficient levels to impact the overall distribution of predation events. Further studies of hunting behaviour at these locations may shed light on the importance of the perimeter fence in hunting strategies of predators in fenced and semi-porous reserves.

With regards to elephant exclosures, we found that, at the conservancy level, predation events were over-represented in or near the exclosures. These results support the hypothesis that there was an increased risk of lion predation in and around exclosures compared to that in the rest of the conservancy. However, upon a more detailed hot spot analysis at the exclosure level, we found that only a few of the exclosures contained hot spots while the majority of the hot spots were found outside the exclosures. Thus, the results of the hot spot analysis did not support the hypothesis that exclosures become prey-traps.

We also noted that predation was over-represented within certain vegetation cover categories consistent with other lion studies (Funston et al. 1998; Hopcraft et al. 2005) and these cover categories were found within the "hot" exclosures. These "hot" exclosures had been created around areas of somewhat already dense vegetation that has become progressively denser with time. However, most exclosures have not developed into fertile hunting grounds for lion possibly because foraging from other browsers has limited the vegetative growth (Sankaran et al. 2013; Staver & Bond 2014) or created thickets that are not conducive to lion hunting (Tambling et al. 2013).

Our findings should give managers the confidence to continue protecting some of the dense vegetation strands with exclosures knowing that there is no generalized increase in the risk of predation.

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GENERAL DISCUSSION

Management interventions

Wildlife conservation can take a wide spectrum of management styles, from a "laissez-faire" or "passive" style, where the minimum possible intervention is the goal, to the other extreme, where a hands-on or "active" style of management dictates nearly endless types of possible interventions (Bothma & Du Toit, 2010). Passive management seeks to prevent human influence while active management involves actively manipulating wildlife and habitat to a specific end goal. In the past, we could have predicted the style of management from geographical location, as East African laissez-faire management style has contrasted sharply with South African micro-management methods, but there is a wind of change in the air. Although some East African ecosystems have managed to survive with little intervention, in recent years, most of East Africa's large ecosystems are under stress from development and population growth. In large ecosystems, such as the Serengeti-Mara, the annual mammal migration traverses both protected reserves and unprotected private lands. For example, on the Kenyan side of the Serengeti-Mara, only 25% of the ecosystem is under some form of protection (through the Masai Mara National Reserve, MMNR), while most of the ecosystem falls under unprotected private or communal lands (Walpole, Karanja, Sitati, & Leader-Williams, 2003). Historically, the communal lands belonged to semi-nomadic pastoralist communities that protected them for grazing, but as time progressed, various economic development policies promoted the parceling of the land to encourage more agriculture. The result is that much of the unprotected pastoral land has transformed to fenced agricultural plots and that there has been a resulting precipitous decline in resident and migrating herbivores due to incompatible land uses inside the migratory corridors, namely: roads, fencing, human settlements, and mining (Ogutu, Owen-Smith, Piepho, & Said, 2011; Ottichilo, de Leeuw, & Prins, 2001; Walpole et al., 2003). So what are the best practices for wildlife managers? If policy makers cannot be counted on to make sensible landscape-wide policies, then it is up to the wildlife managers to do what they can at the conservancy level, tending to their own piece of the commons and trying to avoid any tragedies.

Smaller conservancies function much like fragmented ecosystems in that the restrictive size of their habitat lends itself to increased sensitivity of the wildlife populations to stochastic shocks. Managers in these smaller conservancies are often obliged to be more hands-on due to the dangers of more pronounced fluctuations in wildlife numbers as a result of stochastic events. Thus, managers seek to protect and insulate their wildlife as much they can from these stochastic events by manipulating inputs and propping up populations in times of perceived vulnerability. However, managers often take the role of "emergency help" too far and permanently manipulate and "improve" the habitat. However, the risk is that, as would dictate the "Third Law Of Wildlife Conservation (with apologies to Newton)", an equal and opposite reaction is triggered that may only become apparent later or only by careful monitoring. A classic example is that of improving access to water, where managers might try to reduce the detrimental effects of regular droughts by creating and maintaining artificial watering holes. Maintaining artificial sources of water reduces the impetus to migrate and leads to a disproportionate use of local vegetation, which in turn impoverishes the local habitat for herbivores and leads to increasing predator success and ultimately weakening the stock of wildlife (Davidson et al., 2013; de Boer et al., 2010; Loarie, Aarde, & Pimm, 2009; Shrader, Pimm, & van Aarde, 2010; Smit & Grant, 2009). A more recent type of intervention that has gained traction is the translocation of problem elephant to areas far removed (usually a national park) from where the human-elephant conflict originated. Not only is translocation expensive but elephants very rarely settle where translocated, often roaming or homing (Fernando, Leimgruber, Prasad, & Pastorini, 2012) and recent studies have shown that translocation can causes significant long-term stress to the animals (Jachowski, Slotow, & Millspaugh, 2013; Viijoen, Ganswindt, du Toit, & Langbauer, 2008; Viljoen, Ganswindt, Reynecke, Stoeger, & Langbauer, 2015), higher mortality rates (Pinter-Wollman, Isbell, & Hart, 2009) and acute social disruption that can last for decades (Shannon et al., 2013). These management interventions are just two of the many management interventions that happen regularly inside our study site as well as other smaller managed conservancies. These interventions are specifically targeted to protecting wildlife or enhancing the habitat and range from suppressing the natural the fire regime, mowing and intensive cattle grazing to enhance grass quality, and feeding wildlife during times of intense drought.

Each one of these management interventions should come with a caveat because many of these interventions are ill understood or understudied. Only through vigilant monitoring of possible consequences of past interventions can research inform future managerial decisions. The importance of monitoring is front and centre within an adaptive management framework (Lyons, Runge, Laskowski, & Kendall, 2008). At our study site the level of monitoring is considerably higher than in most managed ecosystems, precisely to better understand the ramifications of management interventions. Interestingly, management itself has not always been supportive of research-led decision-making, viewing scientific research as expensive, slow and often inconclusive. It is in large part by the pressure of supervisory oversight, via donors, management boards or other stakeholders (USAID, The Nature Conservancy, various university researchers or zoo specialists) that management has come to accept and indeed welcome the scientific advisory role in the decision making process. However, scientists have to be ready to answer specific questions in a timely manner and within an often scarce budget (Lyons et al., 2008). A survey of British and Australian conservation management practices revealed that scientific information was not used systematically to support decision making because it is not accessible, or that there was limited monitoring of past interventions resulting in managers making decisions based upon their own personal experience instead of the available research (Pullin & Knight, 2005). In the USA, a review of 53 state-wide wildlife plans revealed that only 25% used an adaptive management plan (Fontaine, 2011) even when nearly all of the people surveyed agreed that an adaptive management framework was superior and implementable. If First World wildlife managers don't use scientific evidence to base their decision making process, how can we expect Third World wildlife managers to hold up a better standard? Allen and Gunderson (2011) took another tack and reviewed projects that used an adaptive management framework but failed. They did so to better understand the pathology and reveal the most common pitfalls in its implementation. They found nine major recurring reasons that science based monitoring failed to inform the decision-making process: lack of stakeholder agreement, the difficulty of designing and carrying out field experimentation (complex large systems, slow to respond to intervention, long temporal or large spatial scales, replication impossible, etc…), unintended consequences (see "Third Law of Wildlife Management"), lack of flexibility in light of changing circumstances, procrastination and calls for "more science", not using what has been learned (i.e. shelving recommendations in favour of experience), risk-averse decision makers, lack of leadership, and finally focusing on planning and not on actions. This list of pathologies bodes well for managers of small conservancies as they neither have they the funds or the time to create elaborate large-scale experiments, rarely call for "more science", are usually led by action oriented people where the focus is squarely on action and not planning. Thus, an adaptive management framework, as long as it is appropriately scaled to the conservancy and supported by a focused group of stakeholders, should be welcomed and useful.

The impact of people

Of course, the largest ecosystem engineer on the landscape is the human. Humans have been molding and changing the landscape to suit their needs from the beginnings of time. Humans have modified migration routes, downgraded top predators to penultimate positions and in most places completely changed the physical landscape. Although my research focused on a human wildlife management tool, I did not actively track the movement of humans on the landscape, and that may be a rich area of future research. Adding the human dimension to the adaptive management framework may help management get a better understanding of the whole ecosystem functioning with people as an integral part of the system.

As a final thought, I recommend a closer coordination of field research with wildlife management issues by pairing field researchers with conservancies in need of pragmatic solution-oriented research. Collaborations such as the one I have enjoyed with this particular study site are key to making research more relevant to management and encourage research-led decision-making.

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Appendix A

The empirical chapters (3,4,5, and 6) in this dissertation are fairly concise and the methodology sections are synoptic, in keeping with the limitations of the peer-reviewed journals in which they appear. Consequently there are a number of interesting analyses that does not appear in these chapters since I opted to give the reader an exact replica of the final published version. With a view to give the reader a more fulsome understanding of some of the omitted spatial analyses that underpinned the conclusions in Chapter 5 and 6, I include a list of figures and maps that may be helpful for replication or further analysis. As I discussed in the preceding chapters, spatial analysis is very sensitive to the neighborhood size and the conceptualization of the spatial relationships. In this Appendix, I illustrate some of the other tools that are useful for further analysis as well as detailing the methods used in chapters 5 and 6. I will use the lion kill data from chapter 6 as an example.

I used ArcMap 10.3 (ERSI, Redlands, California) as the software tool for the spatial analysis. ArcMap's Spatial Statistics Toolbox contains a variety of tools to help the researcher better understand the spatial relationship of the data. The ArcMap toolset is large and varied and knowing how to navigate it is critical to a successful analysis. For example, there is a large menu of various spatial relationships that are offered and choosing a different conceptualization can have drastic effects on your results. For example, from the lion predation data in Chapter 6, choosing the "Inverse Distance" instead of the "Fixed Band" or the "Zone of Indifference" (see Fig 13.) makes a significant impact on the appearance of hot spots while using the Hot Spot Analysis tool:

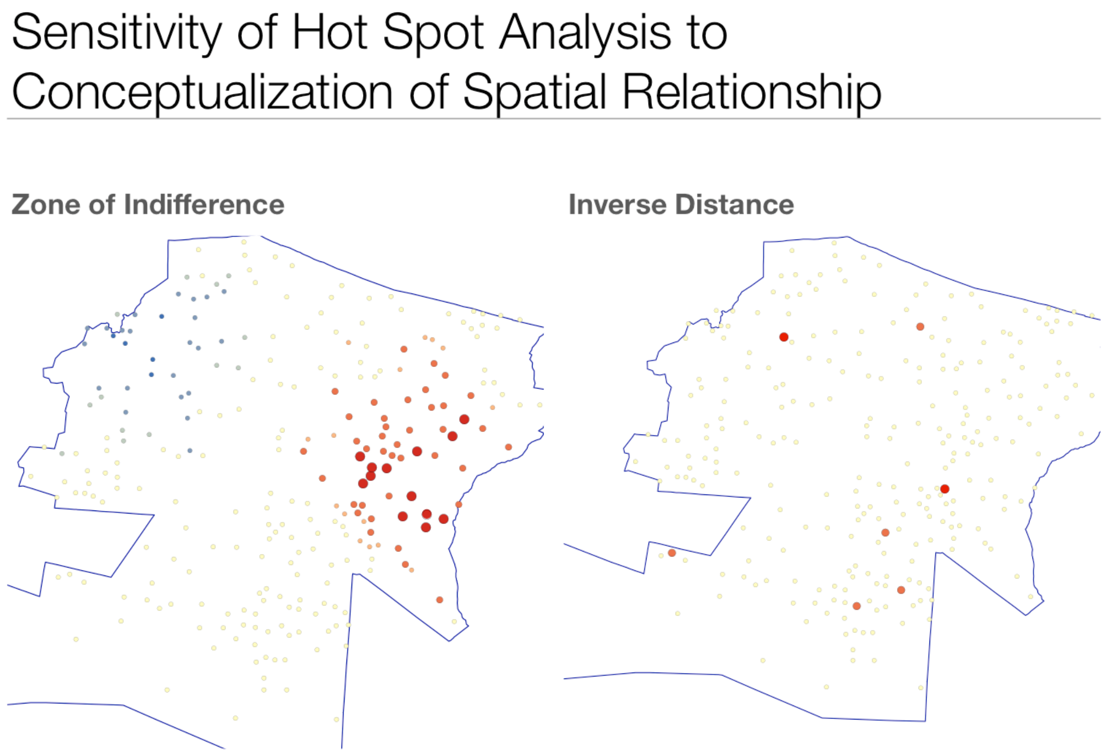


Figure 13- Sensitivity of Hot Spot analysis to different conceptualization of spatial relationships

How and why did I choose to use the "Zone of Indifference"? To answer that question, I will take you step by step through the analysis of how I got to this particular conclusion.

When I first mapped my data, I had a series of points; many of these were coincident points, i.e. at the same location. Simply looking at the map in Fig. 14 gave me a rough indication of clustering and possible patterns, but nothing more:

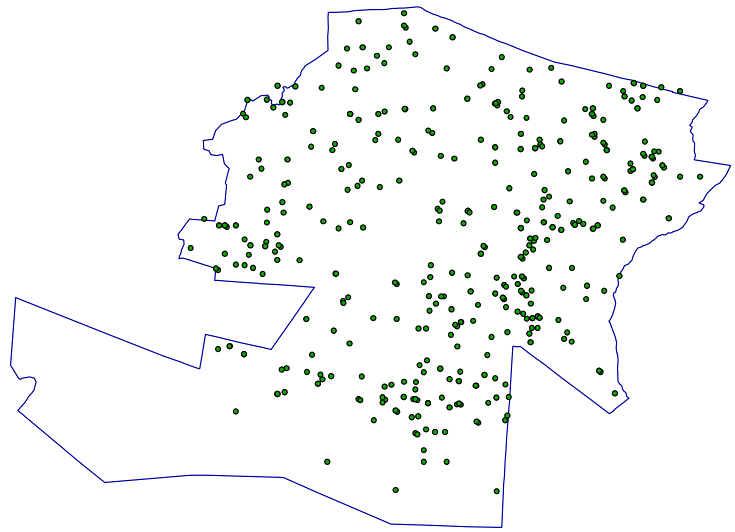


Figure 14- Map of lion kill locations on Lewa (2004-2015)

I then proceeded to aggregate the coincident data, as seen in Fig. 15, as well as the points that were within a 100m radius of each other. Firstly, to better match the actual precision tolerance of the kill data (+/- 50m) and secondly, to create a variance within the incident dataset.

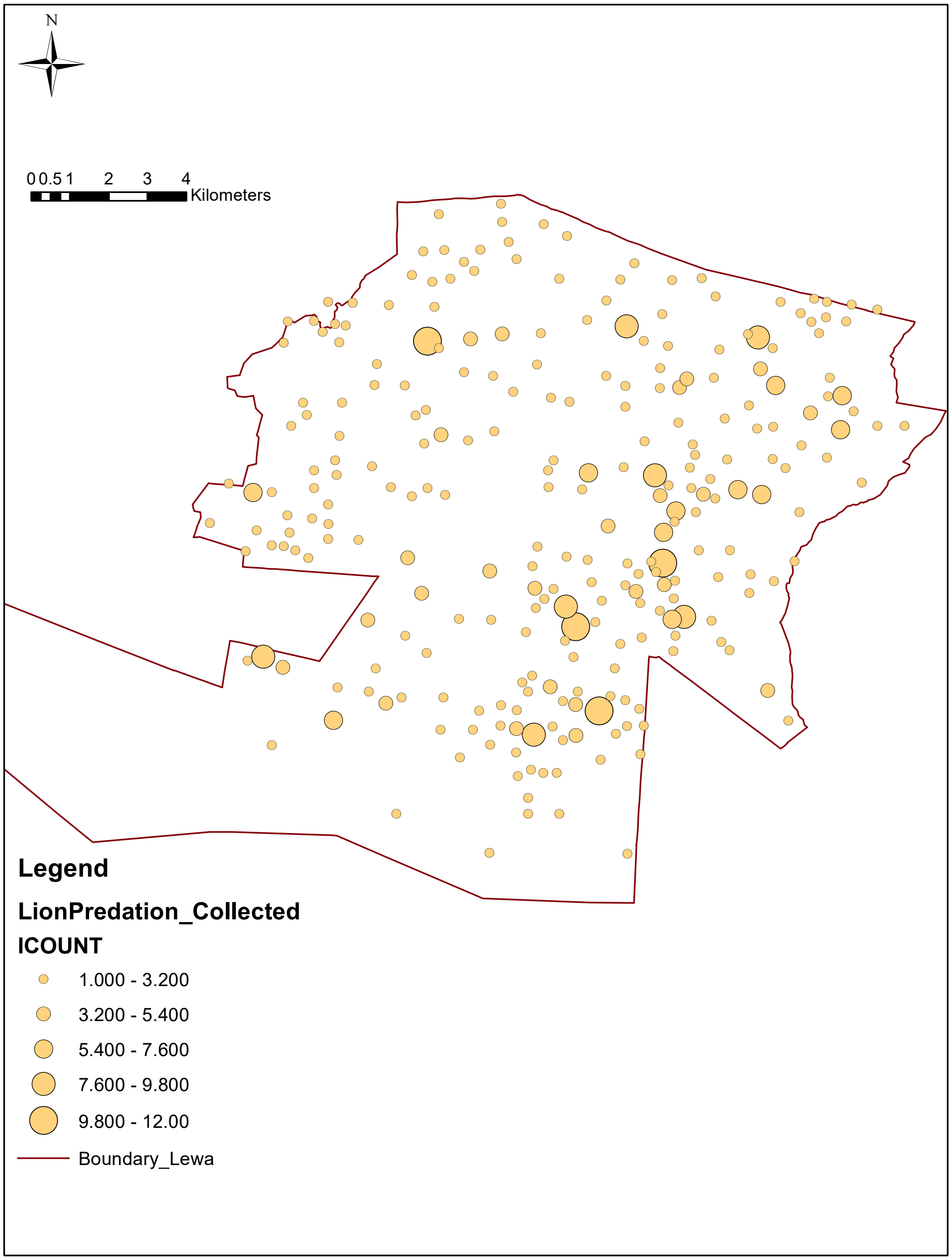


Figure 15 - Lion kill sites, aggregated and collected at 100m radius. (2004-2015)

Figure 15 gives a truer representation of the importance of each kill location and it becomes easier to pick out more important hunting grounds.

I then proceeded to build a heat map, using Kernel Density analysis. The heat map is visualization tool that helps get a first impression of the whole data set. The tool is also sensitive to search radius, and it relies on the user to select a search radius that makes sense to the researcher, e.g. in my case, hunting distance, daily home range size, etc. Each map produces a different output and is a bit of a dead end in terms of statistical inference, as it is mostly based on expert opinion and does not test any location against a norm. Nonetheless, heat maps are extremely useful to gauge the data set and the possible spatial relationships quickly. Figure 16 shows a density analysis at 1000m radius, a good starting distance for the hunting patterns of this species.

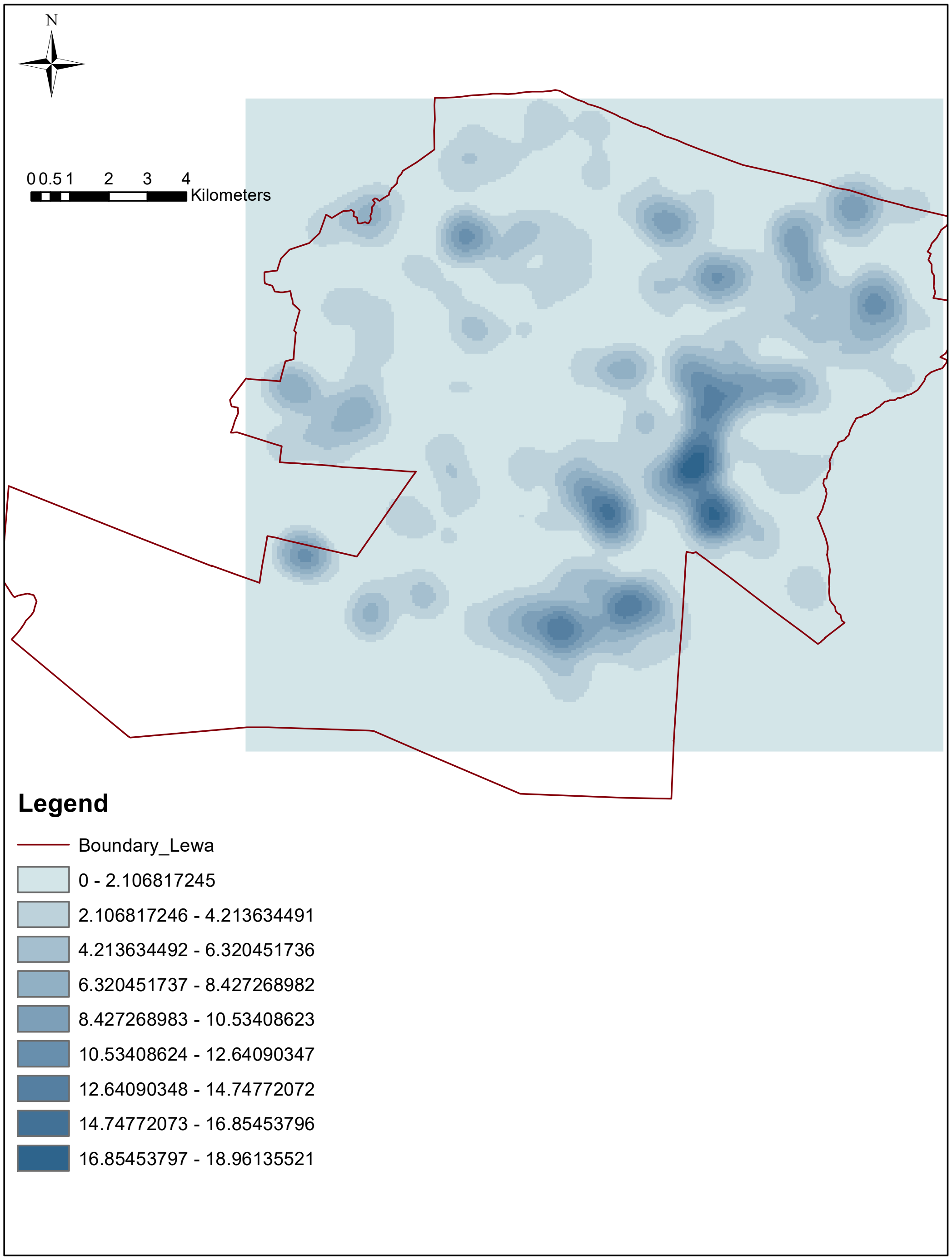


Figure 16- Lion Kill heat map using Kernel Density Analysis at 1000m radius

Figure 17 shows the same kernel density but this time with a search radius of 5000m, more in keeping with a patch disturbance rule for lion (Valeix et al., 2011).

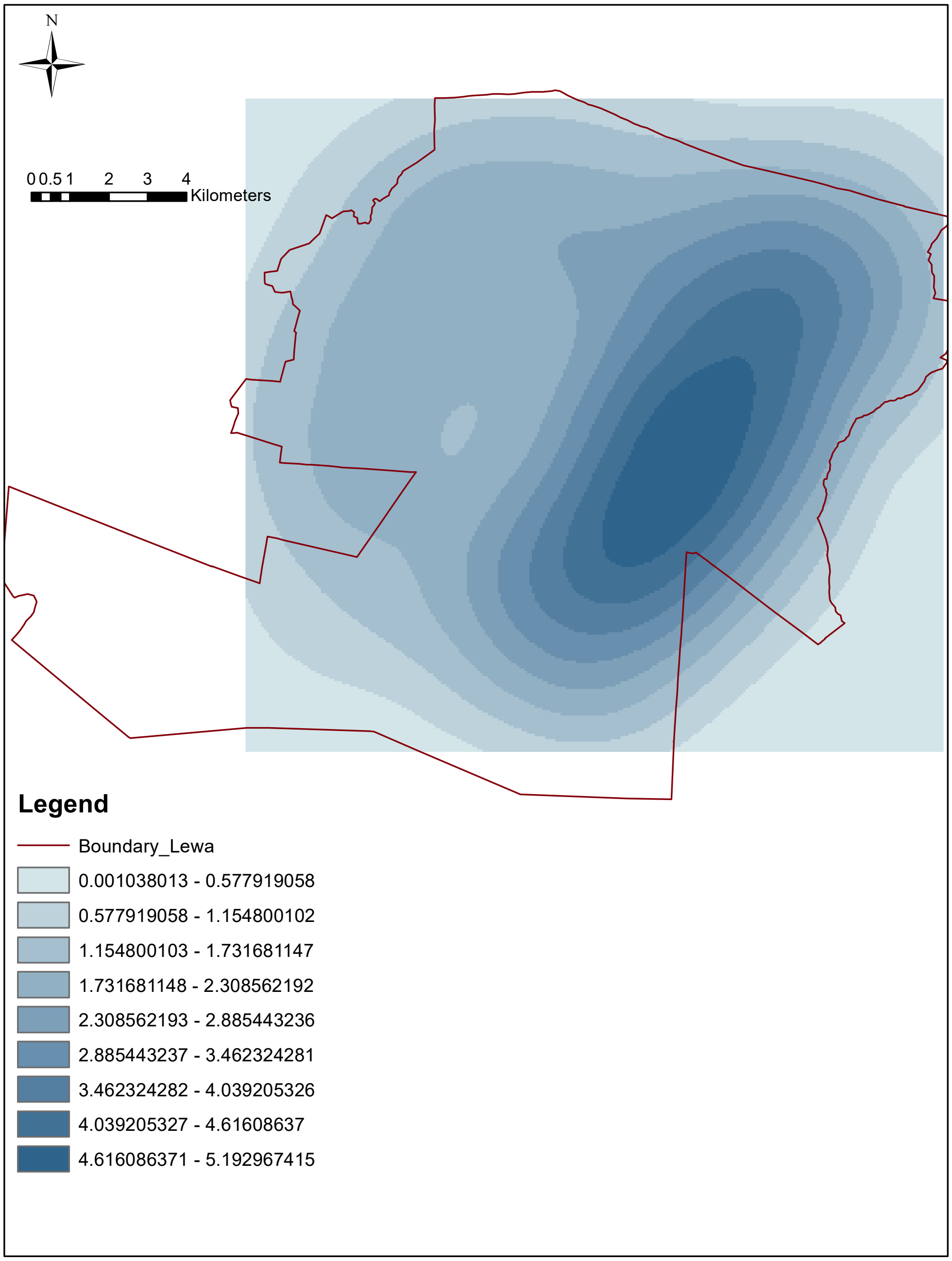


Figure 17- Lion kill heat map at a 5000m radius using Kernel Density analysis

Another excellent tool to analyze clustering is to use a spatial grid superimposed on your data set. This method helps fill the spaces where no data exist, which in my case, is where no kills had happened. I created fishnet grids with various sizes cells, Fig. 18 showing 1 km^2 .

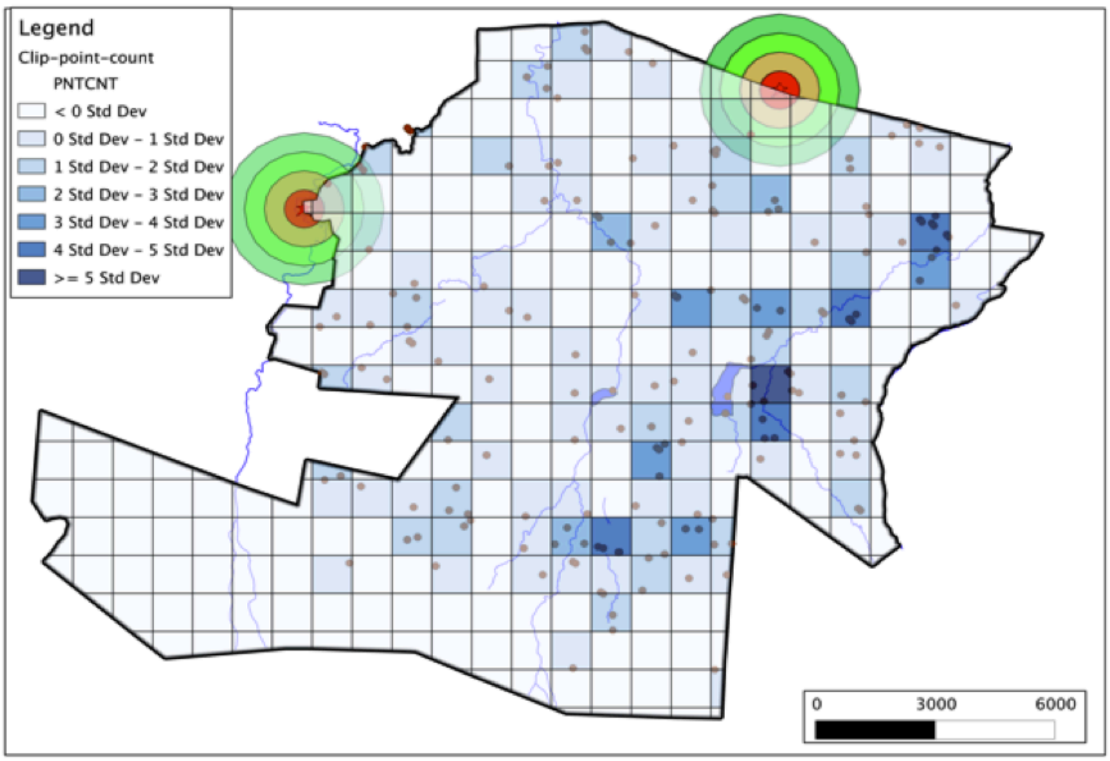


Figure 18-Fishnet spatial grid over the lion kill incident data

So depending upon your desired visualization parameters, you will get a different map. Which one is better? The way I chose to examine the data was to let the data determine the size of the neighborhood. Some of the tools I used were designed to best understand spatial clustering or neighborhoods. I first calculated the distance between collected incident points by using the Average Nearest Neighbor function. Calculating Ripley's K-Function

(Fig. 19) helped me visualize the clustering at various distances, as did performing the Average Nearest Neighbor calculation (Fig. 20).

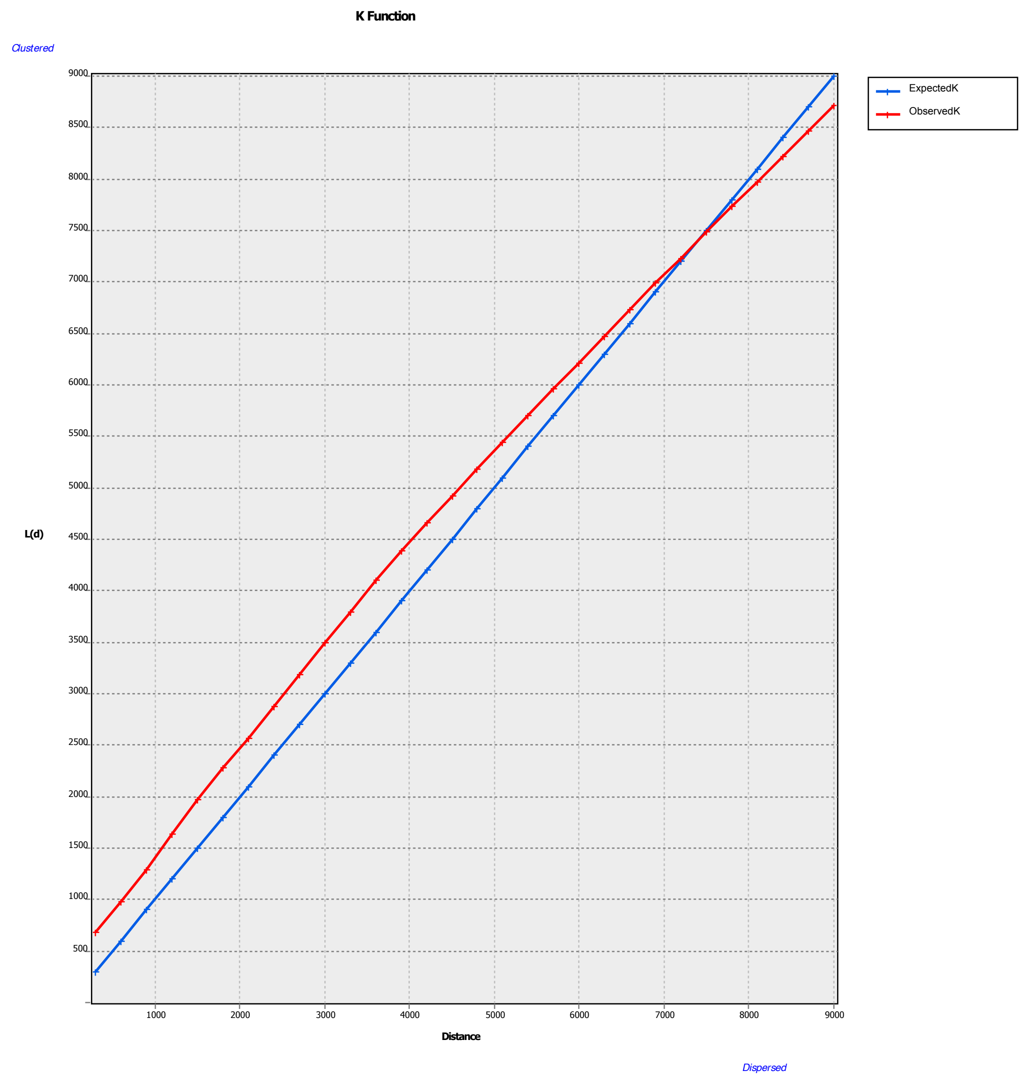
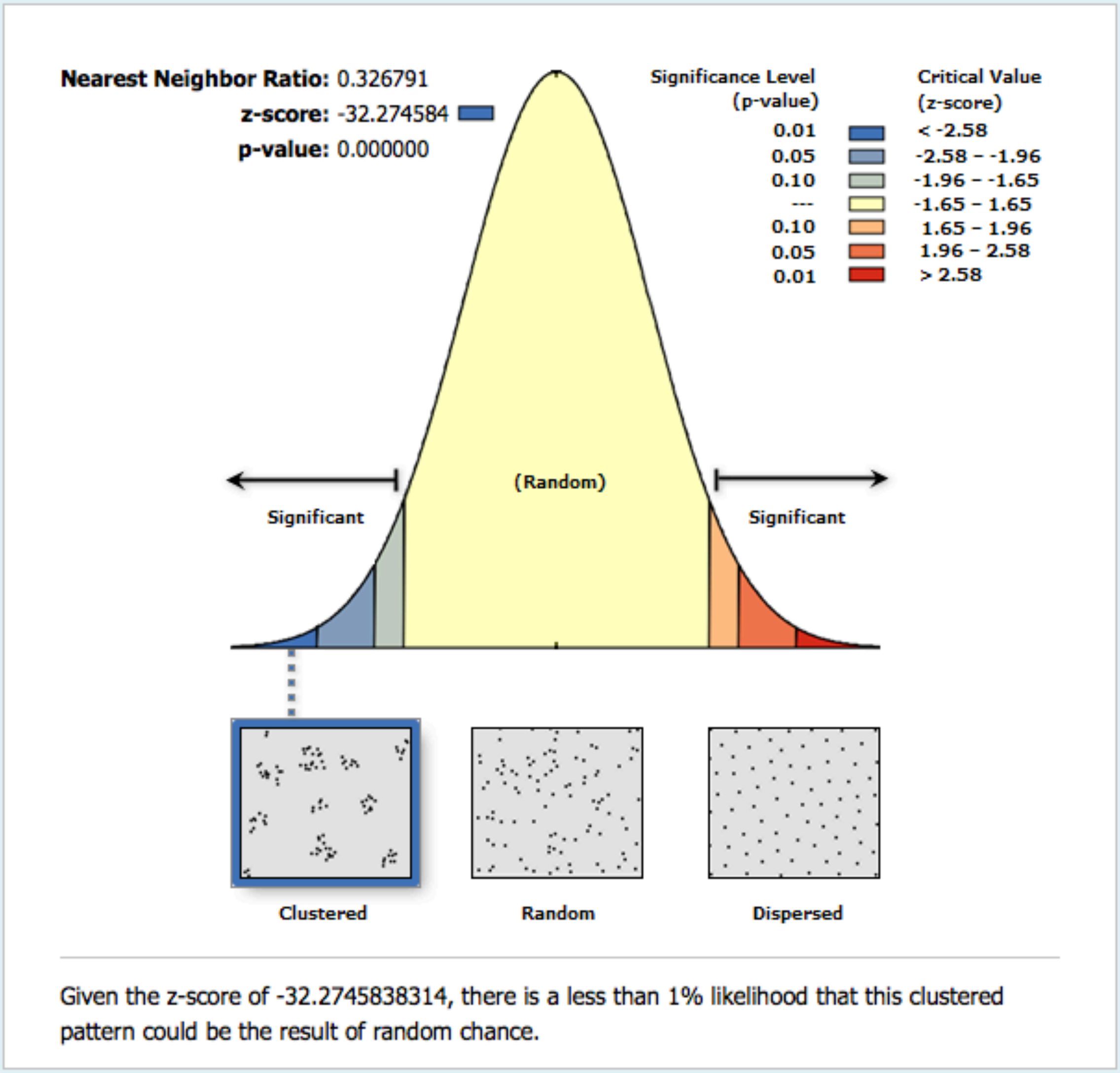


Figure 19- Graph of Ripley's K function for lion kill data

Average Nearest Neighbor Summary



Average Nearest Neighbor Summary

Observed Mean Distance:	105.8040 Meters
Expected Mean Distance:	323.7665 Meters
Nearest Neighbor Ratio:	0.326791
z-score:	-32.274584
p-value:	0.000000

Figure 20- Lion kill data, Average Nearest Neighbor tool, ArcMap 10.3

Using the observed mean distance as calculated in the Average Nearest Neighbor tool as the input distance, I used the Incremental Spatial Correlation tool, to determine the smallest distance at which significant spatial clustering (evidenced by the first significant peak in Global Moran's I statistic).

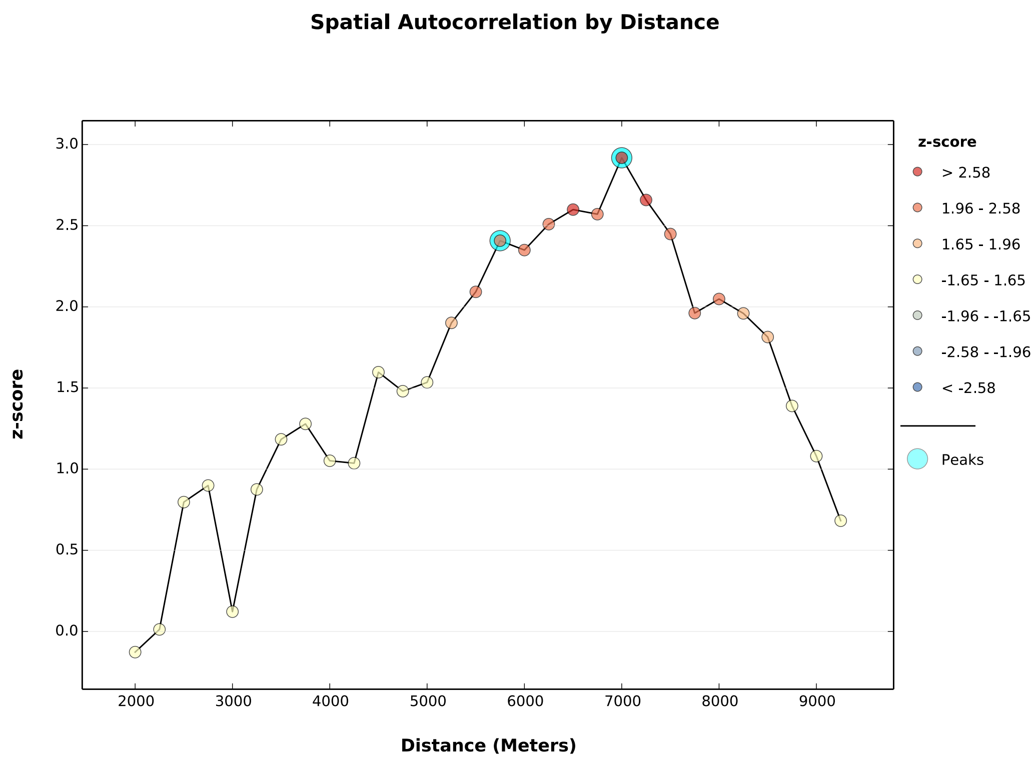


Figure 21- Incremental Spatial Autocorrelation of lion kill data

I then used the first peak distance, as evidenced in Figure 21, as the input distance in the Hot Spot Analysis as detailed in Chapter 6. Interestingly, the size of the neighborhood corresponds very closely to the observed size of the home ranges for lion (using GPS tracking collars and a 95% Kernel Density analysis, Lewa unpublished data) as shown in Fig. 22.

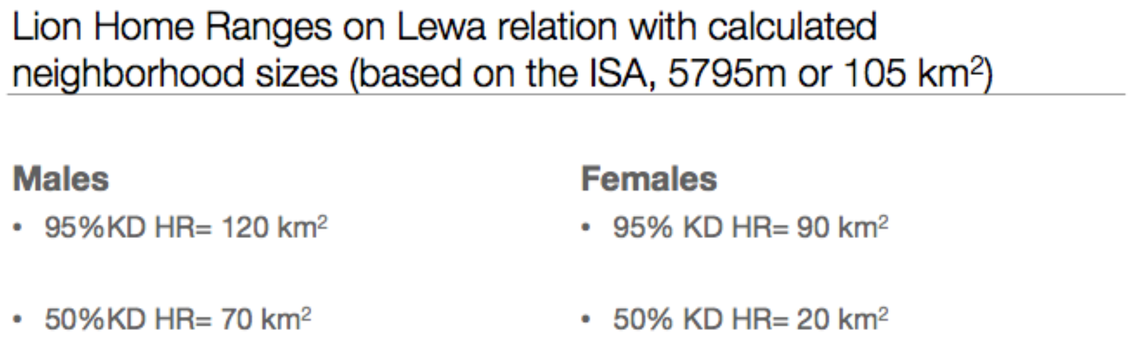


Figure 22- Comparing observed lion home range sizes on Lewa to neighborhood size as calculated by the Incremental Spatial Autocorrelation procedure

Some of the other interesting analyses that did not make it into the final peer-reviewed manuscripts were more descriptive in nature and helped me better understand the data set, although these analyses were not strictly necessary to arrive at my conclusions regarding hunting near the fences. One of the more interesting ways to look at your data is to perform Cluster and Outlier analysis (using the Anselin Local Moran's I). Figure 23 shows the spatial outliers, i.e. hot spots in otherwise cold zones. These outliers highlight specific locations that stand out for being significantly different than their immediate neighbors, although these points will not show up as hot spots in the final analysis because of the coolness of their surroundings. These locations can lead to very interesting further research as there may be landscape traps or other reasons why hunting has been so successful in these specific locations.

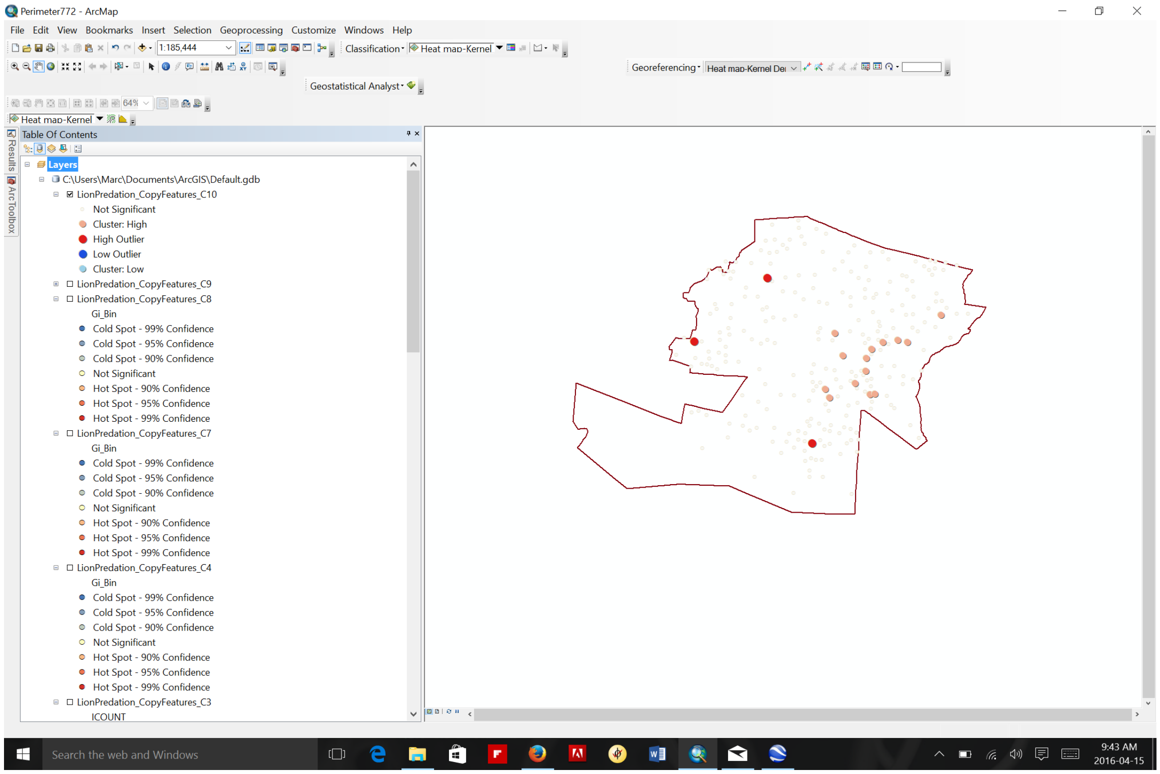


Figure 23-Screenshot of Spatial Outlier Analysis of lion kill data

Another tool that I found very useful was the Directional Distribution within the Measuring Geographic Distribution toolbox. This tool uses standard deviation ellipses to visually bin certain attributes of your data. I used it to visualize individual species kill locations to see if anything looked out of place (Fig. 24).

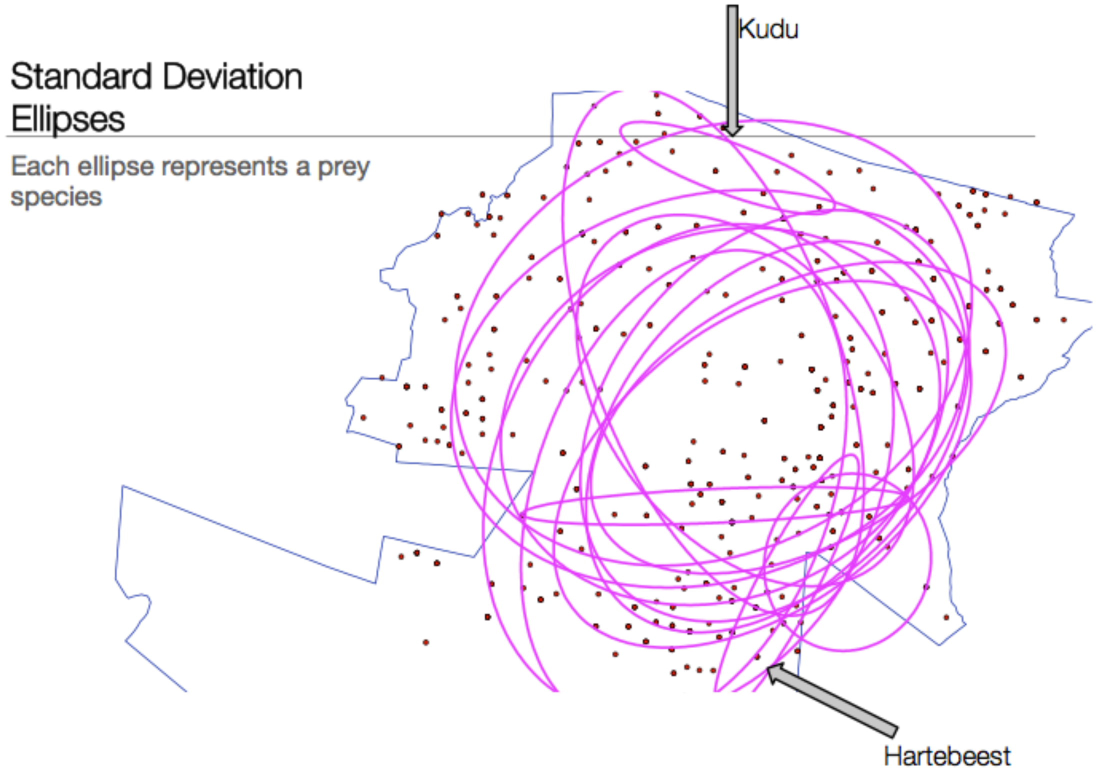


Figure 24- One Standard Deviation ellipses per individual species. Note the small areas for Kudu and Hartebeest

Reference

Valeix, Marion, Chamaille-Jammes, Simon, Loveridge, Andrew J., Davidson, Zeke, Hunt, Jane E., Madzikanda, Hillary, & Macdonald, David W. (2011). Understanding Patch Departure Rules for Large Carnivores: Lion Movements Support a Patch-Disturbance Hypothesis. *American Naturalist, 178*(2), 269-275. doi: 10.1086/660824