# THE MECHANSITIC PATHWAYS OF SPECIES INTERACTIONS IN AN AFRICAN SAVANNA

by

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## Abstract

Quantifying the interactions that govern the abundance and distribution of large African mammals is an opportunity to understand the forces structuring ecological communities and a means to inform conservation practice in a changing world. I paired experimental manipulations with correlative observations taken over expansive scales to quantify the mechanisms shaping interactions between trophic levels in an African savanna. Chapter 2 addresses the non-consumptive effects of predation risk on the behavior of a small and territorial antelope, Guenther's dik-dik (*Madoqua guentheri*). Studies have suggested that mobile prey avoid areas of heightened risk, but few such studies have been carried out on territorial organisms whose movement is constrained by their neighbors. My findings showed that use of familiar areas increased after exposure to a cue of risk, such that predators may reinforce rather than override territoriality in dik-dik. Chapter 3 unifies risk-avoidance behavior in a medium-sized antelope, the impala (*Aepyceros melampus*), and plant defense (thorns) to explain the spatial distribution of plant community structure. My findings showed that plants can persist in landscapes characterized by intense herbivory, either by defending themselves or by thriving in risky areas where carnivores hunt. Chapter 4 explores the cascading effects of wild dog recolonization (*Lycaon pictus*) on dik-dik and trees. Previous work has equated a positive correlation between plant and large carnivore biomass to a trophic cascade, thereby inferring mechanisms by which carnivores suppress herbivores which then releases plants from herbivory. My results showed suppression of herbivores by carnivores and of plants by herbivores, coupled with a positive correlation between carnivore and plant biomass that, together, did not give rise to a trophic cascade. There was no trophic cascade because the effect of herbivory, as measured by replicated herbivore exclosures, was the same in the presence and absence of wild dogs. Chapter 5 summarizes the main findings and limitations of this dissertation, and provides a framework for quantifying trophic cascades in systems dominated by large carnivores. Put together, this dissertation reinforces the vital role of a mechanistic approach to quantifying trophic interactions in large mammals.

# Preface

Chapter 2: A version of this chapter was submitted for peer review on April 14th 2014 and is under revision as of 20-September-2014. Dik-dik capture was performed by Simon Lima and supervised by Jacob Goheen (J.R.G.). Simon Lima monitored the collared dik-dik, under supervision of J.R.G. I designed the experiment, analyzed the data and wrote the associated manuscript. J.R.G. provided editorial support for this manuscript and Peter Komers provided additional comments and suggestions. This study was supported by grants from Natural Sciences and Engineering Research Council (A.T.F., J.R.G.), a Killam Pre-doctoral Fellowship (A.T.F.), the American Society of Mammalogists (A.T.F.), University of British Columbia (A.T.F.).

Chapter 3: A version of this chapter was submitted for peer review on February 27th 2014 (Accepted by Science as of 15-September-2014) and presented as a plenary talk to the American Society of Mammalogists in 2013. This research was performed in collaboration with my advisor, Jacob Goheen (J.R.G.), as well as Tobias O. Otieno (T.O.O.), Todd M. Palmer (T.M.P.), David Ward (D.W.), Rosie Woodroffe (R.W.), Robert M. Pringle (R.M.P.). Impala capture was performed by Kenya Wildlife Service veterinarians and Frontier Helicopters and supervised by J.R.G. Simon Lima monitored the collared impala, under supervision of J.R.G. Thorn-removal experiments were carried out in the field by J.R.G. and T.O.O. Coreen Forbes conducted Acacia spp. density surveys with Simon Lima. R.M.P., J.R.G. and T.M.P. created and funded the UHURU (Ungulate Herbivory Under Rainfall Uncertainty) experiment for which they contributed raw data. R.W. supplied telemetry data and pack compositions of African wild dog packs using MRC. D.W. provided chemical analyses of Acacia spp. I conducted all statistical analyses and wrote the chapter and associated manuscript. J.R.G. and R.M.P. provided editorial support for this manuscript. I received comments and suggestions from S. Buskirk, J. Estes, M. Kauffman, K. Monteith, R. Ostfeld and C. Riginos. This study was supported by grants from Natural Sciences and Engineering Research Council (A.T.F., J.R.G.), a Killam Pre-doctoral Fellowship (A.T.F.), the American Society of Mammalogists (A.T.F.), University of British Columbia (A.T.F.), Keren Keyemet I'Israel (D.W.), South African National Research Foundation (D.W.), University of Florida (T.M.P.) and University of Wyoming (J.R.G.).

Chapter 4: A version of this Chapter was presented at an oral-session to the American Society of Mammalogists in 2014 and is being formatted for submission to a peer-reviewed journal. This research was performed in collaboration with my advisor, J.R.G., as well as T.M.P., R.W., R.M.P. Tim G. O'Brien (T.O.B.), Margaret F. Kinnaird (M.F.K.) and David J. Augustine (D.J.A.). R.M.P., J.R.G. and T.M.P. created and funded the UHURU experiment, for which they contributed raw data. D.J.A. contributed raw data pre- wild dog recolonization. R.W. supplied telemetry data, diets and pack compositions of African wild dog packs using MRC. T.O.B. and M.F.K. supplied raw data on dik-dik densities form 2008-2013. I conducted line-transect sampling and camera trapping. I conducted all statistical analyses. Editorial support for a draft manuscript was provided by J.R.G. and D.J.A.

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## Dedication

To the last light that leaves the eyes, an unending stillness;

To the first spark that enters this world, my unending joy.

# Chapter 1: Introduction

## 1.1 Background

African mammals hold a uniquely important place in the world: from the protagonist in thousands of children's books, to the centerpiece of a multi-million dollar tourism industry, to one of the most commonly studied ecological systems, these animals continue to captivate our imaginations. Despite this attention, populations of many species are facing widespread decline both in human-occupied landscapes (Georgiadis et al. 2007b) and within the protected areas designed to conserve wildlife (Craigie et al. 2010). In addition to species declines, African landscapes are changing rapidly: in some areas woody cover is encroaching into grasslands (Ward 2005), while grasslands are giving way to deserts in other areas (Reynolds et al. 2007), and people are converting vast tracts of wild landscapes into agricultural production (Ramankutty and Foley 1998). Quantifying the mechanisms governing the abundance of large African mammals is thus an opportunity to understand the forces structuring ecological communities and a means to inform conservation practice in a changing world.

A useful place to understand the forces structuring ecological communities starts with the classification of organisms into functionally similar groups based on the types of resources they consume; for example, plants, herbivores and carnivores, or more generally, primary producers, primary consumers and secondary consumers (Elton 1927, Lindeman 1942). Next, organizing these functional groups, or trophic levels, into a linear sequence of resource consumption provides the basis of the food chain model. The food chain model provides a framework with which to understand the flows of energy and matter through ecosystems. I will thus rely on ‘food webs’ (aggregate food chains) as a model to discuss the forces structuring ecological communities, but recognize that there are other, more sophisticated means to conceptualize community structure that account for such processes as detrital food chains, omnivory, and ontogenetic shifts in trophic level (Polis and Strong 1996).

Two forces are thought to structure ecological communities in general, particularly those dominated by large African mammals. First, bottom-up forcing is a resource-limiting constraint on populations, manifesting as a density-dependent decline in fecundity, emigration and/or survival of individuals as the *per capita* availability of nutrients, matter or space declines (Lindeman 1942, Polis and Strong 1996). Thus, longer food chains and a greater abundance of apex predators are more common in more productive environments (Oksanen et al. 1981, Pimm 1984, Fretwell 1987). Second, top-down forcing typically manifests as heightened mortality from predation, but may also include regulation by pathogens and parasites (Hairston et al. 1960). Non-consumptive or risk effects have also been shown to affect the vital demographic rates of populations (Peckarsky et al. 2008, Creel et al. 2009). Organisms exposed to high rates of predation or those living in resource-rich environments are predicted to be regulated by top-down forcing.

Bottom-up and top-down forcing interact to varying degrees among (Hairston et al. 1960) and within trophic levels (Hopcraft et al. 2010). Among trophic levels in savannas, large carnivores are regulated by bottom-up forcing through the abundance of prey while herbivores and primary producers are thought to be regulated by both top-down and bottom up forcing. For example, tree cover in African savannas is regulated by rainfall (i.e. bottom up forcing) below a mean annual precipitation (MAP) of 650 mm, and by fire and herbivory (i.e., top-down forcing) beyond a MAP of 650 mm (Sankaran et al. 2005). Bottom-up and top-down forces also vary within a population. For example, buffalo (*Syncerus caffer*) are more vulnerable to predation when food is limiting, such that bottom-up forcing intensifies the strength of top-down forcing (Sinclair and Arcese 1995a). Finally, variation in bottom-up and top-down forcing also is manifest at the individual level. For example, grazing ungulates titrate risk of predation and forage availability when selecting habitat (Riginos and Grace 2008, Anderson et al. 2010, Burkepile et al. 2013). Some individuals may also experience alternating pulses of resource abundance and predation risk over spatially-expansive migration routes (Fryxell et al. 1988, Fryxell and Sinclair 1988, Mduma et al. 1999). Thus, bottom-up and top-down forcing combine to shape ecosystems at the community, population, and individual-level.

In spite of the growing acceptance that both bottom-up and top-down forcing shape species interactions (Anderson et al. 2010), substantial knowledge gaps remain in the way these two concepts are unified to understand community structure in African savannas. One of the classic concepts outlining how ecological communities are structured is the Jarman-Bell Principle, which explains the allometric partitioning of resources by grazing ungulates (Bell 1971, Jarman 1974). Here, larger-bodied ungulates are constrained by a relatively high-metabolic demand and require large quantities of forage. These species may consume poorer-quality but more abundant forage because of their larger digestive capacity, and often are referred to as ‘bulk feeders’. Conversely, smaller-bodied ungulates have a higher mass-specific metabolic demand and have a lower capacity to digest poorer-quality plant material.

As such, smaller ungulates are considered ‘selective feeders’ as they are more discriminating in the plant material they consume. The generality of the Jarman-Bell Principle has been extended to other ecosystems, where differences in species’ metabolism and environmental heterogeneity promote coexistence through resource partitioning (Damuth 1981, Ritchie and Olff 1999, Ritchie 2009). However, to explain coexistence in herbivores, the Jarman-Bell Principle and its derivatives requires that resources trade-off along an axis of quality and abundance, which may not hold for some trophic levels. Moreover, while it may explain how resource partitioning facilitates coexistence, the Jarman-Bell Principle does not unify bottom-up and top-down forces to explain community structure.

Like the Jarman-Bell Principle, conceptual unification of bottom-up and top-down forcing in the regulation of African ungulates focuses on allometry (Sinclair et al. 2003, Hopcraft et al. 2010). For example, small antelope are more vulnerable to predation (i.e., top-down forcing) than large ungulates, whereas large ungulates are more vulnerable to starvation and water-limitation (i.e., bottom-up forcing) than small antelope (Sinclair et al. 2003, Fritz et al. 2011). While integrating bottom-up and top-down forces, these models focus on population-specific responses and do not inform us about food web dynamics or community structure. For example, Sinclair et al. (2003) found that small antelope like oribi (*Ourebi ourebi*) almost always die from predation, wildebeest (*Connochaetes taurinus*) and zebra (*Equus quaaga*) sometimes do, and buffalo and giraffe (*Giraffa camelopardalis*) rarely do. In this case, removal of a large carnivores should have a greater positive effect on oribi abundance than on giraffe abundance. However, giraffe have a higher *per capita* metabolic demand than oribi, so a minor increase in giraffe abundance could have a more profound effect on the plant community than a relatively larger increase in oribi abundance. Understanding how food webs are structured in African savannas requires an extension of both the coexistence models derived from the Jarman-Bell Principle, along with the population-regulation models (Sinclair et al. 2003, Hopcraft et al. 2010) to account for food-web topology. One of the key hypotheses that can help to unify these two concepts is the trophic cascade (Chapter 5).

Though rarely defined formally in the literature (Terborgh and Estes 2010), a common feature of all trophic cascades is the uni-directional flow of population regulation through at least two sequential trophic levels resulting in the facilitation of a third trophic level. In other words, a trophic cascade is the result of at least two direct species interactions and at least one indirect species interaction. In their archetypal form, trophic cascades arise when plants are indirectly facilitated through the suppression of a herbivore by a carnivore (Hairston et al. 1960, Paine 1980). Trophic cascades generalize to more than three trophic levels (Oksanen et al. 1981), can include both consumptive and non-consumptive effects of carnivores (Schmitz et al. 1997, Preisser et al. 2005), can facilitate species biomass and abiotic processes (Estes et al. 2011) and have been documented widely in a number of marine, freshwater and terrestrial ecosystems (Terborgh and Estes 2010).

The explanatory power of the trophic cascade hypothesis underlies its oft-used application for predicting the community-level consequences of species invasions and extinctions. For example, consistent with the trophic cascade hypothesis, large carnivore restoration led to increased plant biomass in a tri-trophic food chain (Ripple et al. 2001, Hebblewhite et al. 2005b) but decreased plant biomass in a tetra-trophic food chain (Estes et al. 1998). In these two examples, both the plant and the herbivore species were regulated by top-down forcing, but their abundance was ultimately determined by the total number of trophic levels in the food chain. Thus, by formulating a topology of interactions among trophic levels, the trophic cascade hypothesis provides a means to understand and quantify contingencies in the strength of top-down and bottom-up forcing through food webs.

In addition to accounting for food web topology, the trophic cascade hypothesis has been used to integrate phenotypic traits (e.g., body size, behavior, defenses) (Peacor and Werner 1997, Werner and Peacor 2003, Grabowski and Kimbro 2005, Schmitz 2010) and resource heterogeneity (Oksanen et al. 1981, Leibold 1989, Schmitz 1994) when predicting species abundance. For example, well-defended plants can resist herbivory and so tend to be limited by bottom-up forcing while edible plants tend to be limited by herbivory (Leibold 1989). Thus, trophic cascades are commonly stronger in systems dominated by more edible plants (Strong 1992a, Shurin et al. 2002, Shurin et al. 2006). With their episodic drought-rainfall cycles, rapidly changing land-use patterns and diverse assemblages of carnivores and herbivores and plant defense phenotypes, African savannas are a powerful testing ground to evaluate if and how trophic cascades emerge in systems dominated by large carnivores.

The potential for large carnivores to trigger trophic cascades has been used to justify the restoration of these iconic species as both a moral imperative and a means to 're-wild' whole landscapes (Caro 2007, Estes et al. 2011, Ripple et al. 2014). However, there are significant gaps in the empirical support for this claim, particularly when applied to African savannas. Specifically, widespread use of landscape-scale, correlative approaches has made it challenging to attribute changes in plant and herbivore biomass to the effect of carnivore restoration. These correlative approaches or ‘natural experiments’ often lack control and replication and so suffer from confounding variation. For example, Ripple and Beschta (2003) suggest that the recovery of aspen (*Populus* sp.) is driven by behavioral avoidance of risk by elk (*Cervus elaphus*) following the reintroduction of wolves (*Canis lupus*) to Yellowstone National Park, USA. To test the trophic cascade hypothesis, this study focused on the biomass of a single trophic level (plants) before and after restoration of wolves, but in so doing needed to infer the suppression of plants by elk and of elk by wolves. Subsequent studies in this system using more direct measures of wolf-elk interactions found that avoidance of wolves by elk is likely too diffuse and short-lived to facilitate trees (Middleton et al. 2013a), that rates of tree biomass accumulation did not increase with predation risk (Kauffman et al. 2010) and that tree biomass accumulation could also be explained by abiotic factors such as fire and rainfall intervals (Winnie 2012). Moreover, when applied to large, terrestrial carnivores, evaluation of the trophic cascade hypothesis has generally been confined to a small subset of predator species (e.g., cougars, grizzly bears, wolves), herbivores (e.g., large cervids like deer, elk, moose) and broad-leaved trees (e.g., oak, aspen) (McLaren and Peterson 1994, Ripple and Beschta 2003, Hebblewhite et al. 2005, Beschta and Ripple 2007, Callan et al. 2013, Kuijper et al. 2013). In the absence of a more rigorous assessment of the trophic cascade hypothesis, and one which involves a greater diversity of species and biomes, there is a significant gap in our knowledge of food-web dynamics and community structure in African savannas.

The goal of my dissertation research is to fill this knowledge gap using a mechanistic approach to quantifying species interactions between trophic levels. As such, my thesis seeks to understand the causes and consequences of trophic interactions by: addressing the non-consumptive effects of predation risk on ungulate behaviour (Chapter 2), the cascading effects of risk avoidance on the plant community (Chapter 3), and the decoupling of sequential, top down control through a putative trophic cascade (Chapter 4). This effort provides novel insight into the dynamics of predator-prey interactions among large mammals generally, and for browsers in human-occupied savannas, specifically.

## 1.2 Study area

My chosen study area and focal species fill key knowledge gaps related to landscape context and food web dynamics. My research was conducted at the Mpala Research Center (MRC), Laikipia, Kenya (Figure 1.1). There are no formal protected areas within Laikipia and land management is left to private landowners, whereas most of the research addressing the ecology of African mammals has taken place in protected areas (e.g., Serengeti National Park, Tanzania; Hluhluwe–iMfolozi Park, South Africa). As such, my research in Laikipia provides opportunity to integrate different landscape contexts involving human livelihoods, specifically subsistence and commercial livestock management, within the framework of food-web ecology.

MRC is typical of the *Acacia*-bushland areas of East Africa, with a mosaic of grasslands and woodlands. MRC property follows a north-south rainfall gradient from 350 to 650 mm per year and is comprised of two main soil types. The red sand ecosystem is nutrient poor, dominated by a higher diversity of *Acacia* spp. in the overstory, a mix of forbs and grasses in the understory, and high ungulate species richness (Augustine 2010). The black cotton ecosystem has nutrient rich soils, dominated by one *Acacia* species and a few grass species in the understory (Young et al. 1997). This study will focus on the red sand ecosystem.

Traditional land-use practices in Laikipia were once dominated by nomadic pastoralism and have more recently shifted to livestock ranching and ecotourism. MRC contains herds of domesticated cattle (*Bos indicus*), camels (*Camelus dromedaries*) and goats (*Capra aegagrus*), which are managed using traditional Masai herding practices in which livestock are secured in a 'boma' or corral at night to exclude predators and contain the herd.

Large ( >20 kg) carnivores are common in this area, and include leopard (*Panthera pardus*), African wild dog (*Lycaon pictus*), lion (*P. leo*), spotted hyena (*Crocuta crocuta*) and striped hyena (*Hyaena hyaena*), which occur at a combined density of about 35 individuals per 100 km$^2$ (Georgiadis et al. 2007a, O'Brien and Kinnaird 2011, Woodroffe 2011a). Of these, I pay particularly close attention to the ecology of wild dogs, which have recolonized the study area in 2002 and predate upon both of my focal species.

## 1.3 Focal species

In addition to focusing on landscapes within protected areas, studies addressing the ecology of large African mammals are typically situated in more mesic areas dominated by grazing (grass-eating) herbivores (Sinclair 1979, Sinclair and Arcese 1995b). However, such grazing systems are relatively anomalous: browse constitutes a major portion of the diets of 40-60% of the approximately 90 species of ungulates (Jarman 1974, Illius and Gordon 1992, Cerling et al. 2003). My focal species, dik-dik (*Madoqua guentheri*) and impala (*Aepyceros melampus*) (Figure 1.2 and Figure 1.3), are browsers for at least part of the year at MRC (Augustine 2010) and so provide opportunity to complement previous work addressing the ecology of grazing antelope (du Toit and Olff 2014).

Dik-dik (*Madoqua* spp.) are an obligate monogamous and territorial antelope, specializing on C3 (i.e., the photosynthetic pathway of carbon fixation) forbs and trees (Manser and Brotherton 1995, Cerling et al. 2003, Kingdon 2013) and will abandon their territory if woody cover is removed (Boshe 1984). Dik-dik are relatively small for an ungulate, at 4-5 kg adult body mass and a shoulder height of ca. 38 cm. They typically have one offspring every six months, with seasonal modality in birth rates observed in part of the genus' range, and young reach adult height in 8 months and adult mass in 1-1.5 years of age (Kingswood and Kumamoto 1996). As such, it is rare to see a group of > 3 dik-dik in the wild. Territoriality by adult males is related to both mate and resource access (Komers 1996a, Komers and Brotherton 1997). The genus range of dik-dik covers East and North-Eastern Africa, with an outlying population in SW Africa (Namibia). Dik-dik physiology is well-adapted to arid conditions, and they are generally believed to not be water limited (Kingswood and Kumamoto 1996). Because of its diet specialization, physical stature and social organization, understanding the role of top-down and bottom-up forcing on dik-dik provides novel insight on food web dynamics in ungulates – which typically are focused on generalist-feeding, large and gregarious species.

Impala are a medium-sized antelope with an adult body mass of 40-50 kg and a shoulder height of 70-100 cm. Impala typically increase their consumption of C4 grasses in the wet season and consume more C3 forbs and trees in the dry season (Augustine 2010). With their mixed-feeding preferences, impala are often considered an 'edge' species that utilizes both open grasslands and woodlands throughout its species range (Leuthold 1970, Kingdon 2013). Impala typically live in harem-groups or clans, with a dominant male and 5-120 females and sub-adults, and in bachelor herds. Territoriality and harem-defense have both been observed in impala (Jarman 1970, Leuthold 1970, Jarman and Jarman 1973a, Jarman and Jarman 1973b). However, group membership appear to be fluid (Kingdon 2013), and impala may move the distance of several home ranges to track localized pulses in precipitation/ plant growth during dry periods (Augustine 2010). Where they co-occur with pastoralists impala often are observed in abandoned livestock corrals or 'bomas' (Leuthold 1970, Augustine 2004). Because of its diet generalization, larger physical stature and gregarious social organization, research on impala is readily integrated in the established literature addressing community structure in ungulates.

## 1.4 Thesis chapters

The unifying theme of this dissertation is that direct and indirect interactions shape the distribution and abundance of large mammals in an African savanna. Underlying this theme is the use of both mechanistic and correlative field methods to identify both causation and the consequences of species interactions. Mechanistic approaches include use of simulated risk of predation (Chapter 2), manipulated plant defense (Chapter 3), habitat visibility (Chapter 3), and experimental herbivore exclusion (Chapter 4). Correlative approaches include the use of GPS (Global Positioning System) collars to track movement patterns in large mammals

(Chapters 2,3), remote-sensing to quantify habitat types (Chapter 3), and longer-term (>10 years) surveys to measure changes in the abundance of both predators and prey (Chapters 3,4). These approaches are brought to bear on questions regarding the effects of predation risk (Chapter 2 and 3) as well as consumption by a recolonizing carnivore (Chapter 4) on both animal and plant communities. Below I highlight the specific approaches and hypotheses used in my thesis chapters.

In Chapter 2, I quantify how dik-dik perceive and respond to risk of predation. Critically, and unlike typical studies addressing risk in ungulates, in this chapter I use experimental methods to simulate risk and then quantifies fine-scale movement patterns of dik-dik. I test three hypothesis to explain how dik-dik perceive risk including: (1) The Displacement Hypothesis which argues that prey disperse away from areas with heightened risk (i.e., the risky places hypotheses [Creel et al. 2006]) ; (2) the Fidelity Hypothesis, which argues that territoriality reinforces spatial memory and knowledge of areas where crypsis is most effective; (3) the Risk Allocation Hypothesis, which argues that organisms faced with chronic levels of high predation should exhibit limited responses to cues of risk for all but the most immediate of threats (Lima and Bednekoff 1999). Evaluation of these hypotheses highlights the mediating role of the life history of dik-dik as it traverses through spatial heterogeneity in predation risk.

In Chapter 3, I ask three questions to determine if a behaviorally-mediated trophic cascade is occurring via the anti-predator response of impala: (1) do impala select habitat to reduce risk of predation? (2) how do plant defenses affect impala diet selection? (3) does risk of predation to impala explain spatial variation in the distribution of plant defense across the landscape? Using GPS telemetry, I quantify broad-scale habitat selection patterns of impala, one of its predators (wild dogs), and their direct interaction (kill sites). The spatial structure of these carnivore-herbivore interactions are then associated with the distribution of two widespread and abundant species of *Acacia*, each with markedly different anti-herbivore defences. These correlative observations are linked to experimental manipulations that quantify: (1) the effect of risk on habitat selection by impala; (2) the effect of plant defense on the foraging preferences of impala; and (3) the effect of impala on the abundance of *Acacia*. These experimental manipulations provide a mechanistic approach to understand the relative effects of bottom-up and top-down forces, while the correlative data explains how the behavior of impala reverberates to affect the plant community over expansive spatial scales.

In Chapter 4, I report my efforts to test the trophic cascade hypothesis that wild dog recolonization, through suppression of dik-dik, is leading to the facilitation of trees. I decompose this hypothesis into three research questions: (1) do wild dogs suppress dik-dik? (2) do dik-dik suppress trees, and if so, which species? (3) does the effect of dik-dik on trees diminish in the presence of wild dogs. I combine data from studies conducted prior to wild dog recolonization with those started after recolonization. Additionally, in this study I integrate a number of data sources to evaluate alternative explanations to the trophic cascade hypothesis, including other sources (besides wild dog recolonization) of top-down and bottom-up regulation of both dik-dik and trees. This study highlights the critical need to quantify the two direct and one indirect species interactions required that define a trophic cascade.

In Chapter 5, I summarize the main findings from each of the previous chapters, highlighting the need to use both correlation and experimental approaches in studies involving large, terrestrial mammals. I evaluate limitations to my studies and recommendations for future research. I end this chapter with a synthetic view of food web ecology in systems dominated by large carnivores, by creating a framework with which to test the trophic cascade hypothesis.

**Figure 1.1 Map of Mpala Research Center, Laikipia, Kenya.** The legend describes locations of shrub removal plots (Chapter 3), tree survey plots (Chapter 3), the UHURU experiment (Chapters 3 and 4), dik-dik home ranges (Chapter 2), and impala home ranges (Chapter 3).

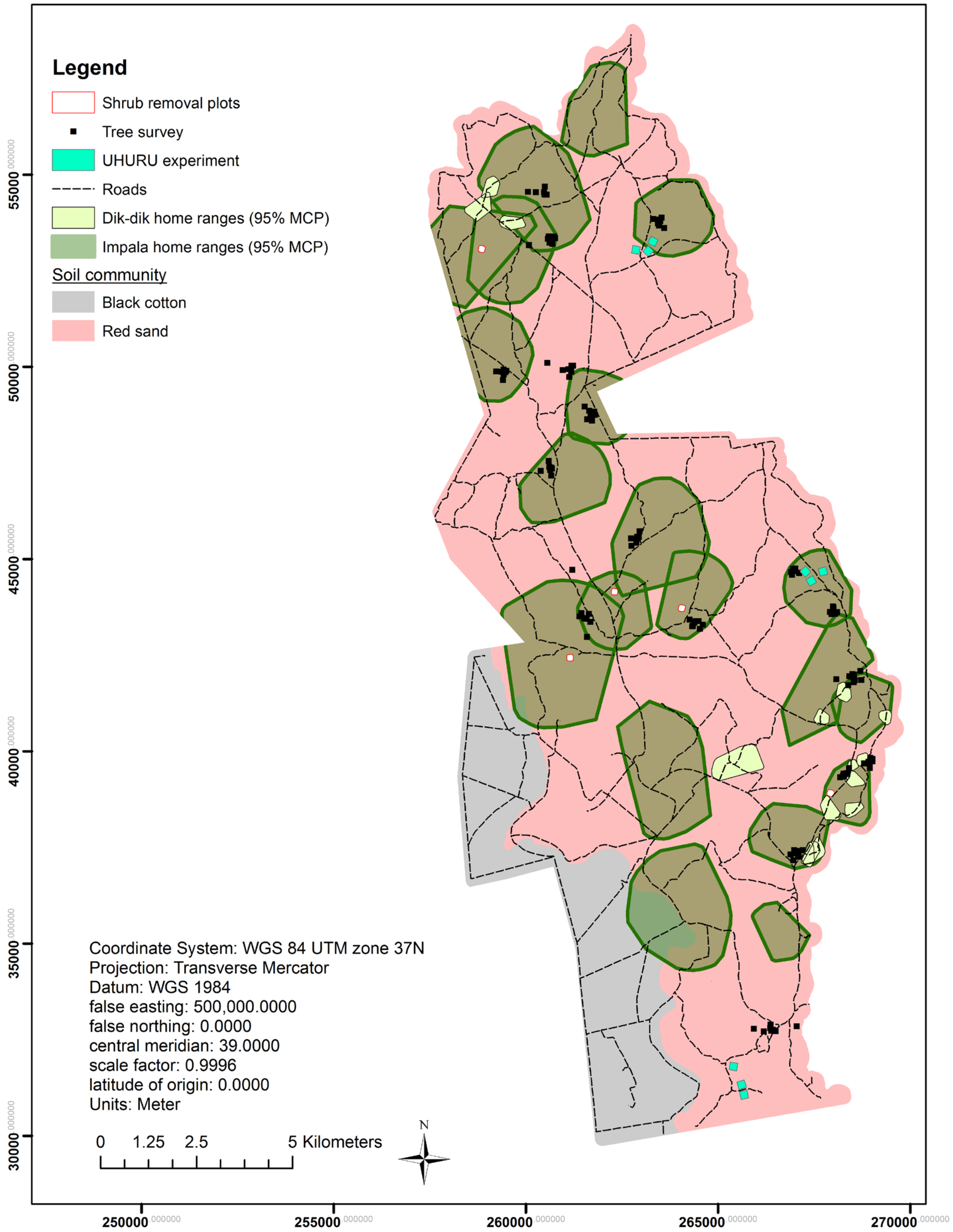


**Figure 1.2 Focal wildlife species in this study, including (a) dik-dik, (b) impala, and (c) wild dogs.**

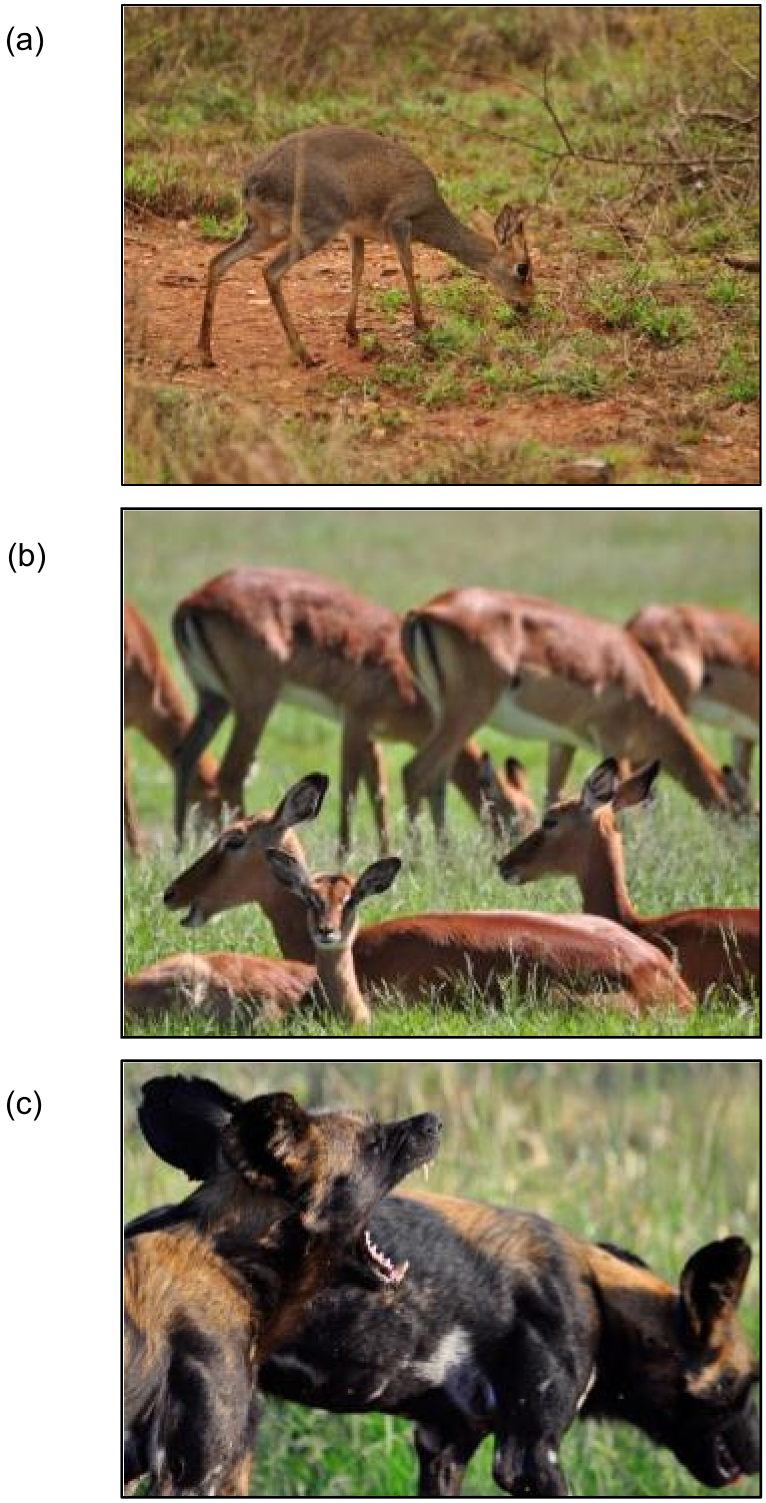
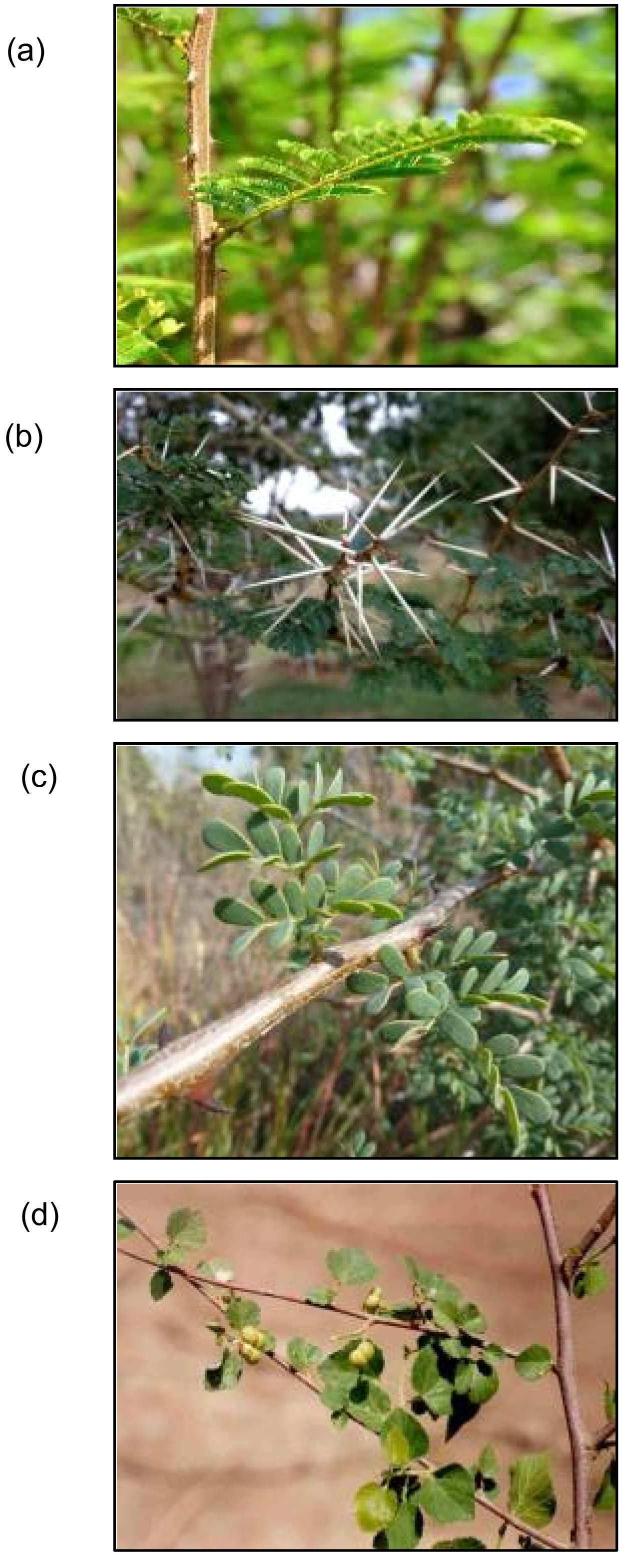


**Figure 1.3 Focal tree species in this study, including (a) *Acacia brevispica*, (b) *A. etbaica* (c) *A. mellifera* and (d) *Grewia* spp.**



# Chapter 2: The landscape of fear for a dwarf antelope, *Madoqua guentheri*: Spatial responses to simulated cues of risk

## 2.1 Introduction

Risk of predation affects the neurobiology (Daskalakis et al. 2013), physiology (Sheriff et al. 2009) and behavior (Lima and Dill 1990) of prey, with consequences for the vital rates of populations and the allocation of biomass through food chains (Schmitz et al. 1997). A key conceptual breakthrough in our understanding of how risk affects ecosystems derives from the 'landscape of fear' [LOF]. The LOF quantifies the spatial avoidance of risk (Laundre et al. 2001), and has been used to understand prey behavior in terrestrial (Brown et al. 2001, Kotler et al. 2002, Brown and Kotler 2004) and marine (Wirsing et al. 2008) systems, and among herbivores (Schmitz 2005, Hodson et al. 2010, Laundre 2010) and carnivores (Cozzi et al. 2012, Broekhuis et al. 2013). Perhaps most intriguingly, the LOF has also been used to understand the cascading effects of risk beyond the focal prey species, including nutrient cycling (Hawlena et al. 2012), material flows (Ripple and Beschta 2012b) and natural disturbance regimes (Eby and Ritchie 2013).

While a LOF has been quantified for a number of taxa, it was originally conceived to explain spatial variation in habitat selection and behavior for mammalian herbivores (elk [*Cervus elaphus*] and bison [*Bos bison*], Laundre et al. 2001) and continues to provide an informative lens through which to understand the ecology of ungulates. For example, the effect of spatial variation in risk on prey behavior has been described for deer (Altendorf et al. 2001, Lingle

2002), caribou (Whittington et al. 2011), guanaco (Marino and Baldi 2008), large (> 40 kg) antelope (Jarman 1974, Underwood 1982, Sinclair and Arcese 1995a, Valeix et al. 2009), elk (Fortin et al. 2005, Middleton et al. 2013a) and moose (Berger 2007, Gervasi et al. 2013). From this body of work, a clear picture is emerging that landscapes of fear are species-specific. For example, sympatric prey species may respond to risk in different ways, even when hunted by the same carnivore (Lingle 2002, Periquet et al. 2012, Gervasi et al. 2013). If the LOF is species-specific, then the functional traits of prey species (e.g., body size, sociality, feeding style) should influence how spatial variation in risk emerges. Indeed, the development of a predictive theory for the role of prey traits in mediating risk-effects is still in its infancy (Creel 2011) and filling this knowledge gap will require field studies covering a broad range of prey traits and species.

Studies quantifying the LOF in ungulates have focused on large (>40 kg), gregarious species that  typically alter their group size in response to risk, avoid risky areas and increase their use of open habitats to facilitate detection of predators (e.g., (Creel and Winnie 2005, Fortin et al. 2005, Proffitt et al. 2009, Anderson et al. 2010, Laundre 2010, Iribarren and Kotler 2012, Kuijper et al. 2013). This emphasis on large species does not represent the diversity of life-history traits among ungulates, of which about 30% have an adult body size < 30 kg (Smith et al. 2003). Gaps in our knowledge regarding the LOF in smaller ungulates are important to address, particularly in light of their abilities to sustain population growth of large carnivores (Hayward et al. 2006, Woodroffe et al. 2007b) and to dramatically change plant communities (Augustine and McNaughton 2004, Goheen et al. 2013).

Because small ungulates tend to be solitary, territorial and cryptic (Brashares et al. 2000, Caro et al. 2004), they may experience a LOF that contrasts with that of larger ungulates. For example, under heightened risk, monogamous species are unlikely to aggregate in groups larger than parents and offspring (Komers 1996a), territorial defense may pre-empt spatial shifts away from risky areas (Brotherton and Rhodes 1996) and crypsis is typically associated with the use of dense cover rather than open habitats (Jarman 1974, Ydenberg and Dill 1986). In addition, smaller species experience higher rates of predation than larger ones (Sinclair et al. 2003, Collins and Kays 2011, Fritz et al. 2011) and this vulnerability to predation is predicted to increase the strength of anti-predator responses (Creel 2011). In spite of the key role that many small ungulates play in ecosystem dynamics, their spatial response to risk is largely unknown.

I report on the spatial responses to risk by a 5 kg, monogamous, browsing, and territorial antelope, the Guenther's dik-dik (*Madoqua guentheri*). I combined high-resolution GPS telemetry (i.e., 10 min relocation intervals) with simulated olfactory cues from both an anthropogenic and natural predator of dik-dik, the African wild dog (*Lycaon pictus*), and then quantified changes in space-use and movement patterns. I confront these data with three hypotheses to explain how dik-dik might respond to simulated risk (Table 2.1). The Displacement Hypothesis argues that prey disperse away from areas with heightened risk. For example, elk (Fortin et al. 2005), deer (Altendorf et al. 2001), moose (White and Berger 2001) and several African ungulates (Thaker et al. 2011) avoid areas where large carnivores hunt. Such risk avoidance may supersede the constraints of territorial defense on movement, similar to some territorial ectothermic (Jones and Paszkowski 1997, Blanchet et al. 2007, Ozel and Stynoski 2011) and avian prey (Dunn et al. 2004). Thus, the Displacement Hypothesis predicts that dik-dik should increase their dispersion when they perceive heightened risk. Conversely, the Fidelity Hypothesis argues that territoriality reinforces spatial memory and knowledge of areas where crypsis is most effective. For instance, risk-avoidance, and not food or mate defense, explained territoriality in migratory robins (*Erithacus rubecula*) (Cuadrado 1997). In addition, many cryptic (but not necessarily territorial) prey also reduce their dispersion under heightened risk (Preisser et al. 2005). Accordingly, the Fidelity Hypothesis predicts that when perceived risk increases, dik-dik should be less dispersive and increase their use of overstory cover. Finally, the Risk Allocation Hypothesis posits that organisms faced with chronic levels of high predation should exhibit limited responses to cues of risk for all but the most immediate of threats (Lima and Bednekoff 1999, Ferrari et al. 2009). Generally, small ungulates persist in a high-risk environment (Sinclair et al. 2003, Fritz et al. 2011) and so may be less responsive to cues of risk than larger ungulates (van der Meer et al. 2012, Kuijper et al. 2014). Consequently, the Risk Allocation Hypothesis predicts that the LOF for dik-dik is not affected by olfactory predator cues.

I further evaluated whether dik-dik movements are affected by predator identity (i.e., humans vs. wild dogs) and diel period (Day: 0630 – 1830; Night: 1830 – 0630). For example, humans can amplify (Proffitt et al. 2009) or attenuate (Cromsigt et al. 2013) anti-predator behavior in ungulates. Risk avoidance behavior in ungulates may change with the heightened activity level of most carnivores at night (Cozzi et al. 2012, Burkepile et al. 2013). Consequently, I included these variables into my analysis to help understand some of the contextual drivers of the dik-dik landscape of fear.

## 2.2 Methods

Adult female dik-dik were captured by MRC technicians during moonless nights between July-August 2010 and August-September 2011 using portable spotlights and long-handled nets, following methods described in (Komers 1996b). Each animal was fitted with a 200 g GPS collar (Savannah Tracking Ltd., Nairobi, Kenya). Handling lasted up to 5 min before the animal was released back into its territory. Individuals were recaptured and collars were removed at the end of this experiment. Handling procedures were approved by the University of Wyoming's Institutional Animal Care Committee and the Kenyan Wildlife Service, and the University of British Columbia, and are in accordance with the American Society of Mammalogists guidelines for handling wildlife. Prior to analysis, I screened and removed GPS relocations that were likely to be inaccurate using an algorithm presented in Bjorneraas *et al*. (2010). This algorithm identifies inaccurate positions when they have an unusually fast step length paired with large turning angles (i.e., spikes).

### 2.2.1 Experimental design

To minimize the potential influence of uncontrolled environmental variation (e.g., rainfall, temperature), I focused on short-term changes to dik-dik behavior. For each individual and treatment combination, I first quantified expected behavior from measurements taken over a 24 h period prior to experimental manipulations, hereafter referred to as the "before" trial period. I then measured deviations from the expected behavior over the following 24 h period (the "after" trial period) under human and wild dog treatments. Each treatment was paired with a sham-control of equal duration to the treatments (Table 2.2).

In the human treatment, I established a grid of scentmarks at the center of each home range using gauze strips (1.3 g each) covered in an equal part mixture of soil and cattle manure. Historically, human use of my field site was associated with nomadic pastoralists who hunted dik-dik for food. Although wildlife hunting has been outlawed here since 2003, illegal snaring of dik-dik is common (Georgiadis et al. 2007a), and dik-dik consistently fled upon approach during my field research suggesting that they maintain at least some fear of people. Thus, both the procedure of applying the scentmarks as well as the presence of a scent cue from cattle can be associated with risk from human predation.

Scentmarks were hung from bushes and grass ca.0.75 cm off the ground in a 5x5 grid spaced at 10 m intervals on the orthogonal (hereafter “scentmark grids”). The area encompassed by scentmark grids is equivalent to 8 ± 1% of the average dik-dik home range in my study area. Scentmark grids were placed within the central feature of each home range using at least 3 days (> 340 locations) of GPS telemetry data per individual. The central feature can be interpreted as the spatial equivalent of a median, and is calculated by identifying the observation that is most central to the distribution of a series of GPS relocations using Geographic Information System (GIS) software (ESRI Inc., Redlands, CA, USA).

For the wild dog treatment, I used the same scentmark grid established for the human treatment, but applied wild dog feces to the gauze strips instead of cattle dung and soil. Wild dogs have occupied MRC since 2002 and about 54% of their diet is comprised of dik-dik

(Woodroffe et al. 2007b, Woodroffe 2011a). Scat was collected from areas where wild dogs rested during the daylight hours. I mixed scats in a solution of 4 parts water and one part scat. Due to a shortage of wild dog scats, I supplemented wild dog scentmarks with a commercial predator odour (Triple Dig-it, Kishel's Quality Animal Scents & Lures, Inc.). I then alternated the wild dog and commercial odour scentmarks within individual dik-dik home ranges.

I created two sham-controls, one each preceding the human and wild dog treatments. During these sham-controls, I measured dik-dik responses over a 48 h period, but without an experimental intervention between the first (i.e., before) and second (i.e., after) 24 h trial period. To control for potential confounds arising from environmental variation (e.g., weather changes), the sham-controls were implemented over the 48 h period preceding application of the scent treatments. Consequently, the 24 h 'after' period of the sham-control was the same as the 24 h 'before' period for the scentmark treatments (Table 2.2). All individuals were exposed to at least one sham-control, and where possible, to both human and wild dog scentmark treatments; however, a few animals were not exposed to the human ($n$ = 1) or wild dog ($n$ = 2) treatments because of battery failure in the GPS collars or mortality.

I did not visit dik-dik home ranges six days prior to or following the establishment of the scentmark grid. I removed scentmarks after six days and did not return to dik-dik home ranges until > 2 weeks had elapsed. At this point, I switched the treatment for the second trial of this experiment. Individuals were randomly assigned to either a human or wild dog treatment at the onset of this study. Because scents were applied to removable markers and hung on vegetation, it is unlikely that there was residual contamination of odours from the first trial on the second trial. To my best knowledge, rainfall and human activity within each home range remained constant over the duration of this experiment.

### 2.2.2 Response variables

I evaluated shifts in the space use and movement pathways of dik-dik in response to human and wild dog treatments and sham-controls (Table 2.1). I quantified three response variables related to space use: dispersion, avoidance of scentmarks, and use of overstory cover. To measure dispersion, I first quantified utilization-distributions (UD) using a Brownian-bridge algorithm (Horne et al. 2007) for each individual and combination of trial period (i.e., 'before' and 'after'), diel period (i.e., day, night), and treatment (i.e., human, wild dog and sham-controls). I then used a UD-overlap algorithm (Fieberg and Kochanny 2005) to calculate the volume of the UD from the before period (i.e., expected dispersion) that intersected with the after period. UD-overlap is largest when dik-dik use the same areas of their territory with the same intensity during the before and after trial periods. Thus, dispersion is defined as 1 – UD-overlap. To measure avoidance of scentmarks, I classified each GPS relocation from the before and after trial periods with a binary variable indicating that the relocation was inside or outside of the scentmark grid. To measure use of overstory cover, I first developed a cover map derived from a high-resolution (ca. 60 $\text{cm}^2$) Quickbird image taken in November 2009. Dik-dik are sensitive to changes in overstory cover (Boshe 1984) and overstory cover facilitates crypsis (Underwood 1982). Overstory cover was thus defined as a binary variable and I determined whether each GPS relocation did or did not overlap with overstory pixels using GIS software.

I measured two properties of dik-dik movement pathways: clustered movement and total distance travelled. To evaluate clustered movement, I first classified sections of dik-dik movement pathways into cluster or inter-cluster movements using a modified version of an algorithm described in Knopff et al. (2010). I defined a cluster as ≥ 3 GPS relocations occurring within 10 m and in less than 60 min from one another. Relocations can be added to a cluster if they are < 10 m away from another GPS relocation already included in the cluster and were recorded < 60 min from any of the GPS relocations already included in the cluster. Sections of pathways with slow and tortuous movement are more likely to be classified as a cluster movement than an inter-cluster movement; thus, a greater propensity for clustered movement indicates greater heterogeneity in dik-dik movement pathways. Conversely, less clustered or homogenous movement pathways characterize dispersive movements (Fryxell et al. 2008). Finally, I calculated the total distance travelled as the sum of all step-lengths (i.e., the sum of the distance between sequential GPS relocations).

### 2.2.3 Statistical analysis

For the human and wild dog treatments, and their respective sham-controls, I compared the response of dik-dik during the 'before' trial period to their response during 'after' trial period. I further divided these data by diel period because dik-dik are less active during the night (Manser and Brotherton 1995), while carnivores are typically more active (Cozzi et al. 2012); these shifting contexts can amplify or buffer treatment effects (Orrock et al. 2004, Luttbeg and Trussell 2013). I used a paired Wilcoxon-signed ranks test to compare dispersion during the human and wild dog treatments with their respective sham-control. I used generalized linear mixed-effects models to analyze (i) avoidance of scentmarks, (ii) use of overstory cover and (iii) clustered movement, with a random effect for individual dik-dik and an auto-regressive correlation term to account for non-independence of residuals over sequential observations made on the same individual (Zuur et al. 2009). The trial period (i.e., before vs. after) was the fixed effect term and separate models were generated for each diel period and treatment. To analyze the total distance traveled, I used non-parametric paired *t*-tests (Wilcoxon signed ranks test) comparing the trial period, with individual dik-dik as the replicate and separate analyses performed for each diel period, treatment and sham-control. All statistical analyses were performed in *R* (R Core Team 2013).

## 2.3 Results

GPS collars were fit on 15 individuals throughout the course of this study: 7 individuals during July 2010 and 8 individuals during August of 2011, which coincided with the dry season for both years. The screening algorithm excluded 16 % ± 3 (mean ± SE) of all GPS relocations per individual due to GPS relocation error. This yielded 61 ± 2.7 GPS relocations per individual for each combination of trial period (before, after), treatment (human, wild dog and sham-controls) and diel period (day, night).

Responses to the wild dog treatment were generally stronger than responses to either human-only or sham-control treatments, but diel period mediated the strength of these responses (Table 2.3). Compared to sham-controls, dispersion decreased by similar magnitudes (ca. 7%) during both the human and wild dog treatments during the day, but significantly so only for the wild dog treatment (Figure 2.1, Wilcoxon signed rank test, $V = 21$, $n = 14$ , $P = 0.049$). This result indicates that movements were more concentrated under heightened risk, at least during the day. Pooled among treatments, about 28 % ± 5 and 39 % ± 6 of dik-dik GPS relocations were located within the scentmark grid during the day and night, respectively. The probability of dik-dik avoiding scentmark grids was significantly greater during the human treatment for the day ($\beta = 0.689$, $n = 13$, $P = 0.003$) and marginally significant at night ($\beta = 0.545$, $n = 13$, $P = 0.054$). Similarly, avoidance of scentmark grids during the wild dog treatment increased for both the day ($\beta = 0.498$, $n = 14$, $P = 0.031$) and night ($\beta = 0.982$, $n = 14$, $P < 0.001$). However, use - rather than avoidance - of scentmark grids increased significantly more than expected from the sham-control preceding the wild dog treatment during the day ($\beta = -0.824$, $n = 14$, $P = 0.004$), but did not change significantly for other sham-controls or diel periods.

Pooled across all treatments, dik-dik use of overstory was similar during the day (18 % ± 1) and night (20 % ± 1). Use of overstory cover decreased significantly more than expected during the night for the wild dog treatment ($\beta = -0.351$, $n = 14$, $P = 0.012$), but not for the human treatment or sham-controls. Pooled across all treatments, clustered movement was reduced during the day (38 % ± 3) compared to the night (61 % ± 3). During the human treatment, the probability of clustered movement increased significantly more than expected during the day ($\beta = 0.897$, $n = 13$, $P < 0.001$) but not during the night (Table 2.3). Conversely, during the wild dog treatment, the probability of clustered movement decreased significantly more than expected during the day ($\beta = -0.489$, $n = 14$, $P = 0.028$) but not during the night. There was no change in propensity for clustered movement during the sham-controls. The total distance moved was generally higher during the day (8035 m ± 566) than night (5602 m ± 302), but not significantly different from expected during any treatment or sham-control (Table 2.3).

## 2.4 Discussion

In support of the Fidelity Hypothesis, dik-dik dispersion was reduced following exposure to a simulated cue of risk, though this effect was minor (i.e., a change of ca. 7 %); however, in support of the Displacement Hypothesis, dik-dik also avoided scentmarks. Counter to all three hypotheses was the decreased use of overstory cover and in support of the Risk Allocation Hypothesis, treatments did not change the total distance travelled. Indicative of predator-discrimination, responses to the wild dog treatment differed from the human treatment; however, these responses also varied by diel period, suggesting that the perceptions of risk are mediated by environmental context. While cues of risk changed dik-dik behavior (i.e., use of overstory decreased) and movement patterns (i.e., clustered movement decreased), risk did not lead dik-dik to increase their use of neighboring territories. Together, my results provide novel insight on how a small, monogamous and territorial ungulate perceives the landscape of fear in ways not entirely predicted by my original hypotheses.

Given the vagility of African wild dogs relative to the territory size of dik-dik, I anticipated that dik-dik would associate scentmarks with risk across an expansive area, rather than simply the scentmark grid itself. For example, wild dogs typically capture larger prey (e.g., impala) within a chase distance of 0.5 - 1.1 km (Creel and Creel 2002) - likely much farther than the chase distances needed to capture dik-dik and greater than the median home range diameter of dik-dik in this study (ca. 330 m, assuming a circular area). Moreover, wild dogs are coursing predators, such that an olfactory cue of their presence should not be indicative of their precise location to dik-dik. Consequently, an individual dik-dik may ‘encounter’ a wild dog – i.e., face an imminent threat - when the wild dog occurs anywhere in its territory (Stankowich and Blumstein 2005). Thus, the lack of dispersion under a perceived increase in risk likely equates to no reduction in the probability of encountering wild dogs, suggesting that encounters may not be the main driver of anti-predator behavior in dik-dik.

At least two explanations point to why dik-dik avoided scentmarks and but did not increase their dispersion under a simulated increase in risk. First, dik-dik may have attempted to move into a neighbouring territory, but defense by neighbours and herding by their mate may have impeded such dispersion. Consequently, dik-dik movements may reflect a tension between avoiding the source of risk (i.e., the scentmark grid) and being repelled by territoriality. Under this scenario, the Displacement Hypothesis may be more applicable in situations when territorial constraints on movement are weaker. For example, extra-territorial movements have been observed when overstory cover (Boshe 1984) or a mate (Komers 1996a) were removed from dik-dik territories. This suggests that, as cover changes or populations of conspecifics fluctuate, dispersion away from risk may become more likely. Territoriality has broad and largely unexplored implications for spatial responses to risk in dik-dik specifically and among other mammals generally (Dunbar and Dunbar 1980, Caro et al. 2004).

A second possibility is that the scentmarks triggered a conditioned response of neophobia in dik-dik. Laboratory experiments conducted on fish and amphibians indicate that cues of risk degrade the exploratory behavior (Brown et al. 2013), memory (Diamond et al. 1999) and novel object recognition (Zoladz et al. 2008) of prey. Additionally, ambient levels of heightened risk – as experienced by many small ungulates (Sinclair et al. 2003, Fritz et al. 2011) - can invoke a stronger neophobic response than lower levels of background risk (Brown et al. 2014). Indeed, dik-dik in this study area co-exist with one of the most abundant and diverse assemblages of terrestrial carnivores faced by any ungulate – there are over 30 individuals of large (> 20 kg ) carnivores from > 8 species per 100 km$^2$ (Georgiadis et al. 2007a, O'Brien and Kinnaird 2011, Woodroffe 2011a), and this estimate does not include the many jackals, baboons and raptors that also prey upon dik-dik in this study area. Thus, rather than a strategy to avoid predators *per se*, constrained dispersion and avoidance of scentmarks following exposure to a risk cue could be a conditioned response to chronic fear, reducing the exploration of novel objects (i.e., the scentmarks) and space (i.e., areas outside of the home range).

Whether dispersion under heightened risk was constrained by neighbours, mates or fear itself, I found a significant reduction in dispersion only during the day and for the wild dog treatment. This diel change in dispersion coincides with an overall 30% decrease in distance moved during the night. Because dik-dik moved less at night than during the day, metrics of risk-avoidance behavior based on patterns of movement are likely to be less sensitive at night. In studies comparing activity amongst different-sized ungulates, smaller species were found to be less sensitive to fluxes in temperature than larger species (du Toit and Yetman 2005), likely because smaller species spend a greater proportion of their time ‘resting’

(Underwood 1982). For dik-dik, the normal patterns of diel activity (i.e., less movement at night) may facilitate risk-avoidance behavior like vigilance or crypsis, without sacrificing time allocated to foraging. As such, the ‘foraging vs. risk avoidance’ trade-off that characterizes much of foraging theory in larger ungulates (Brown and Kotler 2007) may not explain the behavior of small ungulates like dik-dik at night.

Although dik-dik and other small antelope often use crypsis as a strategy to reduce exposure to risk (Jarman 1974, Brashares et al. 2000, Caro et al. 2004), quantifying how this strategy manifests in the space use or movement patterns of individuals is not clear. Crypsis is enhanced by a reduction in movement and increased use of cover to minimize detection by actively hunting predators (Sih 1992, Luttbeg and Trussell 2013). However, I detected no apparent shifts in total distance moved or the use of habitats that facilitate crypsis (i.e., overstory cover) during the wild dog or human scentmark treatment. Instead, dik-dik actually decreased their use of overstory cover during the wild dog treatment, especially at night. This pattern may be explained by dik-dik attempting to increase their visual detection of predators. Though often described as ‘hiders’ (Jarman 1974, Brashares et al. 2000), dik-dik and other small ungulates are known to increase levels of vigilance in response to heightened risk (Dunbar and Dunbar 1980, Coleman et al. 2008, Lea et al. 2008). Using open habitats to facilitate predator detection is not typically associated with cryptic species and suggests that vigilance and crypsis are not mutually exclusive. Indeed, the canonical ‘flee’ vs. ‘hide’ dichotomy of anti-predator behavior in African antelope (Jarman 1974) may be more accurately viewed as a tactical response to avoid capture by an attacking predator rather than as longer-term strategy to reduce the probability of a predator encounter.

Dik-dik responded differently to human and wild dog treatments, particularly with respect to clustered movement. Dik-dik movement pathways were significantly more directed (i.e., less clustered) in wild dog treatments and significantly more variable (i.e., more clustered) in human treatments. The anti-predator benefits of clustered movement may be explained by heightened vigilance or scanning, interspersed with rapid movement between patches of perceived safety (Eccard and Liesenjohann 2008, Ilany and Eilam 2008). Based on the way dik-dik dispersion and use of overstory changed during the wild dog treatment, I also expected to observe an increase in clustered movement under the wild dog treatment, rather than a decrease. While the anti-predator benefits of the more directed movement patterns observed during the wild dog treatment are not clear, it is interesting to note that this response differed from the human treatment. Studies using audio playbacks have shown that dik-dik discriminate predator identity (Coleman et al. 2008, Lea et al. 2008) and anecdotal observations suggest their responses to felid predators differs from their response to canids (Estes 1991). With a diverse assemblage of body sizes, vagilities, and habitat preferences among the carnivores in this study area, there is likely a strong selective pressure for dik-dik to optimize their anti-predator response through predator recognition.

My results highlight how the landscape of fear shapes the movement patterns and behavior of a diminutive antelope. The landscape of fear has been used to conceptualize the way organisms respond to spatial variation in risk in two, non-exclusive ways (Brown et al. 1999, Brown et al. 2001, Laundre et al. 2001). First,  prey modify their behavior while travelling through risky areas, such as increasing their group size or levels of vigilance (Fortin et al.

2005). Second, prey avoid risky areas or otherwise reduce the time spent in them by travelling faster (Lima and Dill 1990). Whether and how these two responses emerge may depend on the traits – such as body size and social organization - of both predator and prey (Creel 2011, Preisser and Orrock 2012). Thus, it is important to consider conducting field research on organisms representative of a wide range of traits hypothesized to affect perceptions of risk.

**Figure 2.1 The effects of simulated cues of risk on dispersion of Gunther's dik-dik over a 24 h period, shown for (a) 15 individuals in 2010 (*n* = 7) and 2011 (*n* = 8). Each bar represents the response over a 24 h period, with increasing dispersion indicative of more wide-ranging movements compared to the preceding 12 h period. I compared dispersion for both a human and wild dog treatment, with dispersion over a random 24 h period (sham-control) using a Wilcoxon signed rank test. Asterisk indicates a significant difference in dispersion (*V* = 21, *n* = 14, *P* = 0.05). To illustrate how risk changes dispersion, (b) shows the utilization distribution of a single dik-dik during the day, before (left column) and after (right column) the wild dog treatment and sham-control. Darker areas indicate greater utilization by this individual and the hashed area shows the location of the scentmark grid. Dispersion for this individual during the wild dog treatment was 0.42 and 0.68 for the sham-control.**

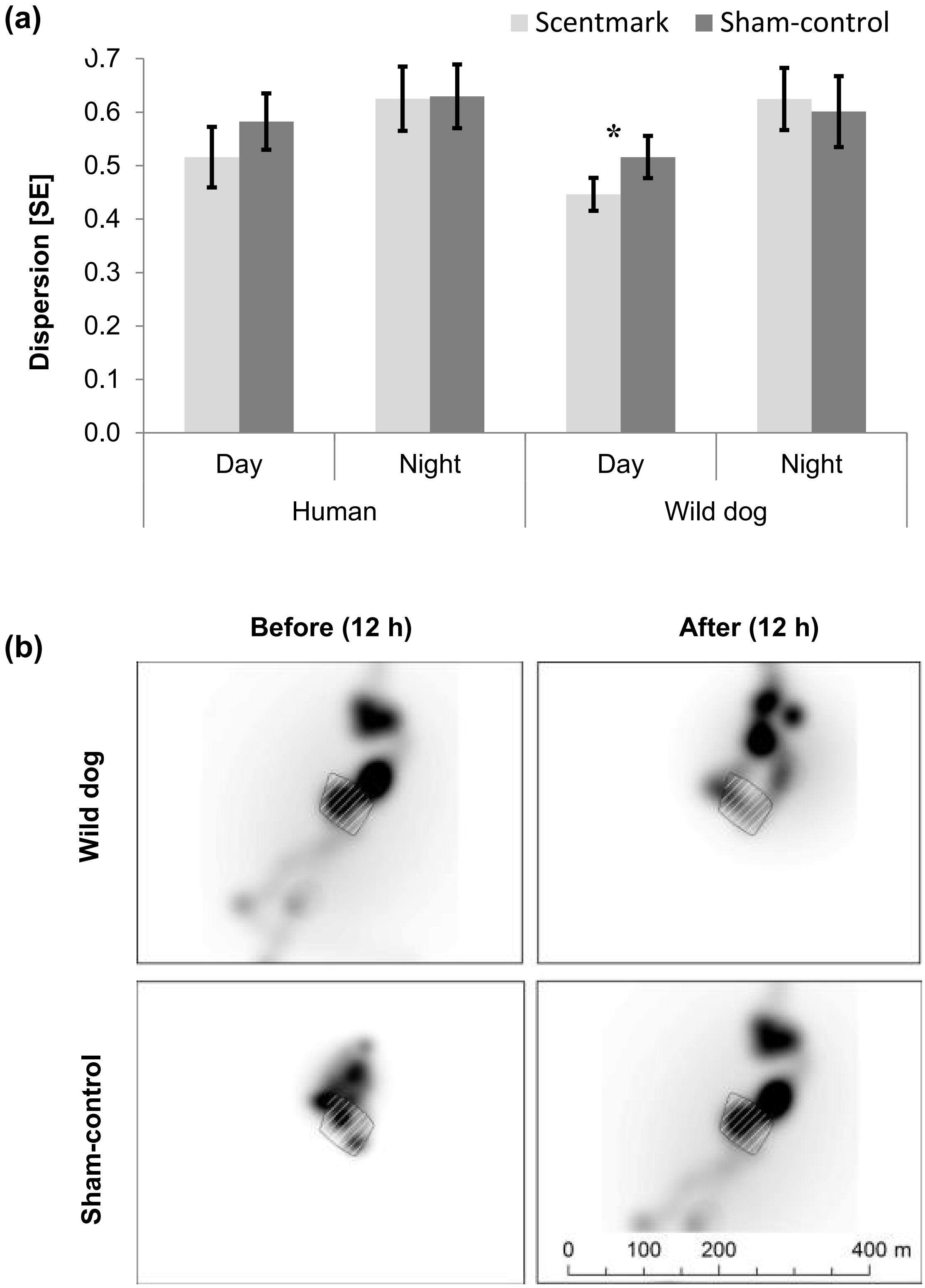

(a)
Scentmark
Sham-control
Dispersion [SE]
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
*
Day
Night
Day
Night
Human
Wild dog
(b)
Before (12 h)
After (12 h)
Wild dog
Sham-control
0
100
200
400 m

**Table 2.1 Prediction matrix for the response of Guenther's dik-dik (*Madoqua guentheri*) to a perceived increase in risk of predation.**

| Hypothesis | Response variables | | | | |
|---|---|---|---|---|---|
| | Space-use | | | Movement patterns | |
| | Dispersion | Scentmark avoidance | Use of overstory | Clustered movements | Total distance travelled |
| Displacement | + | + | 0 | - | + |
| Fidelity | - | 0 | + | + | - |
| Risk allocation | 0 | 0 | 0 | 0 | 0 |
| Statistical test used | Paired Wilcoxon-signed ranks test | GLMM | GLMM | GLMM | Paired t-test |

NOTE: [+] indicates the response variable increases with risk, [-] indicates the response variable decreases with risk, and [0] indicates that the hypothesis does not predict a change for that response variable with heightened risk. GLMM refers to a generalized linear mixed-model.

**Table 2.2 Schedule of research activity and experimental measurements, 2010 and 2011.**

| | | | Trial 1 | | | | | | Trial 2 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Timeline | Start | >6 weeks | -48 h to -24 h | -24 h to 0 h | 0 h | 0 h to 24 h | 6 days | 2 weeks | -48 h to -24 h | -24 h to 0 h | 0 h | 0 h to 24 h | 6 days |
| Research activity | Capture and fitting with GPS collars | Acclimatization of dik-dik to GPS collar | | | Establish first scentmark grid, either human or wild dog* | | Remove first scentmark grid | | | | Establish second scentmark grid, either human or wild dog* | | Remove second scentmark grid |
| Sham-control treatment* | | | Before | After | | | | | Before | After | | | |
| Scentmark treatment * | | | | Before | | After | | | | Before | | After | |

* Order of human or wild dog scentmarks was randomized among individuals.

**Table 2.3 Effects of simulated predator cues on the space use and movement patterns of dik-dik.**

**Bold lettering indicates significant effects at *P* < 0.05.**

| | | | Response variable | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Avoidance of scentmarks | | Use of overstory | | Clustered movements | | Total distance travelled | |
| Trial | Scentmark | Diel period | *β*<br>*(SE)* (1) | *P* | *β*<br>*(SE)* (1) | *P* | *β*<br>*(SE)* (1) | *P* | *V* (2) | *P* |
| African wild dog | Treatment | Day | **0.498**<br>**(0.231)** | **0.031** | -0.030<br>(0.131) | 0.821 | **-0.489**<br>**(0.223)** | **0.029** | 37 | 0.356 |
| | | Night | **0.982**<br>**(0.265)** | **<0.001** | **-0.351**<br>**(0.139)** | **0.011** | -0.001<br>(0.320) | 0.997 | 28 | 0.136 |
| | Sham control | Day | 0.278<br>(0.226) | 0.220 | 0.217<br>(0.132) | 0.102 | -0.107<br>(0.221) | 0.629 | 49 | 0.856 |
| | | Night | **-0.824**<br>**(0.284)** | **0.004** | -0.098<br>(0.129) | 0.445 | -0.161<br>(0.321) | 0.616 | 65 | 0.426 |
| Human | Treatment | Day | **0.689**<br>**(0.234)** | **0.003** | -0.026<br>(0.143) | 0.858 | **0.897**<br>**(0.244)** | **<0.001** | 36 | 0.542 |
| | | Night | 0.545<br>(0.284) | 0.055 | 0.037<br>(0.129) | 0.775 | -0.394<br>(0.337) | 0.242 | 31 | 0.340 |
| | Sham control | Day | -0.233<br>(0.232) | 0.314 | -0.034<br>(0.144) | 0.813 | -0.067<br>(0.229) | 0.768 | 49 | 0.839 |
| | | Night | -0.243<br>(0.259) | 0.349 | 0.014<br>(0.131) | 0.917 | -0.099<br>(0.335) | 0.768 | 38 | 0.636 |

(1) Beta estimates, standard errors and *P*-values are estimated from a mixed-effects logistic regression.

(2) Test-statistic for a paired Wilcoxon-signed ranks test.

# Chapter 3: Large carnivores make savanna tree communities less thorny

## 3.1 Introduction

Few ideas in ecology have been more influential than the Green World Hypothesis (Hairston et al. 1960), which posited that carnivores indirectly benefit plants by suppressing herbivores in what researchers now describe as a 'trophic cascade' (Estes et al. 2011). After more than five decades of testing this hypothesis, alternative explanations have emerged for the manner in which carnivores, herbivores and plants interact to shape a 'green world'. On the one hand, carnivores can both reduce herbivore density and trigger risk-avoidance behaviors that change where and how much plant biomass is consumed (Preisser et al. 2005, Schmitz 2008). On the other hand, plants are not passive victims in the outcome of trophic cascades (Estes and Steinberg 1988, Leibold 1989, Schmitz 1994, Mooney et al. 2010), as many species employ mechanical and chemical defenses that impede herbivory (Coley et al. 1985). Because both predation risk and plant defenses constrain the behavior of herbivores, the ability of plants to thrive in areas that are risky could be functionally equivalent to defenses that reduce herbivory.

To understand how carnivores indirectly influence plant communities, I evaluated the effects of risk-avoidance behavior by impala (*Aepyceros melampus*; a common and widespread ungulate) and plant defenses in mediating a trophic cascade in an African savanna. Impala consume a mixture of grasses and browse (trees) (Augustine 2010) and are preyed upon by several species of large carnivores, particularly wild dogs (*Lycaon pictus*) and leopards (*Panthera pardus*). Habitat visibility is considered to be a major factor in shaping the perceptions of risk from these predators for impala (Pays et al. 2012, Periquet et al. 2012, van der Meer et al. 2012, Burkepile et al. 2013). I combined observations on habitat selection by impala, the spatial distribution of risk and a large-scale manipulation to test the hypothesis that herbivores select habitat to reduce predation risk. I then used feeding trials and an herbivore-exclusion experiment to establish the effect of impala diet preferences on the tree community. Finally, I tested how the proportion of poorly- and well-defended species in the tree community changed with risk of predation to impala across a 200 km$^2$ savanna.

## 3.2 Materials and methods

MRC contains herds of domesticated cattle (*Bos indicus*), camels (*Camelus dromedaries*) and goats (*Capra aegagrus*), which are managed using traditional Masai herding practices in which livestock are secured in a ‘boma’ or corral at night to exclude predators and contain the herd. Traditionally, bomas were constructed from felled trees (*Acacia* sp.), occupied for several months at a time, and were ≥ 1 ha (Augustine 2003). Over the last 10 years, smaller, portable bomas constructed from chain-link have been used at MRC (Porensky 2011). In both cases, manure deposition inside bomas results in elevated nutrient concentrations within both the soil and the mat-forming grasses which colonize these areas during the wet season (Young et al. 1995, Augustine 2004). The elevated nutrient levels in soils and vegetation can persist for decades after the livestock herds have abandoned these sites (Augustine 2003). After colonization by grasses, these former livestock corrals are known as ‘glades’, one of the focal habitat features in this study. I also focused on riparian areas, characterized by dense vegetation 3-100 m wide alongside channels that are (i) normally dry (and were for the duration of this study); (ii) have a sandy substrate; and (iii) can vary in depth from ≤ 0.5 m to 2.0 m.

I focused on the causes and consequences of habitat selection by impala (*Aepyceros melampus*), the second-most abundant species of wild ungulate at MRC. Impala number 20.3 (CV = 17.6) individuals per km$^2$ with a biomass density of 813 kg per km$^2$; only dik-dik (*Madoqua guentheri*) are more numerous (139 individuals per km$^2$, CV = 5.6) and only elephants (*Loxodonta africana*) have greater biomass density (2882 kg per km$^2$; CV = 36.1) (Augustine 2010). These estimates of abundance and biomass do not consider the duration of residency on MRC – both impala and dik-dik have stable, non-overlapping home ranges that are each <1% the size of MRC, whereas elephants occur in the study area only occasionally and have home ranges 769% larger than MRC (Graham et al. 2009). The biomass density of impala is 383% greater than the combined biomass density of other browsing species in its size class (40 kg – 900 kg (Augustine 2010)). Large ( >20 kg) carnivores are common in this area, and include leopard (*Panthera pardus*), African wild dog (*Lycaon pictus*), lions (*P. leo*), spotted hyena (*Crocuta crocuta*) and striped hyena (*Hyaena hyaena*), which occur at a combined density of about 35 individuals per 100 km$^2$ (O'Brien and Kinnaird 2011, Woodroffe 2011a). Most predation of impala at MRC is due to leopards and wild dogs (Figure 3.1).

### 3.2.1 Impala habitat use and selection

I used GPS telemetry and high-resolution (0.36 m$^2$) satellite imagery to quantify habitat selection. I was particularly interested in selection for woody cover, which provides dry-season forage (Augustine 2010), but could simultaneously shape the perception of risk by reducing visibility (Underwood 1982, Matson et al. 2005, Thaker et al. 2011, Pays et al. 2012). Specifically, I focused on how impala utilized two habitat features that represent a wide range of woody cover: (i) ‘glades’, which are ~0.5-ha clearings (woody cover = 8% ± 0.1 [mean ± SE]) derived from abandoned cattle corrals and covered with nutrient-rich grasses (Young et al. 1995, Augustine 2004); and (ii) riparian areas, which are < 100 m - wide strips of dense vegetation (woody cover = 25% ± 1.4) along the edges of dry channels. I then measured how two components of risk changed with increasing woody cover: (i) the *per capita* or individual risk of mortality from predation (Kauffman et al. 2007, Creel 2011), measured as the spatial distribution of kill sites relative to impala abundance; and (ii) the relative probability of encounters with a frequent predator of impala, the African wild dog (Creel and Creel 1995, Woodroffe et al. 2007b), measured with GPS telemetry and resource selection functions.

### 3.2.2 GPS telemetry

In May and June 2011, twenty adult female impala were captured using drive nets (Kenya Wildlife Service) or net guns deployed from a helicopter (Frontier Helicopters, Whakatane, New Zealand) and fitted with GPS collars (Savannah Tracking, Nairobi, Kenya). Handling procedures were approved by the University of Wyoming's Institutional Animal Care Committee, UBC and the Kenya Wildlife Service, and are in accordance with the guidelines established by American Society of Mammalogists (Sikes et al. 2011). Impala home range size averaged (mean ± SE) 393 ha ± 47, which encompassed an average of 7.7 ± 0.8 glades and 37 ha ± 6 of riparian area.

For the duration of this study, changes in home-range size and overlap between herds was minimal, and visual surveys conducted monthly confirmed that each collared individual was representative of movements of roughly 20-60 individuals per herd. These herds were distributed across the Mpala Research Center. The amount of data collected from each GPS collar depended on the timing of mortality events ($n = 3$) or variation in battery power, such that monitoring periods ranged from 46 to 464 days (258 ± 29 days), corresponding to 15278 ± 1794 (range: 3800 - 28000) GPS relocations per animal. GPS collars were programmed to record a location every 20 minutes and positions were screened for inaccuracy prior to analysis using an algorithm presented in Bjorneraas et al. (2010).

### 3.2.3 Mapping glades, riparian areas, and woody cover

I used a Quickbird satellite image (Digital Globe, Longmont, CO, USA), taken in May 2011, with a resolution of 60 cm to create a map of habitat features at MRC. I digitized glades and riparian areas manually and used automatic procedures available in geographic information system software to classify overstory cover (ArcMap v10.1, ESRI, Redlands, CA, USA). Glades and riparian areas are discrete, conspicuous features across the landscape, whereas woody cover is a continuous variable that can be estimated at different spatial scales. For clarity, I collectively refer to glades, riparian areas, and woody cover as "habitat features". Ultimately, based on model selection methods, I transformed overstory cover to a proportional coverage over a circular area with a radius of 40 m, which I refer to as 'woody cover' (see Table 3.1).

### 3.2.4 Habitat use

I used GPS telemetry to evaluate shifts in habitat use over seasons and diel periods. Wet seasons were defined as those with > 50 mm rainfall over the preceding 4 weeks; dry seasons were defined as those with $\leq$ 50 mm rainfall over the preceding 4 weeks. Diel periods were defined as day (0630-1830) and night (1830-630), which were fixed for the duration of this study. To maximize the resolution of habitat use by impala, I calculated the proportion of relocations within each habitat feature using the original 20 minute GPS relocation intervals. I summarized the proportion of individual GPS relocations located within glades and riparian areas and over a classified range of woody cover. Using individual impala as the unit of replication, I employed paired *t*-tests to test the null hypothesis that habitat use was equal between diel periods and seasons.

### 3.2.5 Habitat selection

I used GPS telemetry to evaluate habitat selection for glades, riparian areas, and woody cover. I employed a use-availability design to measure resource selection functions (RSF) for these habitat features (Manly et al. 2002). RSFs address the amount of use relative to the availability of a habitat feature and more directly measure how impala perceive the value of habitat, whereas habitat use is a better measure of the impact impala have in an area.

The area of availability was defined separately for each individual impala as the 95% minimum convex polygon of observed locations (hereafter, “home range”). In analyzing habitat selection, I only used GPS relocations that were $\geq$ 4 h apart to avoid serial autocorrelation, which I confirmed using partial-autocorrelation functions (Zuur et al. 2009, Fieberg et al. 2010). I generated random points equal to the number of observed relocations within each home range, then measured woody cover at each observed and random location (hereafter, “sample points”). Sample points falling within 50 m of a glade or riparian area were considered to occur within that habitat feature. I chose a distance of 50 m to match lengths of transects and plots used in the visibility and tree abundance surveys (see below).

The satellite image classification depicted overstory cover as a binary variable for each 0.36 $m^2$

pixel. Although I expected habitat selection of impala to manifest over areas larger than this, I had no prior expectation for the spatial scale at which impala are most sensitive to variation in cover. Consequently, I defined woody cover as the proportion of 0.36 $m^2$ pixels classified as overstory over a circular area. I then represented woody cover over circular areas with radii of 10, 20, 40, and 80 m, measured impala RSFs for each radius and used Akaike's Information Criterion corrected for sample size (AICc) to discern the model with the best-fitting radius (Table 3.1). Thus, throughout the main text and hereafter, I refer to woody cover as the proportion of a 5027 $m^2$ circular area (i.e., one with a radius of 40 m) occupied by 0.36 $m^2$ pixels classified as overstory.

I used a generalized linear mixed model to estimate RSF coefficients, in which a positive value indicates selection for, and a negative value indicates avoidance of, a habitat feature. I included a random effect for individual in the model and report on the marginal (population-level) coefficients for each habitat feature. I created separate models to calculate RSF coefficients for each habitat feature, diel period and season. I used the R-package lme4 to analyse these data (R Development Core Team 2013).

### 3.2.6 Quantifying risk of predation: visibility

I generated 30 random points across the study area. At each point, I located the nearest glade or riparian area that also occurred within the home range of a collared impala. From each point (i.e., 'location'), I established five 50 m-long transects along which I quantified visibility. For transects located in glades, transects were established at glade edges (Porensky 2011) and extended away from the center of the glade such that transects did not cross one another. For riparian areas, I alternated the side of the water channel on which transects were established, and oriented transects perpendicularly to the channel. Transects associated with riparian areas were separated by 50 m. Using a laser rangefinder every 10 m along each transect, I recorded the distance to nearest obstruction in each cardinal direction at 1.4 m from the ground (i.e., the average height of a female impala) for a total of 24 distances. I quantified visibility as the mean of these 24 distance measurements for each transect.

I assessed habitat visibility for 44 transects near 11 glades, and for 64 transects in 13 riparian areas. I predicted visibility across the landscape as function of woody cover by regressing transect visibility against the satellite-derived estimate of woody cover for the transect midpoint using a linear mixed effects model, with location as a random effect. Predictably, visibility decreased with woody cover (visibility (m) = 36.18 – 69.92 * woody cover; $R^2 = 0.415$; $n = 108$; $P < 0.001$), and was higher in glades (31.0 m ± 2.3) than in riparian areas (17.7 m ± 1.3).

### 3.2.7 Quantifying risk of predation: probability of encountering African wild dogs

Using existing data from a long-term study in central Kenya, I quantified the probability of habitat selection by wild dogs to estimate encounter rates of impala with one their main predators (Hebblewhite et al. 2005a, Kauffman et al. 2007). Wild dogs have occurred at MRC since 2003 (Woodroffe 2011a) and during the course of this study, a single pack (ca. 15 individuals) resided on MRC from 14 September 2011 to 22 January 2012, or about 88% of the days that I monitored impala movements. GPS relocations were collected from a single individual at 30 min intervals during the morning (0600-0800) and evening (1600-2000) hunting periods (Woodroffe 2011b). Analysis of habitat selection (RSF) followed those described above for impala, with area of availability constrained to the portion of MRC encompassed by the home range (i.e., 95% minimum convex polygon) of this pack. Relocations within 500 m of the pack's den were removed from the analysis because these observations are not independent and violate the assumptions of RSF methodologies (Fieberg et al. 2010), resulting in a total of 638 observed GPS relocations. Wild dogs have an average home range that is twice the size of MRC and an average daily movement range of 5.6 km (Woodroffe 2011b). As a result of these high levels of vagility relative to the temporal resolution of the telemetry data, wild dogs were rarely detected within 50 m of a glade or riparian area. Consequently, I used wild dog's RSF coefficient for woody cover ($\beta = 7.57$, SE = 0.64, $P < 0.001$) in estimating the relative probability that impala will encounter wild dogs, given that they were present.

### 3.2.8 Quantifying risk of predation: per capita risk of mortality

Between July 2011 and July 2012, security personnel used handheld GPS units to record the locations of sites where any impala were killed (hereafter "kill-sites"). MRC contains over 300 km of roads that are patrolled daily by security personnel. Kill-sites were located from foot or vehicle by visually identifying a prey carcass or from following predator tracks where they intersected a road. I recorded the locations of 54 kill sites, which were located 112 m ± 14 from the nearest road. Predator identity was assigned based on evidence at the kill location, including tracks, bite marks and fur-removal (Figure 3.1).

The number and distribution of kill sites is constrained by the abundance of prey (Creel and Creel 1995, Hebblewhite et al. 2005a, Kauffman et al. 2007, Creel 2011). Consequently, I was most interested in the relative risk associated with varying levels of woody cover after accounting for differences in the distribution of impala across the landscape, which I refer to as the *per capita* risk of mortality from predation ($r$). To quantify $r$, I first partitioned woody cover values into 8 classes (0.000 – 0.005; 0.005 – 0.020; 0.020 – 0.040; 0.040 – 0.060; 0.060 – 0.080; 0.080 – 0.10; 0.100 – 0.160; 0.160 – 1.000), each of which accounted for 12.5% of GPS relocations pooled across all 20 impala. Second, I calculated the proportion of the 54 kill sites occurring within each class of woody cover. Third, I calculated the ratio of the proportion of kill sites to the proportion of habitat use by impala for each class of woody cover. A ratio $< 1$ indicates that, for a given amount of woody cover, the proportion of kill sites was less than expected by impala habitat use, while a ratio $> 1$ indicates that the proportion of kill sites was greater than expected by impala habitat use. Finally, I regressed these ratios against the value of woody cover at the mid-point of each class. This simple model creates a continuous relationship between probability of detecting a kill site relative to impala habitat use and woody cover ($r = 1.70 + 0.228*\ln(\text{woody cover})$; $n = 8$; $R^2 = 0.792$ ; $P = 0.003$) and allowed me to estimate the *per capita* risk of mortality from predation as a function of woody cover across the landscape. Because kill sites were more difficult to detect in denser vegetation, I note that this model likely underestimates the steepness of the slope for the relationship between $r$ and woody cover. I used a similar methodology to quantify *per capita* risk of mortality from predation at glades and riparian areas using Manly's standardized selection ratios (Manly et al. 2002)

### 3.2.9 Habitat manipulation

To disentangle the confounding influences of forage (i.e., elevated nutrient levels in grass) and safety (i.e., less woody cover) within glades, I cleared all woody cover from five 0.5 ha (70 x 70 m) plots, one in each home range of five individual impala. Thus, relative to their vicinities, these clearings: (i) increased visibility; (ii) eliminated browse; and (iii) did not change grass quantity or quality, at least over the course of this experiment. Clearings were established during dry seasons, one in October 2011 and four in February 2012. Prior to this effort, I used the classified satellite image to identify plots for clearing as areas with a high proportion of woody cover (0.22 ± 0.02, range 0.13 – 0.31) and low observed use by impala. I counted the number of impala relocations within 50 m of plot boundaries, and used GPS relocation data from 60 d before and after removal of woody cover to standardize the monitoring period among animals. I report on the proportional change in use of clearings for each individual.

### 3.2.10 The effect of plant defenses on impala diet preference

I focused on two common *Acacia* that together account for ca. 80% of trees at MRC: *A. etbaica* and *A. brevispica* (Young et al. 1995). I tested the hypothesis that thorn morphology—as opposed to chemical defenses and other leaf characteristics (Table 3.2)—deters herbivory by impala. To measure leaf mass, I clipped 10 leaves from randomly selected branches on 10 different trees for a total of 100 leaves. Leaves were dried in a solar oven for 72 h and weighed to obtain an average leaf mass per species. To measure condensed tannins in leaves, I sampled and air-dried 10 leaves from 10 trees. I then used a standard acid–butanol protocol with quebracho as a standard (see Ward and Young 2002). Results are expressed as percent dry weight in quebracho equivalents (*QE*).

I focused on preferences for two common trees in the genus *Acacia*, *A. brevispica* and *A. etbaica*, that collectively comprise ~80% of all trees in the study area (Young et al. 1995). These trees differ in several traits known to affect herbivory (Coley et al. 1985), with *A. brevispica* exhibiting shorter thorns and higher concentrations of tannins relative to *A. etbaica* (Table 3.2). I measured how these defenses affected diet preference by clipping and removing thorns from groups of *A. etbaica* branches, attaching these thorns to groups of *A. brevispica* branches, and then presenting both types of manipulated branches alongside controls of each species to free-ranging impala in a cafeteria-style feeding experiment.

I cut 2 m branches from *A. brevispica* and *A. etbaica*, ensuring that these branches had not been previously browsed. Four types of branch cuttings were offered to impala: an unmanipulated branch from each species, an *A. etbaica* thorn-removal manipulation, and an *A. brevispica* thorn-addition manipulation. The *A.* e*tbaica* thorn removal was created by clipping the long thorns of *A. etbaica* at their base with wire cutters. The *A. brevispica* spine-addition entailed fixing the long thorns from an *A. etbaica* to an *A. brevispica* branch with bailing wire. Wires were wrapped on all branches to control for handling effects of observers. I placed each branch cutting (two controls, thorn addition, and thorn removal) in separate buckets filled with wet sand and buried the four buckets approximately 1 m apart. I used 10 different glades as experimental sites to maximize the probability of an impala herd encountering the cuttings and each site was used by a different impala herd, as verified by GPS telemetry.

At the beginning of each trial, I marked and then counted the leaves on a randomly selected 30 cm section of each branch in each group. I positioned a motion-activated video camera ca. 5 m from branch cuttings to identify foragers and to monitor preferences by impala. A trial night began in the late afternoon, and concluded when I returned to recount leaves on the marked section in the following morning. I then added water to the buckets to reduce desiccation of leaves, and then returned again for a second morning to recount leaves, at which point I considered the trial finished. Thus, individual branch cuttings were each exposed to two trial nights in this experiment. All herbivory events from this experiment were attributed to impala based on data collected from remote cameras.

I used standardized selection indices to quantify impala diet preference for each of the four types of branch cuttings (Manly et al. 2002). The standardized selection index is a ratio of resource use to availability, which I calculated for each type of branch cutting and trial-night as $\hat{w}_{ij} = o_{it} / \pi_{it}$. Resource use ($o_{it}$) was calculated as the number of leaves removed from a given branch (*i*) divided by the total number of leaves removed over a given trial-night (*t*) from all branch cuttings at a site. Availability ($\pi_{it}$) was the number of leaves on a given branch cutting (*i*) divided by the total number of leaves on all branch cuttings at the start of a trial-night (*t*). I assumed that the leaves of all branches offered to impala were equally accessible at each site and for each night, which is supported by the observation that individuals readily switched among the types of branch cuttings. Availability was recalculated after each night to account for leaf loss from previous foraging. Thus, $\hat{w}_{ij} = 1$ indicates that use (leaf consumption) was proportional to leaf availability, $\hat{w}_{ij} \geq 1$ indicates selection for, and $\hat{w}_{ij} \leq 1$ indicates avoidance of, the leaves on a given branch cutting. I used mixed-effects models and treated each trial-night as a replicate, with the selection index as the response variable and night (first or second) and experimental site as random effects. Fixed effects included *Acacia* species, defense (i.e., long thorns present or absent) and an interaction term. I used the R-package lme4 to analyse these data (R Development Core Team 2013). Because trophic cascades are often defined by an indirect effect on plant biomass (Polis et al. 2000) and leaf biomass varied between these two *Acacia*, I also present data on the amount of leaf biomass removed per 30 cm section of branch by multiplying the number of leaves eaten per trial-night by the mean leaf mass for that species. However, I note that the value for the standardized selection index is the same irrespective of whether use and availability are measured for the removal of leaves or leaf biomass.

### 3.2.11 The effect of herbivory by impala on the abundance of Acacia spp.

I assessed changes in tree abundance over a 3-year period (2009-2012) within an existent large-scale herbivore manipulation (Goheen et al. 2013). Using a series of semi-permeable electrified fences, this manipulation isolates the effect of mesoherbivores (40-900 kg) from that of megaherbivores (> 1000 kg) and smaller herbivores (< 10 kg). In this study area, mesoherbivorous browsers comprise a guild of three species, of which impala account for 79% of the combined biomass density (Augustine 2010). Therefore, differences in tree density attributable to mesoherbivores are almost certainly driven by the diet preferences of impala.

Using existing data from the UHURU enexperiment (Goheen et al. 2013), I asked whether exclusion of impala resulted in changes in stem density for *A. brevispica* and *A. etbaica*. The UHURU experiment consists of 36 1ha fences (and controls) distributed among three sites associated with a spatial gradient in rainfall across the study area. At each site, there are three replicates of four 1ha treatments, in which electrified fences either excluded: (i) all non-volant animals ≥ 5 kg and ≥ 0.5 m tall (TOTAL); (ii) all ungulates ≥ 40 kg and ≥ 1.2 m tall (MESO); (iii) all ungulates larger than 2 m tall (MEGA); (iv) no herbivores (OPEN). Within each 1 ha fence, 36 (49 $m^2$) permanent plots were marked and the number of tree stems recorded in 2009 and in 2012. Further details on the design of the experimental exclosure can be found in (Goheen et al. 2013). I used the difference in stem density per year for each 49 $m^2$ plot as the response variable, impala access as a fixed term, and site as a random term in a linear mixed model. I compared MESO plots (e.g., no impala or mega-herbivores, but allows dik-dik) with MEGA plots (e.g., no mega-herbivores, but allows impala and dik-dik) to isolate the effects of herbivory by impala on trees.

### 3.2.12 Quantifying the distribution of Acacia spp. along a gradient of risk to impala

To understand how the interplay of risk of predation and plant defense manifested across the landscape, I related the abundance and proportion of *Acacia* to spatial variation in satellite-derived estimates of woody cover. I counted stems of *Acacia* and other tree species at 108 transects (200$m^2$) located across the 200$km^2$ study area and centered on randomly-selected glades and riparian areas. I quantified the abundance of *A. brevispica* and *A. etbaica* at the same transects used to quantify habitat visibility by counting the number of stems within 2 m on either side of the 50 m transect line to create 200 $m^2$ rectangular plots (Figure 3.2). I counted stems of all woody species, which included *A. mellifera*, a single *Croton* sp., and a single *Grewia* sp., and then calculated the proportion of *A. brevispica* and *A. etbaica* stems among all woody species at each plot. I compared the arcsine transformed proportion of *A. brevispica* and *A. etbaica* in glades and riparian areas using plot as the unit of replication in a linear mixed-effects model with a random effect for location. To facilitate visual interpretation of these data, I created four classes for the satellite-derived values for woody cover found at the center of each plot and calculated the proportion of *A. brevispica, A. etbaica* and impala GPS relocations found within each class. I used the R-package lme4 to analyse these data (R Development Core Team 2013).

### 3.2.13 Mapping risk of predation and plant defense across the landscape

To illustrate the spatial dynamics of this trophic cascade, I depicted: (i) the distribution of woody cover (derived from satellite imagery), (ii) the predicted distribution of *per capita* mortality from predation (as a function of satellite-derived estimate of woody cover, see above '*Per capita risk of mortality'*), and the predicted proportion of (iii) *A. brevispica* and (iv) *A. etbaica* stems in the tree community. I used linear regression to predict the proportion of *A. brevispica* and *A. etbaica* in the 200 $m^2$ rectangular plots as a function of the satellite-derived estimate of woody cover located at the plot center. Using GIS software, I used these regression equations to create predictive maps for the species composition of the tree community.

## 3.3 Results

Impala displayed a strong, aggregative response to glades, with each individual spending 27% ± 4 of its time in these open areas even though they only occupy about 6% ± 1 of the average home range (Table 3.3). Conversely, impala avoided riparian and other areas with high woody cover (Figure 3.2) This avoidance was more pronounced at night (Table 3.3, Table 3.4) when carnivores are most active (Woodroffe 2011b, Cozzi et al. 2012). Areas of high woody cover were characterized by low visibility and were positively associated with both components of risk: (i) the *per capita* risk of mortality from predation was 653 times greater in riparian areas than in glades (Table 3.5); (ii) wild dogs strongly selected for woody cover ($\beta = 8.76 \pm 0.74$, $P < 0.001$). For example, based on the mean proportion of woody cover in each habitat, the probability of wild dog selection for riparian areas was 219 times greater than selection for glades. Leopards also rely on woody cover to hunt impala (Balme et al. 2007, Pitman et al. 2012*)* and, combined with wild dogs, accounted for 83% of impala kills at MRC (Figure 3.1, Table

3.5). Thus, impala avoided habitats with heightened *per capita* risk of mortality from predation as well as areas that were selected by their primary predators.

Although habitat selection by impala was negatively correlated with risk, this simply may have reflected decisions made to enhance access to the high-quality grasses characteristic of glades. I evaluated this alternative hypothesis by removing woody cover in five 0.5 ha plots, thereby mimicking the high visibility and reduced browse typical of glades, but without the potential confound of nutrient-rich grasses. Using GPS telemetry, I tracked five impala herds for 60-d before and after I created these clearings. Following the removal of woody cover, there was a 160-576% increase in use of clearings by impala (Table 3.6), indicating that nutrient-rich grasses did not drive selection for glades by impala. Additionally, impala will typically increase their consumption of browse during the dry season when grass quality is poor (Augustine 2004), yet I detected no influence of season on utilization of glades versus riparian areas (Table 3.3). A previous study in this area found that impala used glades three times more often in the wet season than in the dry season (Augustine 2004); however, these observations were made prior to the recolonization of wild dogs to this study area (Woodroffe 2011a) and therefore may reflect how impala used habitats in a less-risky landscape. Taken together, these results show that risk avoidance, rather than the availability of nutrient-rich grasses, is the predominant driver of selection for glades and avoidance of woody cover by impala.

Leaf removal from control *A. brevispica* branches was 54% greater than control *A. etbaica*, reflecting diet preferences under natural conditions (Figure 3.4 Table 3.7). This preference was driven by the absence of the large thorns characteristic of *A. etbaica*. Leaf consumption of *A.*

*etbaica* from which thorns had been removed was equivalent to control *A. brevispica*, while leaf consumption of thorn-addition *A. brevispica* was equivalent to control *A. etbaica* (Figure 3.4). These results indicate that thorns, and not tannins or other species-specific differences in leaf properties, underlie preferences by impala for these two abundant and widespread trees.

After accounting for a random block effect, mean stem density of the poorly-defended *A. brevispica* increased by 300% inside exclosures relative to control plots (Figure 3.4; $F = 3.86$, $n = 234$, $P = 0.051$). In contrast, mean stem density of the comparatively well-defended *A. etbaica* decreased by 63% inside exclosures vs. control plots (Figure 3.4), though this difference was nonsignificant ($F = 0.007$, $n = 234$, $P = 0.933$). These results indicate that, despite the demonstrated palatability of leaves from both *Acacia* species (Figure 3.4), thorns effectively buffered the impacts of impala herbivory on tree abundance.

The number of *A. brevispica* stems was 289% greater in riparian areas than in glades (Table 3.8), and increased monotonically with satellite-derived estimates of woody cover (Figure 3.5). Among the species comprising the aggregate tree community, the proportion of *A. brevispica* stems increased with woody cover (Figure 3.6) and was 112% higher in riparian areas than in glades (Table 3.8). Conversely, the number of *A. etbaica* stems was 100% greater in glades than in riparian areas (Table 3.8) and decreased as woody cover increased (Figure 3.5). The proportion of *A. brevispica* (*pACBR*) stems was positively associated with woody cover ($pACBR = 0.257 + 0.850$*woody cover, $n = 108$, adjusted $R^2 = 0.191$, $P \leq 0.0001$, Figure 3.7). In contrast, the proportion of *A. etbaica* (*pACET*) was negatively associated with woody cover ($pACET = 0.269 - 0.592$*woody cover, $n = 108$, adjusted $R^2 = 0.125$, $P = 0.0001$, Figure 3.7). The proportion of *A. etbaica* stems in the tree community decreased with woody cover (Figure 3.6) and was 350% greater in glades than in riparian areas (Table 3.8). Thus, spatial variation in risk of predation determined the relative benefits of carnivores and defenses to trees: with increasing woody cover came greater risk of predation, greater avoidance by impala, and increasing dominance by the poorly-defended and less-thorny *A. brevispica*.

## 3.4 Discussion

The cascading effects of risk on *A. brevispica* arose through a pronounced shift in the distribution of impala away from areas with high woody cover (Figure 3.8). While large mammalian herbivores often attempt to reduce their exposure to risk through labile responses in vigilance (Underwood 1982), aggregation (Hebblewhite and Pletscher 2002), or movement rates (Fortin et al. 2005), it is unclear whether such behaviors result in trophic cascades (Middleton et al. 2013a). Conversely, habitat shifts by herbivores can be potent drivers of trophic cascades, possibly stronger than the consumptive effects of carnivores envisaged under the Green World Hypothesis (Preisser et al. 2005). Such spatial shifts by prey are predicted to occur in systems where predation is associated with a particular habitat feature (Schmitz 2008). Accordingly, risk-averse habitat selection by impala likely occurred because information on at least two components of predation risk (heightened encounter rates with carnivores and higher risk of mortality) were integrated into a single, reliable cue: woody cover.

Thorny defenses attenuated the cascading benefits of risk to *A. etbaica*, but my results also suggest that *A. brevispica* may not be as vulnerable to herbivory as expected by its diminutive thorns. Plant defenses are common in terrestrial systems, and primarily are manifested in chemical (e.g., tannins, alkaloids) and structural (e.g., spines, thorns, trichomes) forms (Coley et al. 1985). A particularly complex defensive strategy emerges through the co-evolution of plant-animal mutualisms. For example, chemosensory cues emitted by milkweed (*Asclepias* spp.) attract carnivorous arthropods to sites where aphids (*Aphis nerii*) have attacked leaves, thereby triggering a localized trophic cascade (Mooney et al. 2010). In an analogous process, riparian and other areas of high woody cover attract carnivores and allow *A. brevispica* to thrive without large thorns in a landscape characterized by intense mammalian herbivory.

Documentation of this trophic cascade did not rely on the extirpation or restoration of large carnivores: spatial variation in risk and tree-community composition emerged within the home ranges of individual impala (Figure 3.8). Trophic cascades involving large mammals typically are inferred at relatively coarse temporal and spatial scales, either by comparing a single area before and after removal of carnivores (Estes and Palmisan 1974, Beschta and Ripple 2009), or between areas with and without carnivores (Croll et al. 2005, Hebblewhite et al. 2005b). While conclusions from these 'natural experiments' often are consistent with the Green World Hypothesis, such studies usually are unreplicated and lack controls. As a result, potential confounds have been identified, spawning a debate over whether and how large carnivores initiate trophic cascades (Mech 2012, Winnie 2012, Beschta and Ripple 2013, Kauffman et al. 2013). Here, I have adopted an approach complementary to such broad-scale natural experiments by manipulating critical links in a food chain comprised of large, free-ranging organisms. As large carnivore populations continue to decline globally, understanding the role that these predators play in shaping a Green World is an urgent priority (Estes et al. 2011, Ripple et al. 2014). I expect that studies integrating risk of predation and plant defenses will constitute a major step towards this goal.

**Figure 3.1 Proportion of impala kills (n = 54) attributed to predation by large carnivores at Mpala Research Center, July 2011 and July 2012. Predator identity was based on evidence at the kill-site, including direct observation of carnivores, tracks, and tooth marks from bites, 'Jackal' refers to black-backed jackals and the 'Hyena' category encompasses both spotted and striped hyenas.**

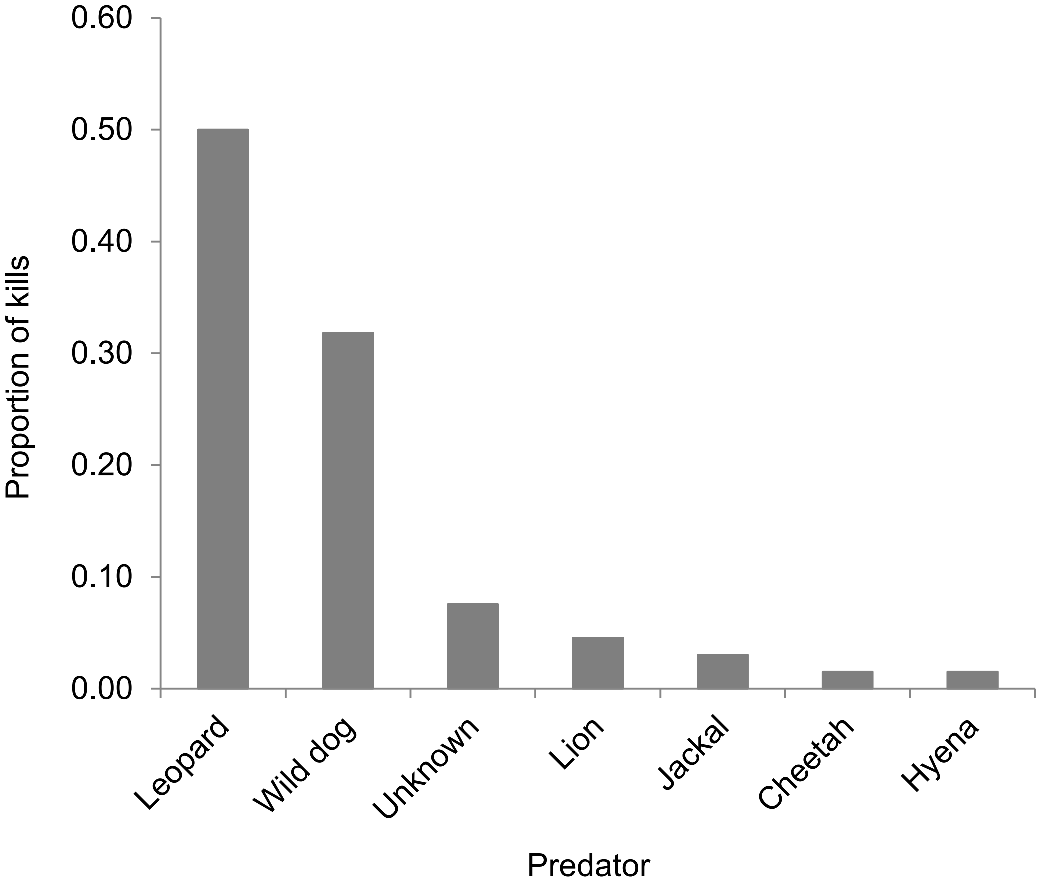


**Figure 3.2 Satellite-derived estimates for woody cover at the mid-point of 200 m$^2$ transects located at (a) glades (*n* = 44) and (b) riparian areas (*n* = 64) and (c) at 1000 random points within each of the 95% minimum convex polygons of 20 adult female impala used in the GPS telemetry study.**

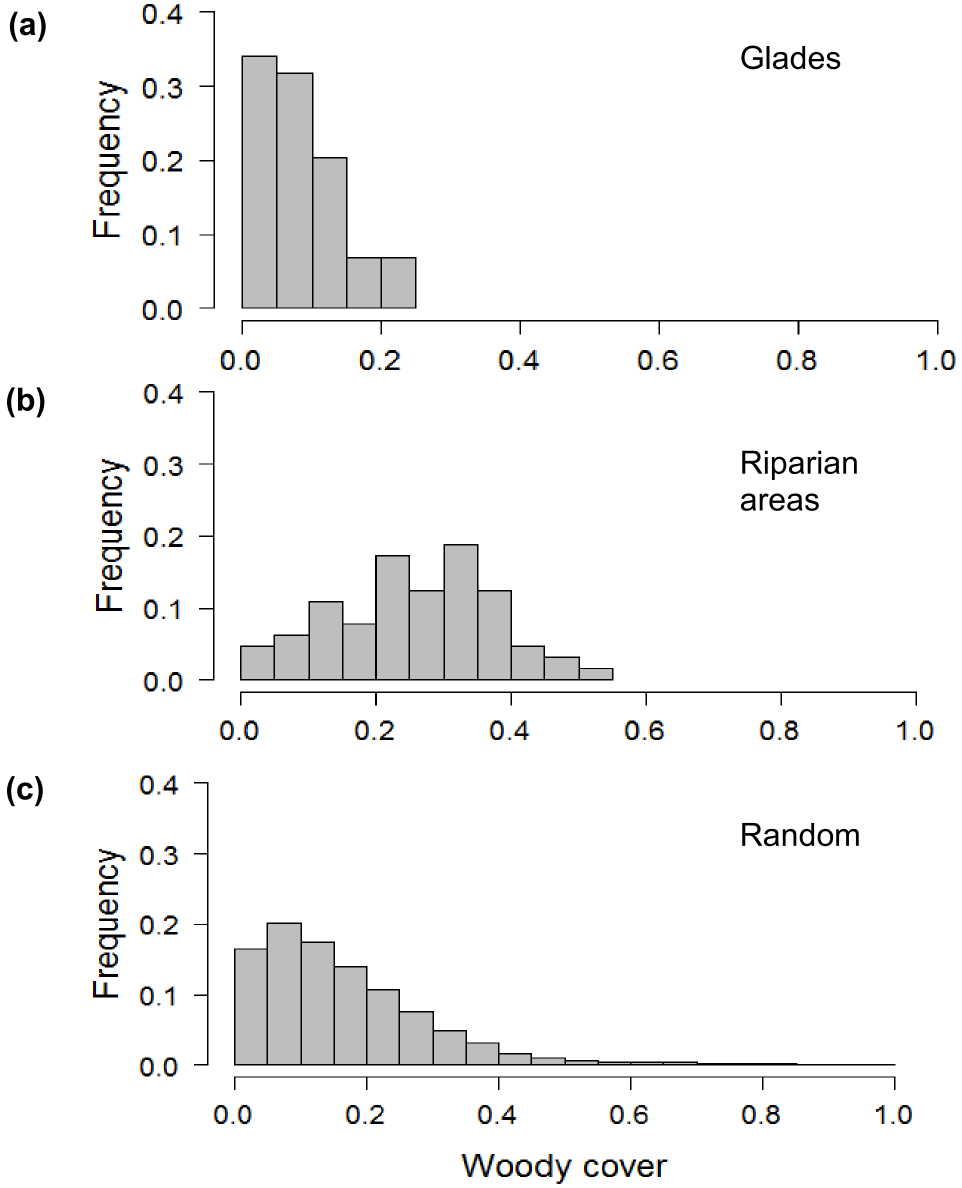


**Figure 3.3 Risk avoidance by impala.** The predicted effect of woody cover on habitat selection by impala (green lines) quantified as the resource selection function [$w(\mathrm{x}) = \exp(-1.99 * \text{woody cover}$, $P < 0.001$], alongside the predicted effect of woody cover on risk [red lines, **(a)** through **(c)**] for: **(a)** visibility, where increasing distance enhances the detection and evasion of predators [visibility (m) = 36.18 - 69.92* woody cover; $R^2 = 0.415$; $P < 0.001$)]; **(b)** probability of habitat selection by wild dogs, quantified as the resource selection function [$\mathrm{w(x)} = \exp(8.76 * \text{woody cover})$; $P < 0.001$]; **(c)** per capita risk of mortality from predation [1.70 + 0.228*ln(woody cover); $R^2 = 0.792$ ; $P = 0.003$], where 1 indicates that the number of kill-sites are expected based on the distribution of impala and values >1 indicates that kill-sites occur more than expected based on the distribution of impala.

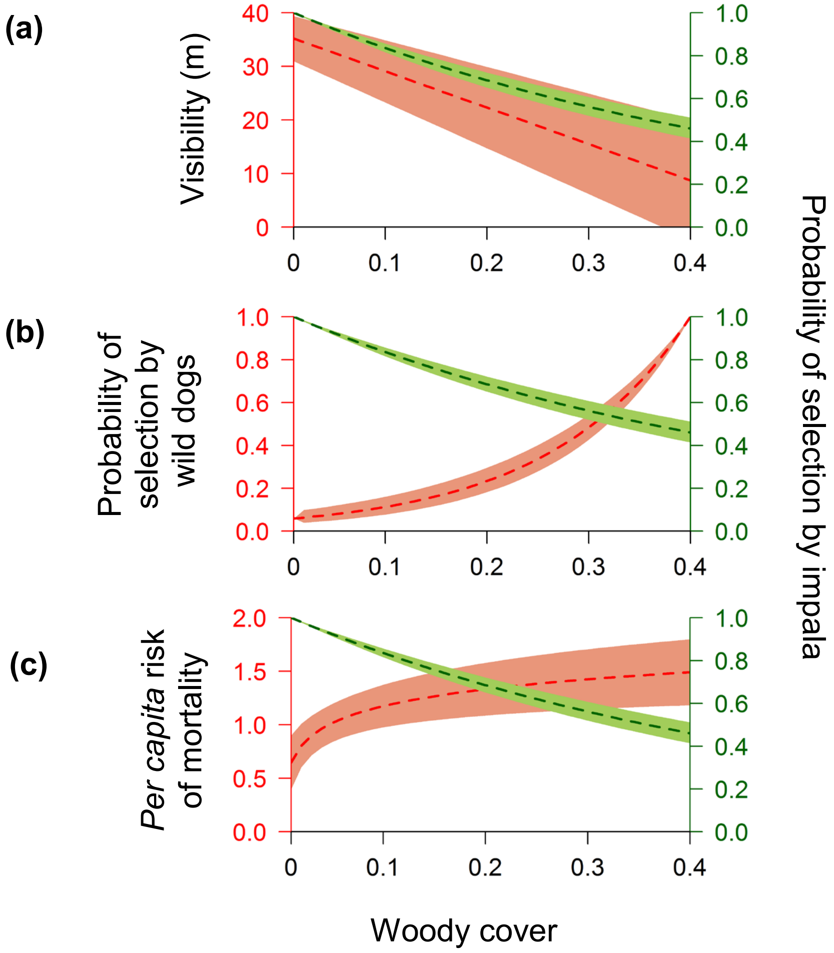


**Figure 3.4 Impala both prefer and suppress the abundance of *Acacia* spp. lacking large thorns**. The effect of thorn morphology on diet preference for (**a**) *A. brevispica* and (**b**) *A. etbaica* was quantified using a cafeteria-style feeding experiment. A value of 1 (dashed line) indicates random leaf consumption among the four treatments, while values >1 indicate diet preference and values < 1 indicate avoidance of leaves. The presence of long thorns ($F$ = 4.70, $n$ = 20, $P$ = 0.033) was a significant factor in probability of leaf consumption, independent of species ($F$ = 0.37, $n$ = 20, $P$ = 0.543). The species x thorn interaction was not statistically significant ($F$ = 0.29, $n$ = 20, $P$ = 0.592). The effect of herbivory on the abundance of (**c**) *A. brevispica* and (**d**) *A. etbaica* stems after 3 years of mesoherbivore exclusion using electrified fencing ($n$ = 234 plots in 36 locations). Controls excluded megaherbivores (elephants and giraffes), but permitted access of mesoherbivores (40-900 kg) as well as smaller-bodied ungulates. Exclosures prevented access of both mega-and mesoherbivores but permitted access of smaller-bodied ungulates. Impala comprise 79% of the biomass density of mesoherbivorous browsers in the study area (Augustine 2010), so the effects of this exclosure experiment are almost certainly driven by impala herbivory.

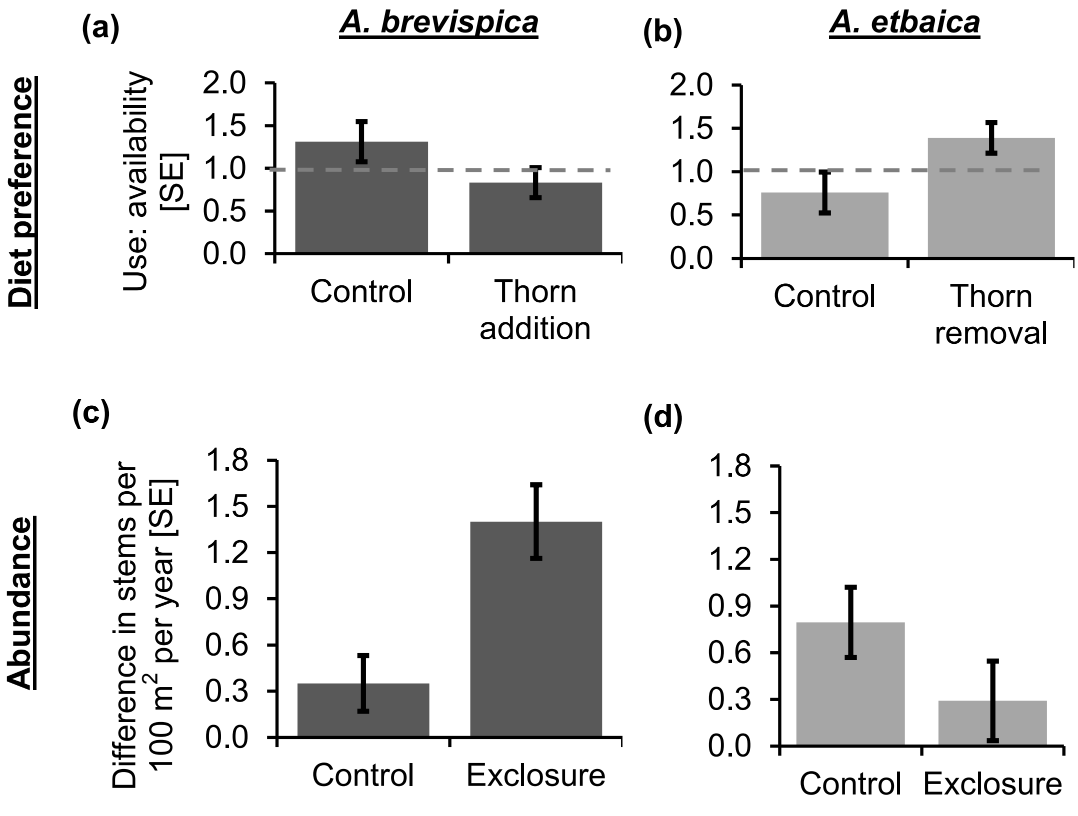


**Figure 3.5 Number of stems measured at $200\text{m}^2$ rectangular plots ($n$ = 108) as a function of the satellite-derived value for woody cover located at the plot center for** (a) **the aggregate tree community of five species or genera (Stems = 2.88 + exp (2.80 * Woody cover), *P* < 0.001);** (b) ***Acacia brevispica*** **(Stems = 1.96 + exp (3.74 * Woody cover), *P* < 0.001);** (c) ***Acacia etbaica*** **(Stems = 1.52 + exp (-1.03 * Woody cover), *P* = 0.011). Poisson regression was used to fit these data.**

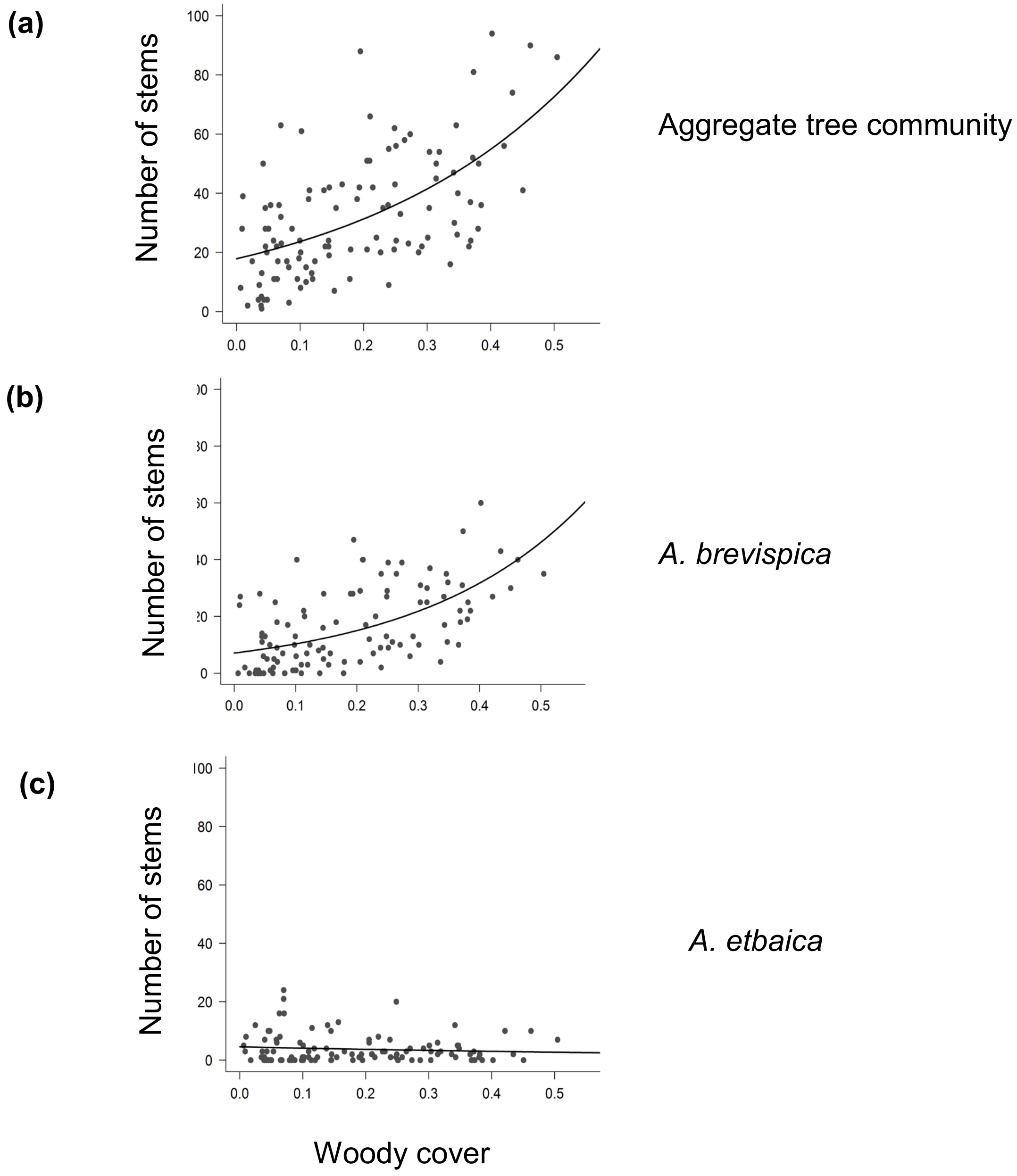


**Figure 3.6 The proportion of poorly-defended *A. brevispica* and well-defended *A. etbaica* stems out of the total number of trees encountered at 108 transects distributed along a gradient of woody cover. Habitat use is defined as the average proportion of GPS relocations per impala located within each of four classes of woody cover for *n* = 20 adult female impala tracked in 2011-12 at 20 minute intervals. The composition of the tree community shifted to dominance by a poorly-defended (*A. brevispica*) species with increasing woody cover, the predominant driver of predation risk to impala.**

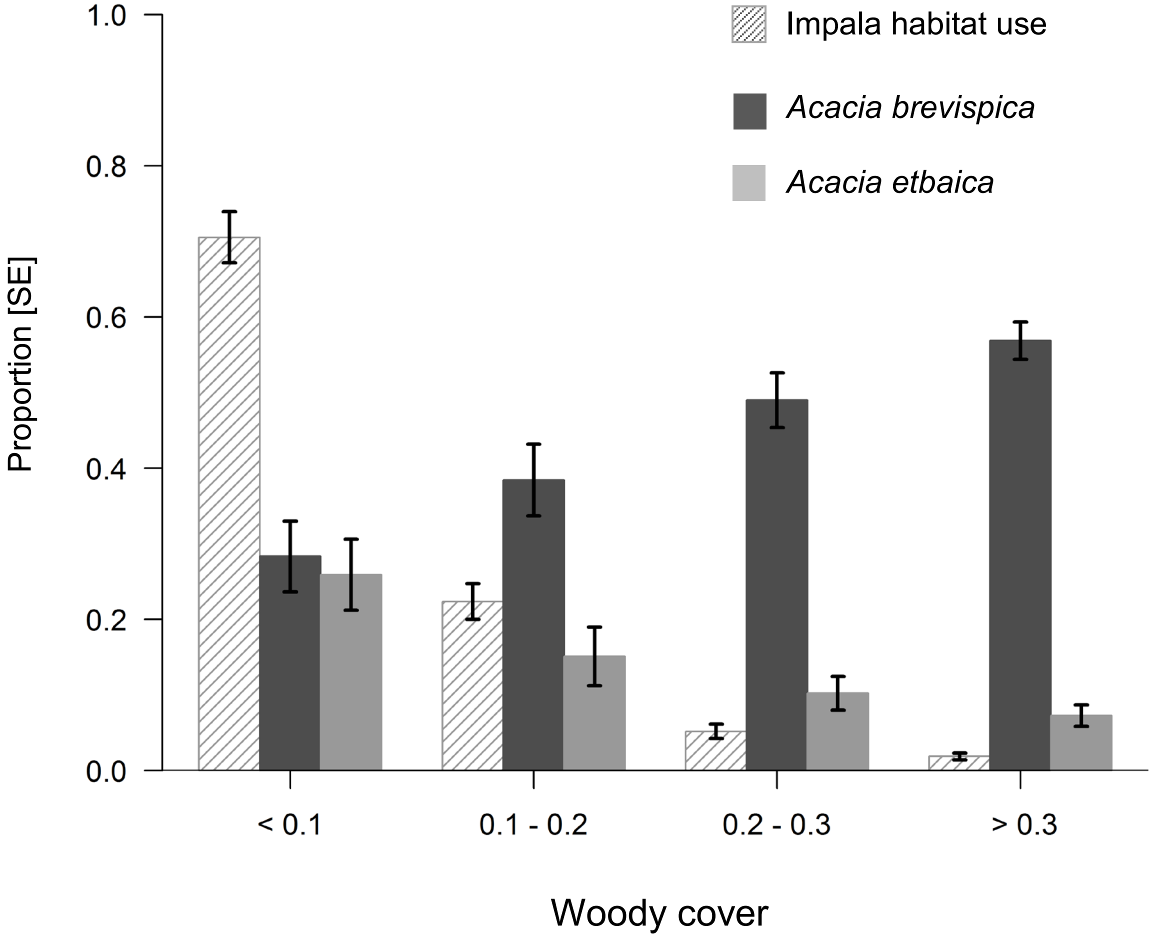


**Figure 3.7 Proportion of stems in the tree community for two *Acacia* sp. measured at 200m$^2$ rectangular plots (*n* = 108) as a function of the satellite-derived value for woody cover located at the plot center. Untransformed data are presented in this figure, and slopes of the fitted lines for the arcsine transformed proportion of stems are significant for both species (*A. brevispica*, $R^2$ = 0.191, *P* < 0.001; *A. etbaica*, $R^2$ = 0.125, *P* = 0.001).**

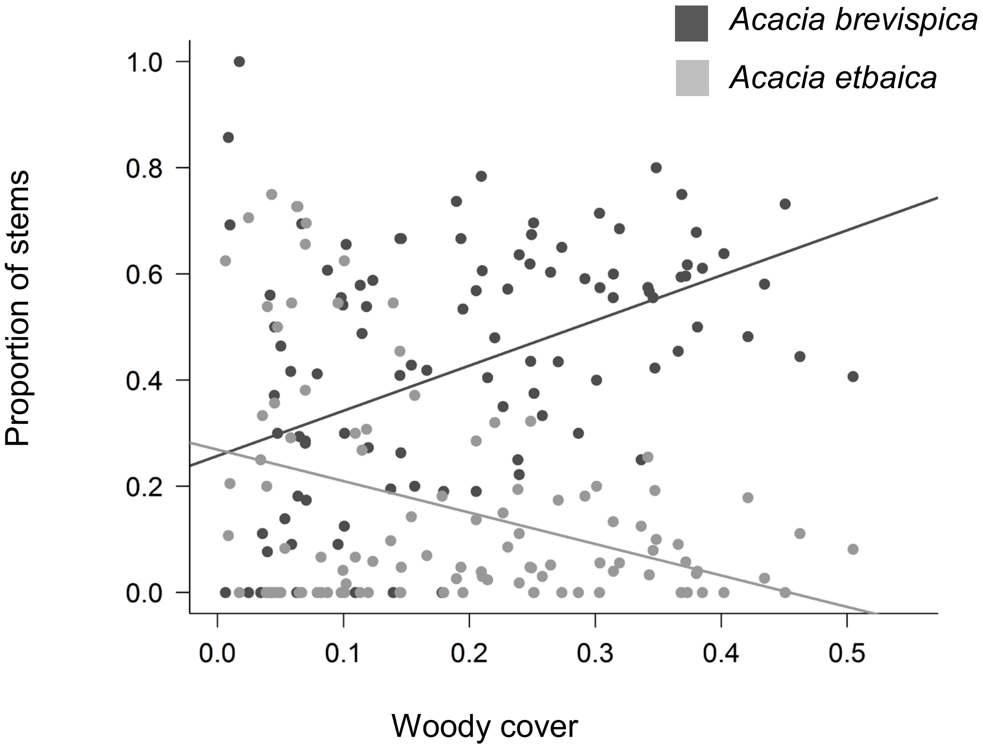


**Figure 3.8 A sample of GPS telemetry relocations (black points) to illustrate the movements of a typical impala, overlaid on maps of (a) woody cover, derived from satellite imagery; (b) the predicted *per capita* risk of mortality from predation (see Figure 3.2); and the predicted proportion of stems in the tree community that are (c) poorly-defended *A. brevispica*; and (d) well-defended *A. etbaica.* Derivation of (c) and (c) is shown in Figure 3.7. Because impala prefer *A. brevispica* (Figure 3.4), I would not expect them to avoid the dark-green areas in (c) if forage availability rather than risk was driving habitat selection. To improve clarity of the figure, I only show a randomly selected portion (15%) of GPS relocations from the entire duration that this individual was monitored between 03-June-2011 to 08-June-2012.**

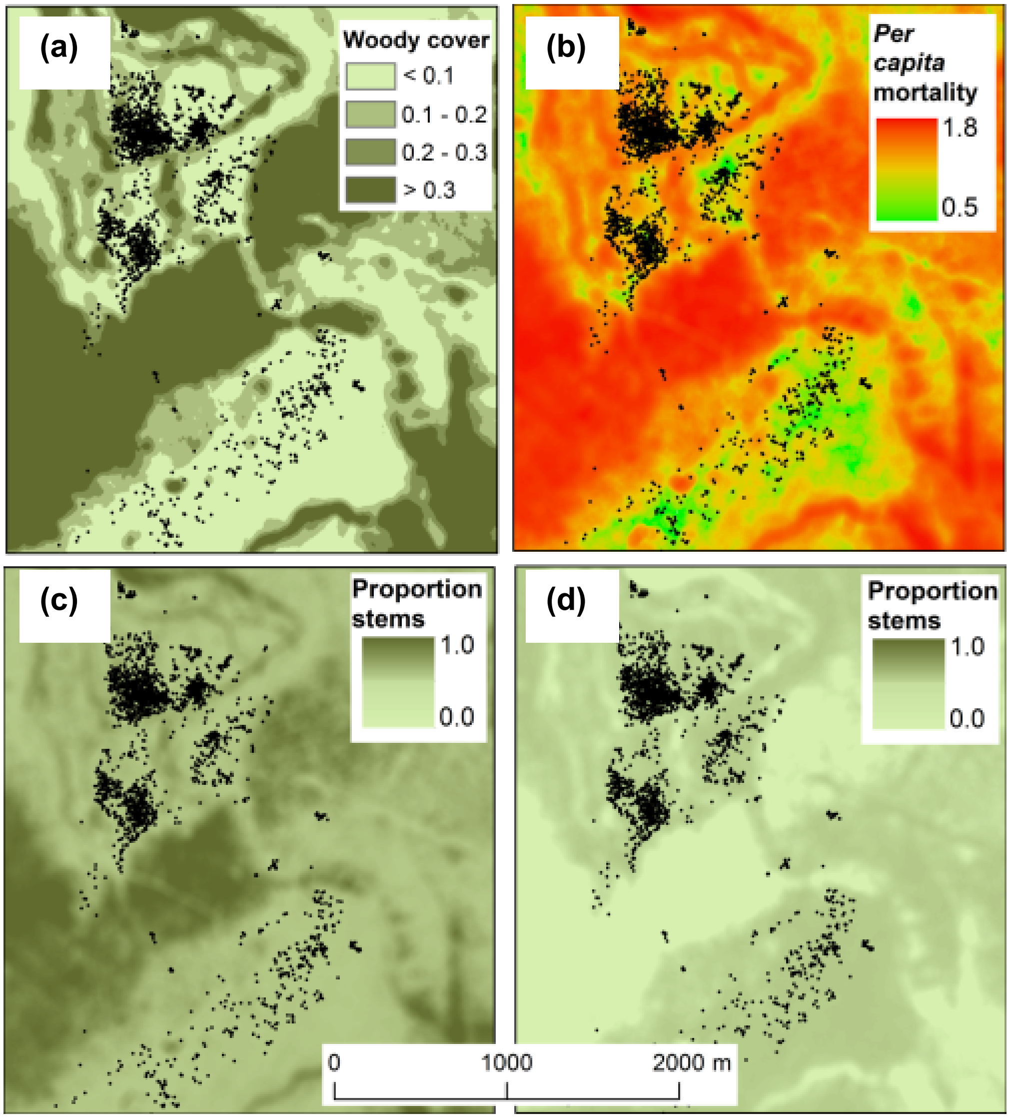


**Table 3.1 Marginal coefficients ($\beta$ ± SE, $n$ = 20) for the resource selection functions of satellite-derived estimates of woody cover, calculated over circular areas with different radii, for adult female impala, May 2011- June 2012.**

| Radius | $\beta$ ± SE | *P* | *AICc* |
|---|---|---|---|
| 10 m | -1.24 ± 0.10 | <0.001 | 57164 |
| 20 m | -1.76 ± 0.12 | <0.001 | 57117 |
| 40 m | -1.99 ± 0.13 | <0.001 | 57112 |
| 80 m | -1.81 ± 0.16 | <0.001 | 57203 |

**Table 3.2 Summary of *A. brevispica* and *A. etbaica* leaf and thorn characteristics (mean ± SE) for 10 leaves, each taken from 10 trees (*n* = 100).**

| Trait | *A. brevispica* (*n* = 100) | *A. etbaica* (*n* = 100) |
|---|---|---|
| Condensed tannins (% Quebracho Equivalents ± SE) | 20.8 ± 2.6 | 1.3 ± 0.3 |
| Leaf mass (g ± SE) | 0.336 ± 0.028 | 0.030 ± 0.003 |
| Mechanical defenses | Short straight thorns (< 0.6 cm) | Long straight thorns (< 6 cm) and short recurved thorns (< 0.6 cm) |

**Table 3.3 Habitat use, defined as the proportion of GPS relocations (mean ± SE, *n* = 20) located ≤ 50 m from habitat features, by diel period and season, for adult female impala living in distinct herds, May 2011- June 2012. Glades occupy 6.6% ± 0.7 and riparian areas 8.6% ± 0.9 of the average impala home range (393 ha ± 47, *n* = 20), measured as the 95% minimum convex polygon of GPS relocations.**

| | | Diel period(1) | | | Season(2) | | |
|---|---|---|---|---|---|---|---|
| Habitat feature | All | Day | Night | $P^{(3)}$ | Dry | Wet | $P^{(3)}$ |
| Glade | 0.27 ± 0.04 | 0.16 ± 0.02 | 0.39 ± 0.05 | <0.0001 | 0.25 ± 0.04 | 0.28 ± 0.04 | 0.220 |
| Riparian area | 0.03 ± <0.01 | 0.04 ± <0.01 | 0.01 ± <0.01 | <0.0001 | 0.02 ± <0.01 | 0.03 ± <0.01 | 0.050 |

(1) Diel period: Day (0630 – 1830); Night (1830 – 0630)

(2) Season: Dry (≤ 50 mm rainfall in previous 4 weeks); Wet (> 50mm rainfall in previous 4 weeks)

(3) *P*-values show the results of paired *t*-tests comparing the proportion of impala GPS relocations found within each habitat feature between diel period or season.

**Table 3.4 Habitat selection, defined as the marginal coefficients ($\beta$ ± SE; $n$ = 20) for resource selection functions of adult female impala living in distinct herds, May 2011- June 2012. Separate models were created for each habitat feature, diel period and season.**

| | All | Diel period$^{(2)}$ | | Season$^{(3)}$ | |
|---|---|---|---|---|---|
| Habitat feature | | Day | Night | Dry | Wet |
| Glade | 0.21 ± 0.02 *** | 0.07 ± 0.04 * | 0.32 ± 0.03 *** | 0.21 ± 0.03 *** | 0.17 ± 0.03 *** |
| Riparian area | -0.30 ± 0.06 *** | -0.21 ± 0.07 *** | -0.47 ± 0.10 *** | -0.37 ± 0.08 *** | -0.23 ± 0.07 *** |
| Woody cover $^{(1)}$ | -1.63 ± 0.24 *** | -0.47 ± 0.27 * | -4.17 ± 0.47 *** | -1.51 ± 0.35 *** | -1.49 ± 0.30 *** |

(1) Woody cover: excludes sampling locations ≤ 200m from glades and riparian areas.

(2) Diel period: Day (0630 – 1830); Night (1830 – 0630)

(3) Season: Dry (≤ 50 mm rainfall in previous 4 weeks); Wet (> 50 mm rainfall in previous 4 weeks)

(4) * $P < 0.100$; ** $P < 0.050$; *** $P < 0.001$

**Table 3.5 Derivation of *per capita* risk of mortality from predation as standardized selection indices for kill-site ($n$ = 54) occurrence in glades and riparian areas.**

| Habitat feature | Impala habitat use (1) ($\pi$) | Kill-sites detected | Kill-site proportion(2) ($\theta$) | Selection index(3) ($\hat{w}$) | Standardized index(4) ($\beta$) |
|---|---|---|---|---|---|
| Glades | 0.270 | 11 | 0.204 | 0.756 | 0.133 |
| Riparian areas | 0.030 | 8 | 0.148 | 4.933 | 0.867 |

(1) Based on mean values for $n$ = 20 GPS collared impala pooled across diel periods (Table 3.3)

(2) A total of 54 impala kill sites were found, e.g., $\theta_{glades} = 11/54$

(3) $\hat{w} = \theta/\pi$

(4) $\beta$ = Manly's standardized selection index (Manly et al. 2002)

**Table 3.6 Use of clearing plots as measured by GPS telemetry of 5 distinct herds of impala, 60 days pre- and post-tree removal.**

|  | Pre-removal |  | Post-removal |  |  |
|---|---|---|---|---|---|
| Animal | Relocations per day inside plot | Total observed relocations during 60 d | Relocations per day inside plot | Total observed relocations during 60 d | Proportional increase of GPS relocations inside plot |
| A | 0.005 | 3883 | 0.014 | 4122 | 1.60 |
| B | 0.016 | 3963 | 0.047 | 257 (1) | 1.89 |
| C | 0.003 | 3972 | 0.019 | 3897 | 5.76 |
| D | 0.001 | 4007 | 0.004 | 4056 | 1.96 |
| E | 0.007 | 3903 | 0.038 | 2589 | 4.68 |
| mean ± SE | 0.006 ± 0.002 | 3946 ± 23 | 0.024 ± 0.008 | 2984 ± 737 | 3.18 ± 0.85 |

(1) Animal was killed by poachers within 48 h of tree removal.

**Table 3.7 Summary of *Acacia* thorn manipulation experiment.**

| Species - Treatment | Mechanical defense | Initial leaf density (leaves · cm $^{-1}$ ± SE) | Biomass density [(1)] at onset of experiment (g · cm $^{-1}$) | Leaf removal per night (% ± SE) | Biomass removal per night (g · cm$^{-1}$ ± SE) |
|---|---|---|---|---|---|
| *A. brevispica* – control | No long thorns | 0.91 ± 0.14 | 0.297 ± 0.048 | 54.0 ± 8.8 | 0.123 ± 0.037 |
| *A. brevispica* – thorn addition | Long thorns | 0.60 ± 0.06 | 0.200 ± 0.021 | 35.0 ± 7.7 | 0.055 ± 0.017 |
| *A. etbaica* – control | Long thorns | 1.19 ± 0.10 | 0.033 ± 0.003 | 27.7 ± 5.4 | 0.009 ± 0.002 |
| *A. etbaica* – thorn removal | No long thorns | 1.14 ± 0.09 | 0.032 ± 0.003 | 46.7 ± 7.8 | 0.011 ± 0.003 |

(1) Estimated from mean leaf mass (Table 3.2).

**Table 3.8 Distribution of *Acacia* spp. stems by habitat feature at 200m$^2$ rectangular plots ($n$ = 108).**

| Species | Habitat feature (number of plots) | Density (stem per m$^2$ ± SE) | Proportion of stems in tree community (mean ± SE) | $P$ (1) |
|---|---|---|---|---|
| *A. brevispica* | Glade (44) | 0.038 ± 0.007 | 0.273 ± 0.040 | 0.003 |
| | Riparian area (64) | 0.109 ± 0.009 | 0.515 ± 0.021 | |
| *A. etbaica* | Glade (44) | 0.026 ± 0.004 | 0.273 ± 0.038 | <0.001 |
| | Riparian area (64) | 0.014 ± 0.002 | 0.080 ± 0.013 | |

(1) P-value derived from a linear mixed model comparing the within-species differences of arcsine transformed proportion of stems in glades and riparian areas.

# Chapter 4: Sequential top-down forcing does not trigger a trophic cascade following the recovery of a globally endangered carnivore in a savanna ecosystem

## 4.1 Introduction

Carnivores can powerfully shape ecosystems through their direct effect on herbivores, and through their indirect effect on plants, nutrient cycling and rates of natural disturbance (e.g., (Hairston et al. 1960, Estes et al. 1998, Schmitz et al. 2004, Croll et al. 2005). In ecosystems dominated by large mammals, these 'trophic cascades' often are used to justify and predict the outcome of restoring populations of large carnivores (Estes et al. 2011, Mech 2012, Winnie 2012, Ripple et al. 2014). Although the restoration of these iconic species is justifiably heralded as a conservation success story, mechanistic evidence linking the abundance of large, terrestrial carnivores to plant biomass is scant.

Field studies demonstrating the cascading effects of large, terrestrial carnivores have been confined to a few ecosystems, and typically hinge on "natural experiments" in which replication and control are lacking. For example, several studies document a recovering wolf (*Canis lupus*) population, followed by the suppression of a large, gregarious cervid (e.g., deer [*Odocoileus* spp., *Capreolus capreolus*], elk [*Cervus elaphus*], moose [*Alces alces*]) prey, and the release of woody plants (e.g., willow [*Salix* spp.], aspen [*Populus* spp.], oak [*Quercus* sp.]) (McLaren and Peterson 1994, Ripple and Beschta 2003, Hebblewhite et al. 2005b, Beschta and Ripple 2007, Callan et al. 2013, Kuijper et al. 2013). Additional cascades have involved similar prey (e.g., deer, elk) and different predators (cougars [*Puma concolour*], brown bears [*Ursus arctos*]) (Ripple and Beschta 2008, 2012a).

Even within this rather narrow representation of ecological communities, controversy surrounds the standards of evidence used to support or reject the trophic cascade hypothesis. In perhaps the most well-known example of such a controversy, the reintroduction of wolves to the Greater Yellowstone Ecosystem has been interpreted as leading to the recovery of aspen via risk-avoidance behavior and suppression of elk (Ripple et al. 2001, Ripple and Beschta 2007). More recent studies found that elk suppression could also be explained by the intensity of human hunting and predation by large carnivores other than wolves (Mech 2012, Winnie 2012, Middleton et al. 2013b), while aspen growth could also be explained by longer growing seasons and disturbances like drought and fire (Kauffman et al. 2010, Winnie 2012). Covariation in bottom-up (i.e., pollutants) and top-down (i.e., disease, alternative sources of predation) factors associated with the return of a large mammalian predator has confounded testing of the trophic cascade hypothesis elsewhere, such as the Pacific near shore (Estes et al. 1998, Kuker and Barrett-Lennard 2010). Consequently, the claim that trophic cascades are ubiquitous in driving ecosystem structure and function (*sensu* Terborgh et al. 2010) may be premature without studies on a broader suite of species, combined with greater efforts to falsify alternative hypotheses.

The African wild dog (*Lycaon pictus*) is a globally-endangered carnivore inhabiting < 7% of its historic range through sub-Saharan Africa (Woodroffe 1998). After an absence of 20 years, wild dogs naturally recolonized the Laikipia Plateau in central Kenya, where they now co-occur with an assemblage of abundant large carnivores (i.e., 8 species > 10 kg, with a combined density of

≈ 30 individuals 100 km$^{-2}$ (Georgiadis et al. 2007a, O'Brien and Kinnaird 2011, Woodroffe 2011a). A key driver of population growth for wild dogs is the availability of prey (Woodroffe 2011a, b), of which dik-dik (*Madoqua guentheri*) are the most common prey item (> 62% of prey biomass) in Laikipia. Dik-dik are a 5 kg, territorial antelope that suppress the growth of trees and other woody plants (Augustine and McNaughton 2004, Augustine 2010, Goheen et al. 2013, Sankaran et al. 2013). Given the importance of dik-dik as prey for wild dogs, and the documented suppression of trees by dik-dik, strong potential exists for the recovery of wild dogs to trigger a trophic cascade via an indirect, positive effect on trees.

In spite of the potential for top-down forcing following the recolonization of wild dogs, food-web theory suggests that trophic cascade may not occur for at least three reasons: reticulate food chains, donor control and environmental heterogeneity (Murdoch 1966, Ehrlich and Birch 1967, Strong 1992a, Polis 1999, Polis et al. 2000, Finke and Denno 2004, Borer et al. 2005, Mooney et al. 2010, Schmitz 2010). Reticulate food chains are characterized by high numbers of species with similar resource requirements within a given trophic level (Polis and Strong 1996, Tschanz et al. 2007, Thibault et al. 2010). Following the decline of a single species from a consumer trophic level, functional or numerical compensation by species within that trophic level may buffer against a trophic cascade (Finke and Denno 2004). The high species richness of large carnivores and herbivores in Laikipia may comprise a reticulate food chain, and could nullify the cascading effects of wild dog recovery.

Donor control arises when organisms are defended (e.g., secondary compounds or defensive armaments) or otherwise impede (e.g., risk avoidance behavior in animals) the upward flow of energy through the food chain (Polis and Strong 1996, van der Stap et al. 2007, Mooney et al. 2010). In Laikipia, donor control is manifest in the plant defenses in dik-dik forage (Seifert and Palmer, in press) and the anti-predator behavior of dik-dik (Coleman et al. 2008, Lea et al. 2008, Chapter 2). Thus, wild dog recovery may not facilitate tree abundance if trees are defended or if dik-dik reduce their susceptibility to predation through behavioral responses.

Environmental heterogeneity - particularly variation in light, soil nutrients and rainfall - can impose stronger limitations than herbivory on biomass accumulation of plants (Leibold 1989, Schmitz 1994). For example, and across African savannas, tree abundance is constrained by rainfall below 650 mm mean annual precipitation (MAP), and by herbivory and fire above this threshold (Sankaran et al. 2005). Different parts of Laikipia straddle this critical threshold (Goheen et al. 2013), suggesting that tree abundance may not be regulated by herbivory in at least some areas. Moreover, episodic droughts are frequent in Laikipia, and variation in rainfall can cause dramatic shifts in tree recruitment, potentially accentuating bottom-up control (Augustine and McNaughton 2004, Sankaran et al. 2005, Bond 2008, Augustine 2010). Thus, environmental variation, and particularly variation in rainfall, may override any indirect effects of wild dog recovery on trees.

I evaluated the hypothesis that the recovery of wild dogs initiated a trophic cascade, manifesting as an indirect, positive effect on tree abundance in Laikipia. Specifically, I asked the following questions to test my hypothesis:

1. Do wild dogs suppress the population density of dik-dik?
2. Do dik-dik suppress tree abundance?

(3) Is the effect of dik-dik on tree abundance reduced in the presence of wild dogs?

To answer Question 1, I measured the population density of dik-dik prior to (1999-2002) and following (2008-2014) the recovery of wild dogs (2002) across an 84 km$^2$ area in Laikipia. I complemented these spatially-expansive observations with an intensive, 3 month assessment of dik-dik abundance near an active wild dog den – i.e., a period of heightened mortality for dik-dik (Woodroffe et al 2007). I evaluated evidence that other carnivores or variation in rainfall could just as readily explain reductions in dik-dik density as the population of wild dogs recovered.

To answer Question 2, I employed a series of size-selective herbivore exclosures (permitting access by dik-dik, but not larger herbivores) to identify which tree species responded to browsing by dik-dik *per se*. In assessing the effects of herbivory, I focused on changes in the abundance of trees rather than the degree of browsing (Polis et al. 2000, Halaj and Wise 2001), and examined both community and species-specific responses (Polis et al. 2000, Halaj and Wise 2001).

To answer Question 3, I employed the use of separate herbivore-exclusion experiments—one initiated prior to (1999-2002) and one following (2009-2012) the recovery of wild dogs—to quantify whether the effect of dik-dik on tree abundance had diminished since wild dog recovery. I evaluated alternative hypotheses that tree abundance could be explained by the density of other browsers, or by variation in rainfall.

## 4.2 Methods

In this section I highlight the methods used to quantify this trophic cascade, including documentation of wild dog populations, dik-dik and the response of trees to herbivory.

### 4.2.1 Recovery of wild dogs

Estimated biomass of wild dogs on MRC was derived from an ongoing study of > 30 packs, distributed over a 12,000 km$^2$ area (Woodroffe 2011a). Using GPS and VHF telemetry, I quantified the movement patterns, denning periods, and composition of 9 packs at MRC since 2002. Tracking collars were fit on 1-2 individuals in each pack. Because packs are highly cohesive, I interpreted the telemetry data from collared individuals as representative of the entire pack. To quantify the biomass density of wild dogs on MRC, I first calculated the composition of adults (ca. 23 kg) and juveniles (5-22 kg) in each pack, and summed the estimated mass of these individuals to quantify pack-level biomass. The biomass estimate of individual juveniles was adjusted over time as they matured (Woodroffe 2011a). I used telemetry to calculate the number of days that each pack spent at MRC, yielding an estimate of wild dog biomass days (in kg days) over the study area. I performed this calculation for the 6 months preceding each population survey for dik-dik (see below) up to January 2013, as well as in January and June of the years where surveys for dik-diks were not conducted (2003-2007). Using GPS telemetry and field observations, I identified a denning event from a single wild-dog pack comprised of 19 adults and 12 pups in 2011, during which time individuals foraged intensively within 3 km of their den (Figure 4.1).

### 4.2.2 Population density of dik-dik

A previous study performed line-transect sampling (Buckland et al. 2007) to estimate dik-dik density along four transects (1.5-3.3 km each) in 2000 and six transects (1.5-3.3 km each) in 2001-2002 (Augustine 2010). In each survey, transects were each driven four times in 2000 and six times in 2001-2002, for a total effort of 35.9 km to 92.8 km per survey. A total of six surveys

(3 in 2000, 2 in 2001, 1 in 2002) were performed prior to wild dog recovery. Beginning in June 2008 (i.e., 5 years after wild dogs had recolonized MRC) the same study area as Augustine (201) was monitored. Each of these surveys consisted of 20, ca. 2 km transects that were sampled once each per survey, for a total effort of ca. 40 km per survey. A total of 12 surveys were performed at a rate twice per year between June 2008 and January 2014.

Line transect sampling was always performed with two observers and one driver, from a vehicle travelling at 20 km·h$^{-1}$. Distances to animals were estimated using a laser rangefinder and bearings were estimated using a handheld compass. Density estimates and confidence intervals were calculated in Program DISTANCE using a hazard function and cosine series expansion, with observations filtered to a maximum of 72 m from the transects. I filtered data to meet the assumptions of the distance sampling (Buckland et al. 2005), resulting in the removal of 5% of dik-dik observations.

### 4.2.3 Suppression of dik-dik by wild dogs

I compared the population density of dik-dik before and after recolonization of wild dogs using a generalized least squares (GLS) analysis. I then evaluated three lines of evidence to assess how wild dogs affected the dik-dik population. First, I quantified the effect of the estimated consumption of dik-dik by wild dogs on the population growth rate of dik-dik. I estimated consumption of dik-dik based on the energetic demand of wild dogs combined with the caloric return of an adult dik-dik (Woodroffe et al. 2007a). An average-sized wild dog (23 kg) feeding exclusively on dik-dik requires 0.61 individuals per day. Because dik-dik account for ca. 62 % of prey biomass in the diets of non-denning wild dog diets at our study site (Woodroffe et al.

2007a), the predicted demand of dik-dik per kg day of wild dog is 0.015 individuals. I calculated the population growth rate of dik-dik as $r = \frac{N_{t2}-N_{t1}}{t2-t1}$, where *N* is the mean population density estimate from the dik-dik population survey at time *t*, and *t2* is more recent than *t1*. I assumed the number of dik-dik consumed per wild dog has remained constant among all dik-dik population surveys. However, foraging theory suggests that the rate of predation on dik-dik may decline with their density (Holling 1959). Thus, I tested for an interaction of the estimated consumption of dik-dik by wild dogs and the population density of dik-dik on *r*.

Second, following Augustine (2010), I used the proportion of dik-dik groups consisting of ≥ 3 individuals as an index of recruitment for each population survey. I used a GLS regression to test for the effect of consumption by wild dogs on the recruitment index. For all statistical analyses using a GLS test, I tested for serial autocorrelation of residuals between population surveys using auto- and partial-auto correlation functions. Following Zuur et al. (2009), I incorporated both correlation and variance structures into the model, evaluating parsimony using restricted-maximum likelihood estimation and model selection methods. I evaluated model significance using a likelihood ratio test for the top-ranked model, re-fit with maximum likelihood estimation. The likelihood ratio test evaluated a model with the variable of interest against a null (intercept-only) model.

Third, I capitalized on the serendipity of a wild dog den that was established mid-way through a line-transect sampling effort conducted in 2011-2012. This 2011-2012 line transect survey was in addition to the population surveys used to estimate dik-dik density across MRC. I quantified encounter rates between observers and dik-dik along a 14 km road transect before, during, and after a wild-dog den was established. The den was established in December 2011, occupied by 31 individuals and was abandoned after 28 days during a natural dispersal event in January 2012. While denning, wild dogs increase their consumption of dik-dik by 10% (Woodroffe et al. 2007a) and forage almost exclusively within 3 km of the den site (Figure 4.1). This shift in the diet and movement patterns of wild dogs allowed me to quantify short-term responses of dik-dik to a pulse of intense predation. Because the dik-dik population is expected to fluctuate without predation by wild dogs, I compared encounter rates near the active den to a control area where dogs did not forage as frequently (Figure 4.1). The transect in the control area was 17 km and adjacent to the denning range of wild dogs. To quantify encounter rates, I drove at 20 km $h^{-1}$ with two dedicated observers and one driver to locate dik-dik. Transects were every sampled every 60 days from November 2011 to March 2012. Typically, distance sampling methods are preferred to encounter rates because the former provides an estimate of variance. However, due to lack of temporal replication of transects within each pre-, active- and post-denning survey period, distance sampling methods resulted in inordinately high variance in density estimates, and therefore were not appropriate. I verified that the encounter rate of dik-dik served as a reasonable index of population density using the 16 population surveys conducted across MRC between 1999 and 2013 ($n = 16$, $R^2 = 0.873$, $P < 0.0001$). I used an Exact Test with a Poisson distribution to evaluate the null hypothesis that the encounter rate during the active denning phase was the same as the pre-denning and post-denning period. I performed separate tests for the area near the den and the control area. In addition to encounter rates, I also compared the recruitment index in the denning and control areas over these three periods using a Proportion Test, which tests the null hypothesis that recruitment did not change over time.

### 4.2.4 Other drivers of dik-dik density: reticulate food chains, donor control and environmental heterogeneity

I considered the possibility that a reticulate food chain formed by other large carnivores likely to consume a significant number of dik-dik (i.e., leopards [*Panthera pardus*] and black-backed jackals [*Canis mesomelas*]) could either dampen or confound the effect of wild dog recovery on dik-dik abundance. For example, if the abundance of other large carnivores increased concurrently with wild dogs, then causation for any observed decline in the population of dik-dik cannot be unequivocally traced back to wild dog recovery. To measure if the relative abundance of other dik-dik predators has increased with wild dog recovery, I compared the number of detections from a camera-trapping survey conducted in 2002-2003 (7364 trap hours at 19 sites) with a survey conducted in 2011 (48513 trap hours at 97 sites). Camera traps were placed in random sites throughout the study area. I used a lag time of 6 minutes between sequential camera images to identify unique camera trap events. I used an Exact Test with a Poisson distribution to evaluate if the detection rate of large carnivores – excluding wild dogs – has changed between these two periods. Following wild dog recovery, an increase in the relative abundance of other large carnivores could obfuscate an effect of predation by wild dogs on dik-dik density.

I considered another possibility that donor control of dik-dik forage has intensified, thereby reduced the quality of dik-dik diets. Following Hebblewhite et al. (2005), I assessed diet quality for dik-dik using fecal nitrogen samples collected before (1999-2001; $n$ = 20) and after (2011; $n$ = 5) the return of wild dogs (but see Monteith et al. 2014). Dung samples were analyzed for nitrogen content (%N) by Dumas combustion using a Carlo-Erba CN Autoanalyzer (Milan, Italy). I equated higher dietary nitrogen as indicative of greater nutritional intake (Hebblewhite et al. 2005b). Following wild dog recovery, a decrease in forage quality for dik-dik could limit their population densities and confound any effect of predation by wild dogs.

I considered a third possibility that environmental heterogeneity, specifically rainfall, covaried with the recovery status of wild dogs. Water can limit population growth of ungulates in African savannas (Mduma et al. 1999, Ogutu and Owen-Smith 2003, Georgiadis et al. 2007b, Augustine 2010), and while dik-dik populations are not normally considered to be water-limited (Kingswood and Kumamoto 1996, Augustine 2010), I related rainfall to population densities of to test this possibility. I regressed rainfall and an interaction of rainfall with the estimated consumption of dik-dik by wild dogs (individuals $km^{-2}$) on the population growth rate of dik-dik. I measured the cumulative rainfall (mm) over a six month period ahead of each dik-dik population survey to represent the average inter-birth period of dik-dik (six months, Kingswood and Kumamoto 1996). Following the recovery of wild dogs, a combination of decreased rainfall and a significant, positive effect of rainfall on the population growth rate of dik-dik would obfuscate any effect of predation by wild dogs on the population density of dik-dik.

### 4.2.5 Suppression of tree abundance by dik-dik

I assessed the effects of dik-dik on three individual species of tree as well as the aggregate tree community. In our study area, *A. etbaica, A. mellifera* and *Grewia spp.* are browsed almost exclusively by dik-dik and not larger browsers (Figure 4.2; (Augustine and McNaughton 2004)). *A. etbaica, A. mellifera* and *Grewia spp.* comprised 24%, 21% and 8% of woody cover in our study area, respectively (Chapter 4). In addition, I measured the community-level response to dik-dik by pooling the response of all woody plants (32 species).

To measure the effect of dik-dik *per se* on tree abundance, I used data from a replicated series of exclosures as part of the UHURU experiment. The UHURU experiment was initiated in 2009 (Goheen et al. 2013) and consists of 36 1-ha fences distributed among three sites spread across a spatial gradient in rainfall. At each site, there are three replicates consisting of four 1 ha treatments each, in which electrified fences either exclude: (1) all ungulates ≥ 5 kg and ≥ 0.5 m tall (TOTAL); (2) all ungulates ≥ 40 kg and ≥ 1.2 m tall (MESO); (3) all ungulates > 2 m tall (MEGA); or (4) no large ungulates (OPEN). To maintain consistency with the study area from the pre-wild dog exclosure experiment (see below), I did not include the northern and more arid plots from the UHURU experiment in our analyses. Dik-dik have a standing height of ca. 1 m, and their exclusion releases their preferred forage into height classes taller than 1.0 m (Augustine and McNaughton 2004). Thus, within each 1 ha replicate, the number of tree stems in the 1.0 - 2.0 m height class were recorded in 2009 and in 2012.

The initial abundance of trees differed between treatments because of random variation in the distribution of trees. Thus, to quantify the effect of browsing on tree abundance, I calculated the net difference in stem density (stems 100 $m^{-2}$ $yr^{-1}$) between 2009 and 2012 as the response variable, with treatment as the predictor variable in an ANOVA. If dik-dik suppressed trees, then I expected to see a greater increase in the net difference in stem density in TOTAL plots (i.e., excludes all browsers) relative to MESO plots (i.e., accessible to dik-dik, but not larger browsers).

### 4.2.6 The effect of dik-dik on tree abundance in the presence and absence of wild dogs

As part of an existing study (Augustine and McNaughton 2004), I measured the effect of total browser exclusion on woody stems 1.0 - 2.0 m tall between 1999-2002, prior to wild dog recovery. The Augustine experiment consisted of three 0.5 ha electrified fences that excluded all browsers > 3 kg (TOTAL plots), and were paired with 0.5 ha unfenced controls (OPEN plots). I compared the effect of dik-dik exclusion on tree abundance in the absence (using the Augustine experiment) and presence (using the UHURU experiment) of wild dogs. For this analysis, I examined only the OPEN and TOTAL plots in the UHURU experiment for consistency with the Augustine experiment. I focused on the response of *A. etbaica*, *A. mellifera*, *Grewia* spp., and the tree community in aggregate to dik-dik exclusion. If wild dogs mediated the effect of dik-dik on trees, then the difference in tree abundance between OPEN and TOTAL plots from the Augustine experiment between 1999-2002 should be greater than that observed in the UHURU experiment between 2009-2012, particularly for the species most responsive to herbivory by dik-dik.

I tested this prediction using an ANOVA, with the net difference in stem density (stems 100 $m^{-2}$ $yr^{-1}$) as the response variable, and an interaction between treatment (OPEN vs. TOTAL plots) and the status of wild dog recovery (pre- vs. post-; hereafter “recovery status”) as predictor variables. I conducted separate analyses for *A. etbaica, A. mellifera, Grewia* spp. and the tree community in aggregate. I assessed the best-fitting model using Akaike’s Information Criterion, corrected for small sample sizes. High-ranking models which included the interaction term between treatment and recovery status may indicate that wild dogs have suppressed the effect of dik-dik on trees. Thus, if models containing this interaction term had strong support (i.e., Δ AICc

< 2), I proceeded to compare pairwise differences for each combination of treatment and recovery status using a Tukey's Honestly-Significant-Difference Test. Finally, I compared the mean difference between TOTAL and OPEN plots for both herbivore exclosure experiments, and used a pooled standard error to quantify uncertainty in grouped means (Quinn and Keough 2002). A large mean difference between TOTAL and OPEN pre-wild dog recovery relative to post-wild dog recovery is evidence for a trophic cascade. Conversely, if these mean differences are similar, it indicates that the effects of herbivory *per se* have not changed with the recovery status of wild dogs.

### 4.2.7 Other drivers of tree abundance: reticulate food chains and environmental heterogeneity

I considered the possibility that a reticulate food chain, consisting of other browsers (particularly, impala [*Aepyceros melampus*], giraffe [*Giraffa camelodopardalis*], and elephants [*Loxodonta africana*]) could either dampen or confound the effect of dik-dik on the abundance of trees. For example, if the density of browsers (besides dik-dik) increased with wild dog recovery, it may negate a potential indirect effect of wild dogs on dik-dik forage. Likewise, if the density of browsers (besides dik-dik) has decreased with wild dog recovery, our ability to ascribe changes in tree abundance to dik-dik *per se* would be compromised. Therefore, I compared the energetic demand of all non-dik-dik browsers pre- (2000-2002) and post-recovery (2008-2011) of wild dogs. Densities of these species were quantified while performing the dik-dik population surveys between 2000-2002 (Augustine 2010) and 2008-2011 (O'Brien and Kinnaird, unpublished data). Biomass was estimated using the mean adult body size of each species. To estimate energetic demand of all browsing ungulates, I calculated the mass-specific field metabolic rates as

$FMR = \sum_{j=1}^{n} 4.82 \cdot D_j^{0.734}$, where $M$ is the mean biomass density (g·km$^{-2}$) of species $j$ and $FMR$ is the energetic demand in kJ·day$^{-1}$ (Nagy 2005).

I considered a second possibility that environmental heterogeneity, especially rainfall, covaried with the recovery status of wild dogs. Rainfall mediates the effect herbivores on savanna plants in general (Sankaran et al. 2005, Bond 2008, Louthan et al. 2013). In particular, higher rainfall post-wild dog recovery could enhance tree survival, growth, and reproduction, thus muddling the indirect effect of wild dogs on trees. I compared records for monthly rainfall during pre- and post-wild dog recovery periods using a GLS model with a first-order autoregressive term to account for serial correlation in residuals.

## 4.3 Results

In this section I describe the results of the three main research questions for this chapter, along with alternative hypotheses for the observed patterns.

### 4.3.1 Do wild dogs suppress the population density of dik-dik?

The biomass density of wild dogs peaked between June 2007 and January 2008 at 3938 kg·days·km$^{-2}$, with an average mean biomass density of 1600 ± 266 kg·days·km$^{-2}$ (mean ± SE) since recovery in 2002. Dik-dik density was 145 ± 4 (individuals·km$^{-2}$) before wild dog recovery (1999-2002) and 97 ± 7 (individuals·km$^{-2}$) since 2008, corresponding to a mean decline of 33% ($F = 27.9$, df = 14, $P < 0.001$; Figure 4.3).

The recruitment index declined from 0.17 ± 0.02 (1999-2002) to 0.10 ± 0.01 (2008-2013), and decreased with increasing energetic demand of wild dogs (Figure 4.3). Similarly, the population growth rate of dik-dik was not affected significantly by dik-dik density (Likelihood ratio = 0.65, df = 13, $P = 0.421$), but was negatively affected by the energetic demand of wild dogs (Likelihood ratio = 4.05, df = 13, $P = 0.044$), suggesting a lack of functional response of wild dogs to dik-dik density (see Table 4.1).

Encounter rates with dik-dik decreased significantly by 58% near the active wild-dog den relative to the pre-denning period (Figure 4.3, Poisson rate parameter ($\lambda$) ± [95% CI] = 0.525 [0.36,0.74], $P < 0.001$), while the encounter rate in the control area did not change over the same period of time ($\lambda = 1.01$ [0.82,1.25], $P = 0.916$]). Sixty-days following the abandonment of the den by wild dogs, the proportional difference in encounter rates compared to the pre-denning period was similar near the den (22%) and in the control area (19%). Likewise, the recruitment index declined by 20% relative to the pre-denning period near the active den, while there was a fivefold increase in the recruitment index over the same period in the control area (Figure 4.3; $\chi^2 = 5.75$, $P = 0.008$). The recruitment index in the control area and near the den was the same pre- ($\chi^2 < 1$, $P = 0.999$) and post-denning ($\chi^2 < 1$, $P = 0.500$). Thus, over both expansive (82 km$^2$, 11 years) and restricted (31 km, 180 days) spatio-temporal scales, wild dogs had a pronounced, negative effect on the abundance of dik-dik.

### 4.3.2 Other drivers of dik-dik density: reticulate food chains, donor control and environmental heterogeneity

The decline in the dik-dik population following the recovery of wild dogs could not be explained by reticulate food webs, donor control or environmental heterogeneity. Compared to pre-wild dog recovery, the relative abundance of species most likely to consume dik-dik was either the same (leopard, $\lambda = 1.13$ [0.265, 10.260], $P \geq 0.999$) or significantly less following the recovery of wild dogs (black-backed jackal, $\lambda = 0.13$ [0.041,0.419], $P < 0.001$). This suggests that the observed decline in dik-dik density was not likely caused by an increased abundance of predators other than wild dogs.

Fecal nitrogen was similar pre- (2.04% ± 0.08%, $n = 20$) and post- (2.2% ± 0.16%, $n = 5$) wild dog recovery ($F = 0.43$, df = 23, $P = 0.519$). While the power to detect a difference between these two periods is somewhat limited by sample size, these results suggest that diet quality has not changed following the recovery of wild dogs. On average, 23% more monthly rainfall occurred post-wild dog (58.3 ± 4.5 mm, 2003-2013) compared to pre-wild dog recovery (47.3 ± 6.2 mm, 1999-2002), but this difference was not statistically significant (Figure 4.4; $t = 1.12$, df = 187, $P = 0.264$). Moreover, I did not find support for an effect of rainfall on population growth of dik-dik, nor for an interaction between rainfall and the estimated consumption of dik-dik on the population growth of dik-dik (Table 4.1). Together, my results suggest that the observed decline in dik-dik density was not caused by declining resource availability or quality.

### 4.3.3 Do dik-dik suppress tree abundance?

By themselves, dik-dik significantly reduced stem density of *A. mellifera* but not of *A. etbaica*, *Grewia* spp. or the aggregate tree community (Figure 4.5). Over a three-year period, the net difference in *A. mellifera* stems in TOTAL plots increased by 84% relative to MESO plots that were accessible only to dik-dik and no other browser. The net difference in stem density for *A. etbaica, Grewia* spp. and the aggregate tree community increased by 54%, 52% and 40%, respectively, in TOTAL plots relative to MESO plots (Figure 4.5). A combined probability test (Whitlock 2005) of *A. mellifera*, *A. etbaica ,*and *Grewia* spp. indicated that these collective differences were statistically significant (*P* =0.011). The aggregate community response was not included in this combined test because it is not independent of the response of the other three species. Thus, between 2009 and 2012, dik-dik *per se* contributed to the suppression of individual tree species and the aggregate tree community, but exerted their most consistent effect on *A. mellifera* (Figure 4.5).

### 4.3.4 Is the effect of dik-dik on tree abundance reduced in the presence of wild dogs?

The effect of herbivore exclusion was not reduced in the presence of wild dogs. When comparing just the OPEN plots (Figure 4.6), a combined probability test for *A. mellifera*, *A. etbaica*, and *Grewia* spp. indicated a significant, collective effect (*P* =0.035). This result appears to suggest that the recovery of wild dogs has a positive indirect effect on stem density. However, none of the best-fitting models I tested included a treatment (i.e., OPEN vs. TOTAL) x recovery status term (Table 4.2). Treatment was included in all best-fitting models, suggesting that browsing had a strong effect on stem density both pre- and post-wild dog recovery. Moreover, recovery status was included in the best-fitting models for *A. mellifera*, *A. etbaica* and the aggregate tree community, reflecting a systematic increase in stem density within TOTAL plots (Figure S4). Indeed, when comparing just the TOTAL plots (Figure 4.6) between experiments, a combined probability test (Whitlock 2005) of *A. mellifera*, *A. etbaica*, and *Grewia* spp. indicated a marginally significant collective effect ($P = 0.052$). In other words, there was a tendency for heightened stem density in the absence of herbivory, irrespective of recovery status. The mean difference between OPEN and TOTAL plots was 35%, 34%, 42% and 3% greater following the recovery of wild dogs for *A. mellifera*, *A. etbaica, Grewia* spp. and the aggregate tree community, respectively (Figure 4.7). Thus, there was an overall increase in the effect of herbivory on stem density following the recovery of wild dogs.

### 4.3.5 Other drivers of tree abundance: reticulate food chains and environmental heterogeneity

The biomass density of browsers (excluding dik-dik) increased slightly since wild dog recovery from 4129 kg·km$^{-2}$ pre-wild dog recovery to 4178 kg·km$^{-2}$ post-wild dog recovery (Table 4.3). Our estimates of biomass density do not account for the duration of residency, and resident browsers should have a more persistent, chronic effect on tree growth than transient species. When examining only the resident browsers (excluding dik-dik as well as transient giraffe and elephant), the biomass density was 949 kg·km$^{-2}$ pre-wild dog recovery and 1140 kg·km$^{-2}$ post wild dog recovery, an increase of 20%. When I converted biomass density to metabolic load, there was a 7% increase for all browsers and a 20% increase for resident browsers following wild dog recovery. This suggests that herbivory by browsers other than dik-dik may have intensified with the recovery of wild dogs. In addition, there was a non-significant, 36% increase in mean rainfall during the post-wild dog exclosure experiment (44.8 ± 6.7 mm [1999-2002] vs. 60.9 ±

7.6 mm [2009-2012]; $t = 1.09$, df = 94, $P = 0.278$). Since 2008, increases in the abundance of other browsers and heightened rainfall may explain why the effect of dik-dik on trees was not reduced by the recovery of wild dogs.

## 4.4 Discussion

In spite of the suppression of dik-dik by wild dogs, and of trees by dik-dik, I did not find support for a trophic cascade triggered by the recolonization of wild dogs to the Laikipia Plateau. Trophic cascades can arise when plant biomass is enhanced by top-down forces through at least two sequential trophic levels. Critically, these forces must be demonstrably stronger than other factors that regulate species abundance. The decline in the dik-dik population could not be explained by hypotheses more parsimonious than heightened mortality from predation by wild dogs. Contrary to the trophic cascade hypothesis, wild dog recovery did not dampen the extent to which dik-dik suppressed tree abundance. Below, I evaluate potential mechanisms which may have buffered against a trophic cascade, and highlight the implications of these findings for large carnivore restoration in savanna ecosystems.

### 4.4.1 Do wild dogs suppress dik-dik?

I attributed the main effect of wild dogs on dik-dik to heightened mortality from predation. I acknowledge that data on vital rates of dik-dik (lacking in my study) could have provided even stronger inference. For example, data on the disappearance or survival rates of individuals in the presence and absence of wild dogs (e.g., Estes et al. 1998, Hebblewhite et al. 2005b). However, the declining population density and recruitment of dik-dik after wild dog abundance at a local

(180 days, 34 km) spatio-temporal scale strongly suggests that wild dogs are the causal agent of dik-dik decline at an expansive (11 years, 82 $km^2$) scale (Figure 4.3).

In addition to directly killing dik-dik, wild dogs may also have changed the anti-predator behavior or dispersion of dik-dik, thereby causing a perceived decline in the population. Dik-dik are thought to rely on crypsis to evade predators (Estes 1991, Brashares et al. 2000), so it is possible that they are less apparent when wild dogs are in the vicinity. However, experiments conducted on free-roaming dik-dik indicate that vigilance (Coleman et al. 2008) and use of open habitats (Chapter 2) increases with  risk of predation. Thus, under heightened risk of predation, dik-dik should be more conspicuous following the recovery of wild dogs. Moreover, if dik-dik are less conspicuous because of risk of predation by wild dogs, then the detection distance (i.e., distance at which dik-dik seen by observers) from these surveys should have decreased following the recovery of wild dogs; however, the detection distances were nearly the same pre- (22.7 ± 0.4 m) and post-wild dog recovery (24.4 ± 0.5 m). Thus, I do not believe that changes in dik-dik behavior are the reason why fewer dik-dik have been observed following the recovery of wild dogs.

Another possibility is that dik-dik avoided risky areas, particularly within the home range of denning wild dogs (Figure 4.1). Larger prey (e.g., impala, Greater kudu [*Tragelaphus strepsiceros*]) may occur at lower densities near active wild dog dens, either because dens are established in areas with low prey densities or because these prey avoid denning wild dogs (Romañach and Lindsey 2008, Mbizah et al. 2014). However, because dik-dik are territorial and have home ranges that are ca. 100-300 m in diameter, dispersion out of denning home range is highly unlikely. Indeed, I observed a contraction in home ranges for dik-dik following exposure to a cue of risk from wild dogs (Chapter 2). Thus, heightened predation by wild dogs almost certainly explains why the dik-dik population declined over the course of our 14-year study. Still, I considered factors coincident with wild dog recovery that may also have caused a decline in the dik-dik population.

I tested three alternative hypotheses to explain why dik-dik declined with the recolonization of wild dogs, including reticulate food chains, donor control and environmental heterogeneity. Resource limitation is not predicted to drive the abundance of small antelope like dik-dik (Hopcraft et al. 2010) and I found that variation in diet quality and rainfall could not explain why the population density of dik-dik has declined since the recolonization of wild dogs. Thus, donor control and environmental heterogeneity do not explain the decline in the dik-dik population. The most likely explanation for the declining dik-dik population - other than predation by wild dogs *per se* – is a reticulate food chain and heightened predation from other carnivores.

To assess the importance of wild dogs relative to other predators requires data on the proportion of dik-dik in the diets for a number of carnivores over time (e.g., Sinclair et al. 2003, Kauffman et al. 2007, Kortello et al. 2007). In the absence of these data, I quantified the relative abundance of carnivores and found no increase that could explain heightened predation of dik-dik. I also found no evidence of prey switching by wild dogs, as the predicted effect of wild dog predation on $r$ did not change with dik-dik density (Table 4.1), nor did alternative prey (impala) decline with wild dog recovery (Table 4.3). Assuming that that the *per capita* consumption of dik-dik by other predators has not increased over time, the importance of wild dogs in shaping dik-dik density has likely remained unchanged since they recolonized the study area. Thus, I did not find compelling evidence that factors - other than predation by wild dogs specifically - were responsible for the observed decline in the dik-dik population.

### 4.4.2 Do dik-dik suppress trees?

To determine if wild dogs enhance tree abundance, it was necessary to determine if dik-dik, on their own, have the capacity to suppress trees. In other words, dik-dik needed to be sufficiently abundant to lower tree abundance, and their effect needed to be isolated from that of other browsers. Through a series of size-biased herbivore exclosures, I documented that browsing by dik-dik *per se* is sufficient to suppress *A. mellifera* (Table 4.2), consistent with Augustine and McNaughton (2004) who also attributed significant browsing damage of *A. mellifera*, *A. etbaica* and *Grewia* spp. to dik-dik. However, I did not find evidence that dik-dik, on their own, significantly decreased the abundance of *A. etbaica*, *Grewia* spp. or the aggregate tree community over a three-year period (2009-2012).

Where trophic cascades have been documented in systems with multiple species of herbivores, ecologists typically have discounted species-specific sources of herbivory (Ripple and Larsen 2000, Ripple et al. 2001, Hebblewhite et al. 2005b). However, pooling sources of herbivory may not preclude evaluation of a community-level trophic cascade (*sensu* Polis et al. 2000) if species are similar in their vulnerability to predation. For example, concluding that wolves in the western North America enhance plant abundance via predation of the herbivore guild (i.e., deer, elk, moose) is consistent with a community-level trophic cascade. Concluding that enhanced plant growth occurred because of the suppression of an individual species of herbivore (e.g., elk) requires information on that species' contribution to plant suppression, relative to that of other herbivores (e.g., deer and moose; Ripple and Larsen 2000, Ripple et al. 2001, Hebblewhite et al. 2005). Such species-specific effects are particularly important to identify when species differ in their vulnerability to predation. In Laikipia, for example, populations of impala and elephants have comparable energetic requirements to that of the dik-dik population (Table 4.3) and browse on the same trees species (Goheen et al. 2013). However, wild dogs strongly reduce dik-dik abundance, weakly reduce impala abundance, and have no effect on the abundance of elephants (Woodroffe et al. 2007a, Hopcraft et al. 2010). Thus, to evaluate if wild dog recovery could have triggered a trophic cascade via suppression of dik-dik, it was first necessary to demonstrate that dik-dik *per se* suppressed trees (Figure 4.5) and that the abundance of other browsers did not decline with declining dik-dik densities (Table 4.3).

### 4.4.3 Is the effect of dik-dik on trees reduced in the presence of wild dogs?

I did not find evidence for a trophic cascade triggered by wild dog recovery, in spite of evidence for top-down suppression through two sequential trophic levels. At least two possibilities exist as to why wild dog recovery did not generate a trophic cascade. First, the forage released by the suppression of dik-dik may have been consumed by remaining dik-dik or other herbivore species (Table 4.3). Consequently, browsers in Laikipia may constitute a reticulate food web that at least buffered, if not nullified, any cascading effects of top-down forcing caused by the recovery of wild dogs (Polis and Strong 1996, Tuscans et al. 2007, Thibault et al. 2010 ).

Second, the 33% decline in the dik-dik population across our study area may not reflect more localized changes in population density. Wild dogs hunt over expansive home ranges (mean =

27790 ha) (Woodroffe 2011b) compared to the relatively small extent of our herbivore exclosures (0.5- 1.0 ha for each replicate) and the home ranges of dik-dik (ca. 8 ha, Ford unpublished data). As a monogamous and territorial antelope, the effect of dik-dik browsing is typically driven by no more than 2 adults and 1-2 young individuals in a given area. As such, it is unclear if the 33% decline in the dik-dik population across the study area is reflected by a proportional change in herbivory by dik-dik at the scale of our herbivore exclosures. For example, wild dogs would need to consistently hunt within the vicinity of the exclosures and consume 1/3 of each family group. Conversely, a change in the population of larger ungulates should more closely reflect the intensity of herbivory at a local scale. Many larger ungulates (e.g., deer, elk) are gregarious, non-territorial and have expansive ranges which combine to homogenize the intensity of herbivory over a broad area (Kauffman et al. 2007, Ritchie 2009). For this reason, trophic cascades associated with large ungulates may be more tractable compared to the effect of a declining dik-dik population caused by the recovery of wild dogs.

Third, variation in rainfall during the pre- and post-wild dog herbivore experiments was similar in that both included unusually dry (2000, 2001, 2009) and wet years (2001, 2010, 2011), but the 23% increase in mean monthly rainfall after wild dogs recovered may have overridden any signal of reduced browsing by dik-dik. Indeed, when comparing the TOTAL plots between Augustine and UHURU experiments, the net difference in stem density was greater post-wild dog recovery (Figure 4.6). This suggests that conditions have become more favorable for trees with time, irrespective of the reduction in browsing pressure by dik-dik. In general, tree abundance in African savannas is limited by rainfall below a MAP of 650 mm, and by herbivores and fire above 650 mm (Sankaran et al. 2005). During the pre-recovery exclosure experiment, MAP was below this threshold (537 ± 100 mm) but exceeded it following wild dog recovery (730 ± 146 mm). Consequently, the importance of browsing for tree abundance may actually have increased following the recovery of wild dogs.

In systems dominated by large carnivores, evidence for trophic cascades is typically sought by correlating biomass of herbivores to plants over vast areas with and without large carnivores (Estes and Palmisan 1974, Terborgh et al. 2001, Croll et al. 2005), or over a span of years over which carnivore biomass has changed (McLaren and Peterson 1994, Beschta and Ripple 2009). Because correlative approaches usually lack replication and control, they can suffer from confounding variation in evaluating the trophic cascade hypothesis (Terborgh et al. 2010, Winnie 2012). However, correlative approaches often are the only option available to investigate trophic cascades at scales commensurate with the movements of large carnivores and their prey. Even within the framework of a correlative approach, studies on trophic cascades involving large carnivores often are limited in two fundamental ways.

The first limitation arises when studies fail to document the population dynamics of the three (or more) trophic levels that comprise a trophic cascade. By definition, trophic cascades involve at least two direct species interactions (e.g., carnivore-herbivore, herbivore-plant) and one indirect interaction (carnivore-plant), each of which should be quantified. Even through an ostensibly correlative approach, it is still possible to measure variation in the biomass of one- (e.g. total herbivore exclusion), two- (e.g., carnivore-free areas or times) and three-level food chains (e.g. post-restoration of carnivore), ideally each paired with a control (Estes et al. 1998, Hebblewhite et al. 2005b, Kauffman et al. 2007, Kauffman et al. 2010). These approaches contrast with other studies, in which a positive correlation between plant and carnivore biomass is interpreted as evidence for trophic cascade (Ripple et al. 2001, Callan et al. 2013, Kuijper et al. 2013). Missing from these approaches is explicit quantification of the response of herbivores to carnivores, and of plants to herbivores. In using herbivore exclosures (i.e., a 1-level food chain) anc control plots accessible to herbivores in the absence (i.e., a 2-level food chain) and presence (i.e., a 3-level food chain) of wild dogs, it allowed me to quantify whether and how a trophic cascade has occurred on this landscape. Had I simply compared tree abundance in the presence and absence of wild dogs (e.g., pre- and post-wild dog recovery in OPEN plots, Figure 4.6), I would have concluded (incorrectly) that the increase in tree abundance was caused by wild dog recovery.

The second limitation in many correlative studies lies in the difficulty of testing alternative explanations for variation in plant and herbivore biomass. For example, Kuker and Barrett-Lennard (2010) highlight that alternative sources of predation, environmental contamination, and diseases are all plausible and untested explanations for the trophic cascade hypothesized in Estes et al. (1998). In the Greater Yellowstone Ecosystem, alternative explanations to wolf restoration for why elk have declined and aspen have increased has resulted in a productive debate in the peer-reviewed literature (Mech 2012, Winnie 2012, Beschta and Ripple 2013, Kauffman et al. 2013, Marris 2014). Identifying the species that interact most strongly to generate trophic cascades may be critical when species have high economic (e.g., elk) or conservation (e.g., wolves, brown bears, wild dogs) value.

### 4.4.4 Conclusion

East African savannas are compelling systems to apply both conservation practice and ecological theory to our evaluation of trophic cascades. Here, tree cover is a key determinant of both ecosystem dynamics and rural livelihoods. For example, tree cover alters nutrient cycles (Belsky 1994, Treydte et al. 2007) and surface water retention (Scholes and Archer 1997, Smit and Rethman 2000), provides forage availability for both wild and domestic herbivores (Odadi et al. 2009, Odadi et al. 2011) and forms an important source of household fuel in many areas (Chambers and Longhurst 1986). Rainfall, soils, natural disturbance and herbivory are notable drivers of tree cover (Sankaran et al. 2005, Bond 2008). Claims that trophic cascades are a fundamental property of ecosystems (Terborgh et al. 2010) are supported by growing evidence for a positive association between the biomass of broad-leaved trees and large carnivores in temperate systems (Beschta and Ripple 2009); however, I caution that it is premature to conclude that large carnivores indirectly facilitate tree cover in African savannas.

The restoration of large carnivores can be highly divisive among local communities and often attracts a disproportionate amount of conservation funding, leading to controversy over the role of these species in facilitating ecosystem services (Andelman and Fagan 2000, Clark and May 2002). For the discipline of community ecology to remain relevant in resolving these debates, I suggest that researchers adhere to the basic tenants of the scientific method, including replication, control, and testing of multiple hypotheses. While some may claim that the restoration of large carnivores is a moral imperative (Ripple et al. 2014), I add that scientific rigour is both the duty and responsibility of all ecologists. The extent to which large carnivores trigger trophic cascades is a testable hypothesis, not an exclusive one.

**Figure 4.1Location of transects near and away from an active wild dog denning site. The left panel shows wild dog utilization during the pre-denning period while the right panel shows the same area during the active denning period. In the left panel, black lines are roads, and in the right panel black lines are roads in the near den area, while white lines are roads in the control area. I used a length weighted mean utilization of 0.005 to partition the near den and control areas. White points show GPS relocations (30 min interval) of a single adult male from this pack. There are no GPS relocations available in the post-denning period but the den was not being used during this time.**

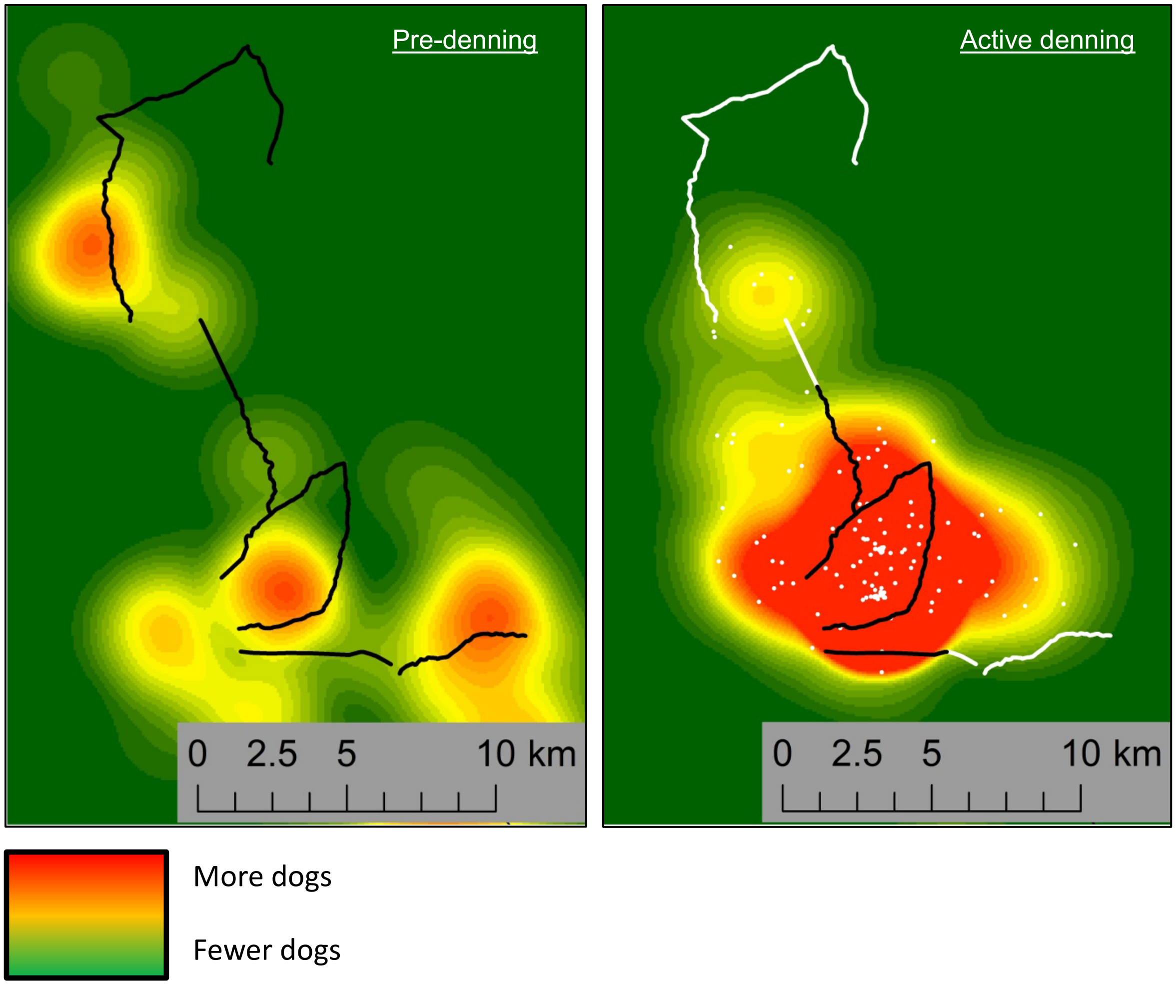


**Figure 4.2 Twig biomass accumulation of two *Acacia* spp. as a function of tree height and herbivore exclusion. Between 1999-2002 (i.e., prior to recolonization by African wild dogs), browsing pressure was most pronounced within the range at which dik-dik commonly forage (a) < 0.5 m, and not at heights exceeding this range (b) 1-1.25 m, for *A. etbaica* (ACET) and *A. mellifera* (ACME). TOTAL plots excluded all herbivores > 3kg, while OPEN plots were accessible to herbivores (redrawn with permission from data published in Augustine and MacNaughton 2004).**

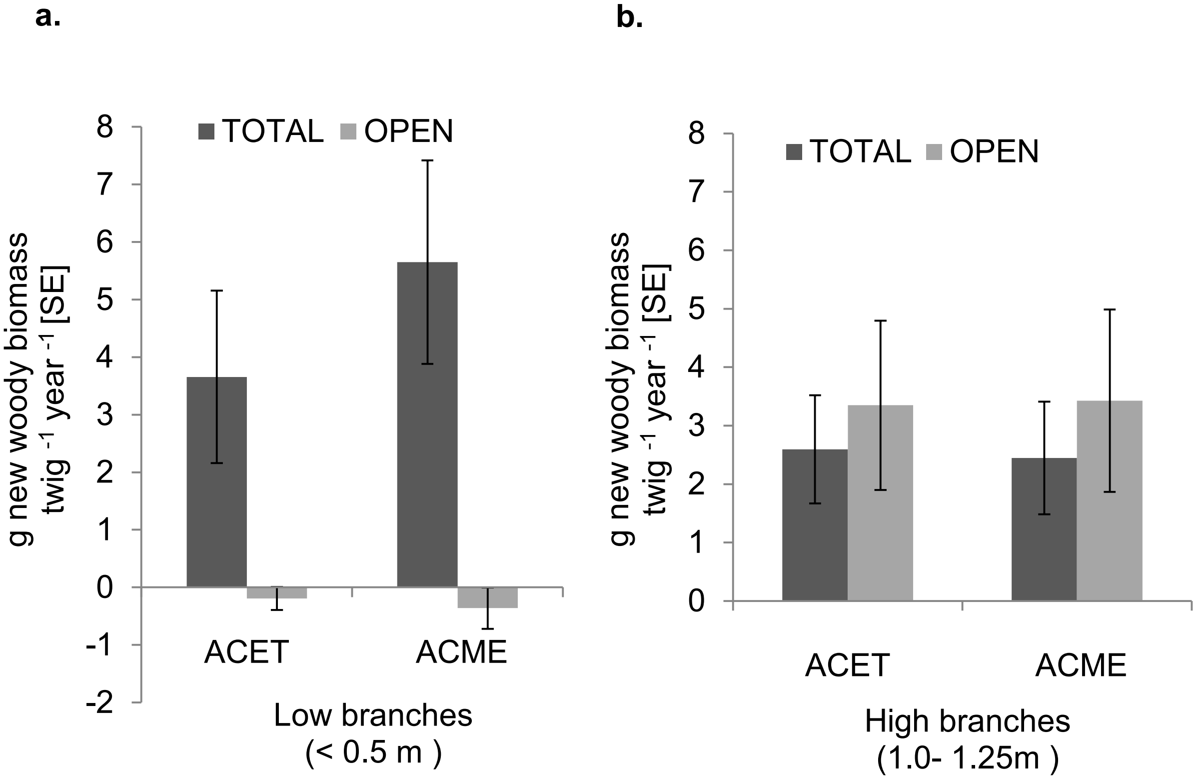
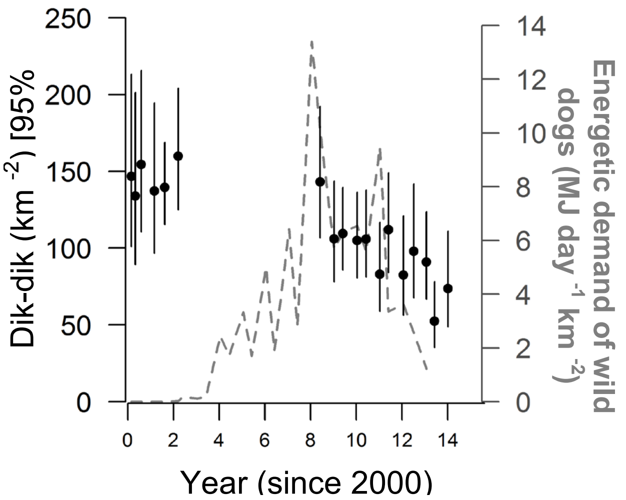
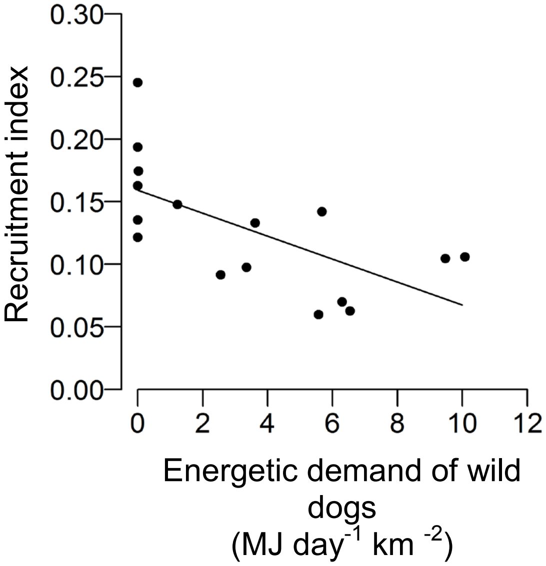


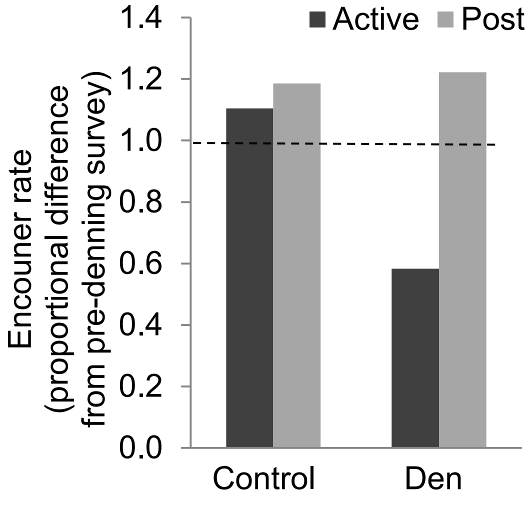
**Figure 4.3 The suppression of dik-dik by wild dogs, over an 11-year period and 82 km$^2$ area, shown as (a) dik-dik density in black and the energetic demand of wild dogs since 2000 in gray; (b) the energetic demand of wild dogs, which had a significant effect on the recruitment index (proportion of families with ≥3 individuals) ($n = 14$, $R^2 = 0.368$, $P = 0.007$). Over a relatively fine spatio-temporal scale (180 days, 34 km), suppression of dik-dik by wild dogs was evident on (c) encounter rates (dik-dik km$^{-1}$), which decreased by 42% near an active wild dog den and increased by 10% in a nearby control area where wild dogs foraged much less frequently (Figure 4.1.); and on (d) the recruitment index, which decreased by 50% near the den and increased by 375% in the control area during the same time. I show the proportional change from pre-denning to the active- and post-denning periods because of initial differences between control and denning areas in the pre-denning surveys. Responses during the active and post-denning surveys are equal to the pre-denning surveys at a value of 1 (dashed line).**

**a.**


Dik-dik (km -2) [95%
250
200
150
100
50
0
Energetic demand of wild dogs (MJ day -1 km -2)
14
12
10
8
6
4
2
0
0 2 4 6 8 10 12 14
Year (since 2000)

**b.**


Recruitment index
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0 2 4 6 8 10 12
Energetic demand of wild dogs
(MJ day-1 km -2)


Encouner rate
(proportional difference
from pre-denning survey)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Active
Post
Control
Den

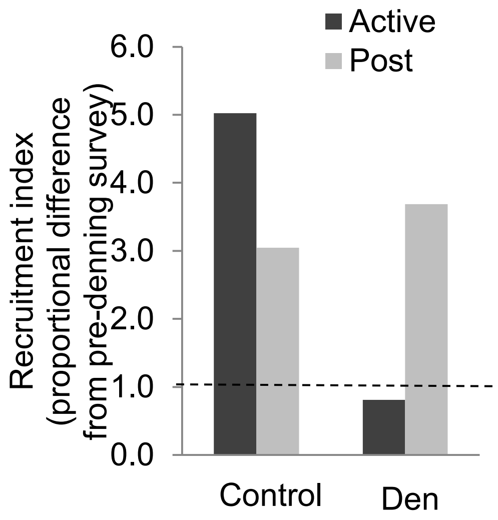

Recruitment index
(proportional difference
from pre-denning survey)
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Active
Post
Control
Den

**Figure 4.4 Mean monthly rainfall during each year of this study. Wild dogs recolonized the area in 2002 and began denning on Mpala Research Center in 2003. Shaded sections show the years during which the two herbivore exclosure experiments were conducted. I estimated population density of dik-diks in 1999-2002 and from 2008-onwards.**

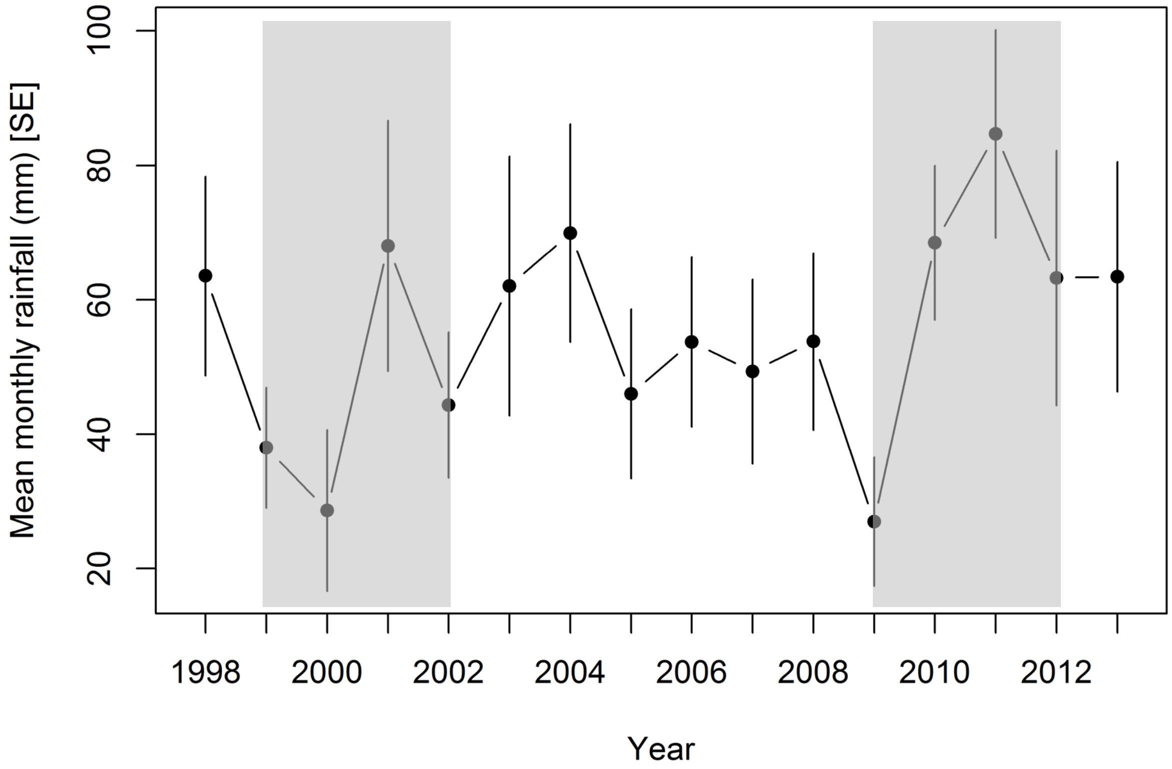


**Figure 4.5 Suppression of trees by dik-dik over a three-period, shown as changes in stem density for trees between 2009-2012. Plots excluded all mammalian herbivores >3 kg (TOTAL) or permitted access by dik-dik (5 kg) and smaller herbivores, but not larger herbivores (MESO). The effects of dik-dik exclusion were significant for *A. mellifera* (*F* = 8.31, df = 10, *P* = 0.016) but not for *A. etbaica* (*F* = 1.88, df = 10, *P* = 0.201), *Grewia* spp. (*F* = 2.22, df = 10, *P* = 0.167) or the pooled response of the tree community (*F* = 0.920, df = 10, *P* = 0.360).**

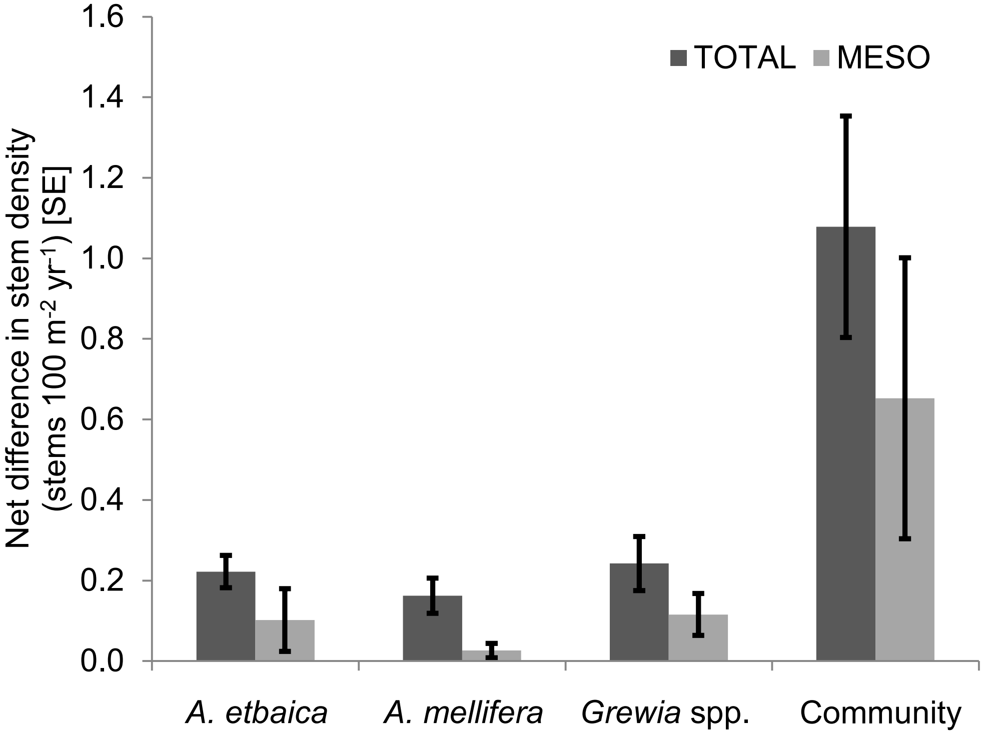


**Figure 4.6 The net difference in density (stems 100 m$^{-2}$ yr$^{-1}$) for stems 1 – 2 m tall, over a 3-year period pre- (1999-2002) and post- (2009-2012) recovery of wild dogs for (top panel) three species of tree and (bottom panel) the aggregate tree community consisting of ca. 30 species. Note difference soin the scale of the y-axis between top and bottom panels. TOTAL plots excluded all herbivores > 3kg, while OPEN plots were accessible to herbivores.**

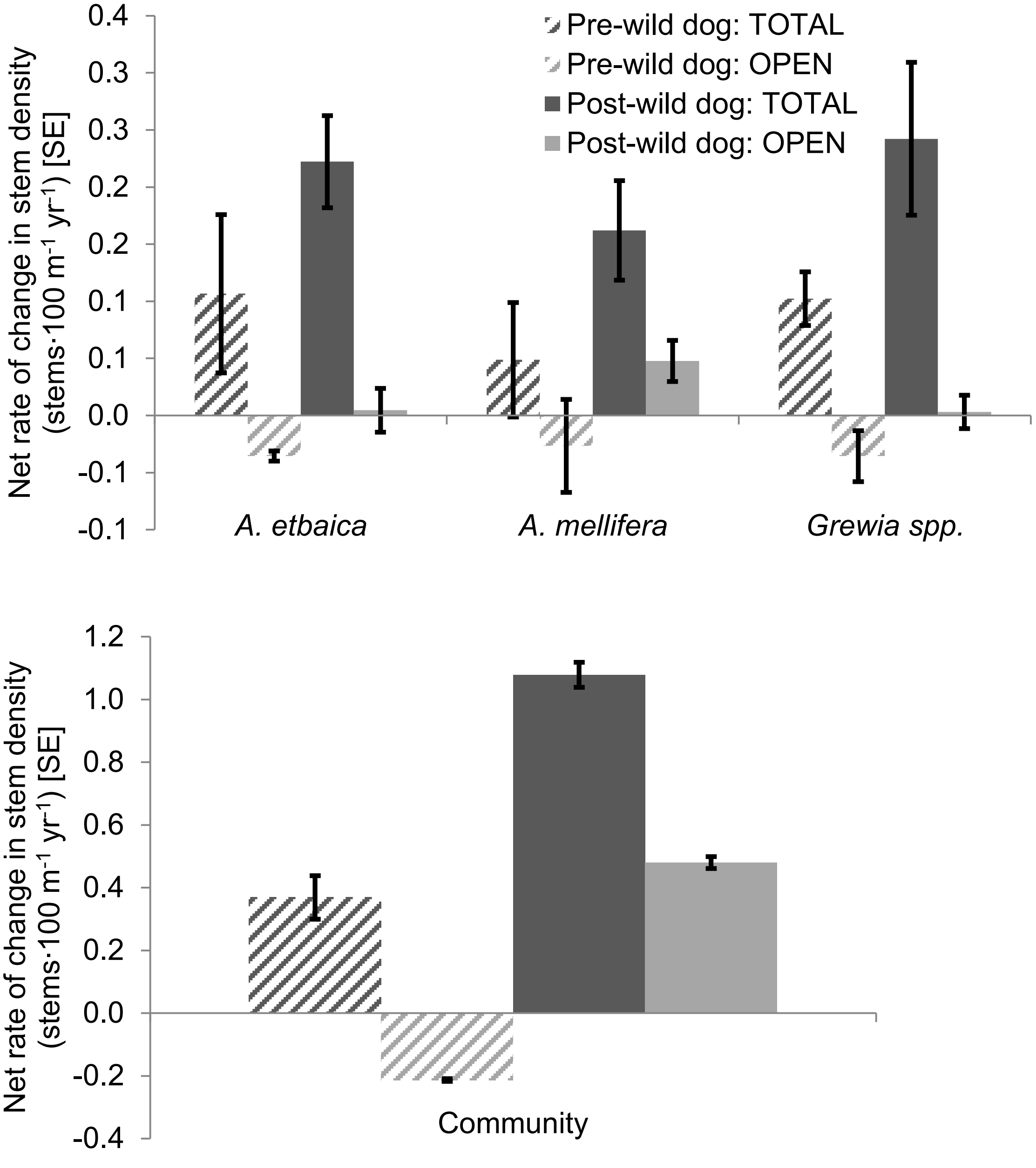


**Figure 4.7 The difference between the mean of TOTAL and OPEN plots for the net difference in stem density (stems 100 m$^{-2}$ yr$^{-1}$) over a 3-year period, pre- (1999-2002) and post- (2009-2012) recovery of wild dogs. The net difference in stem density for each combination of treatment (TOTAL vs OPEN) and experiment (pre- vs. post wild dog recovery) is shown in Figure 4.6.**

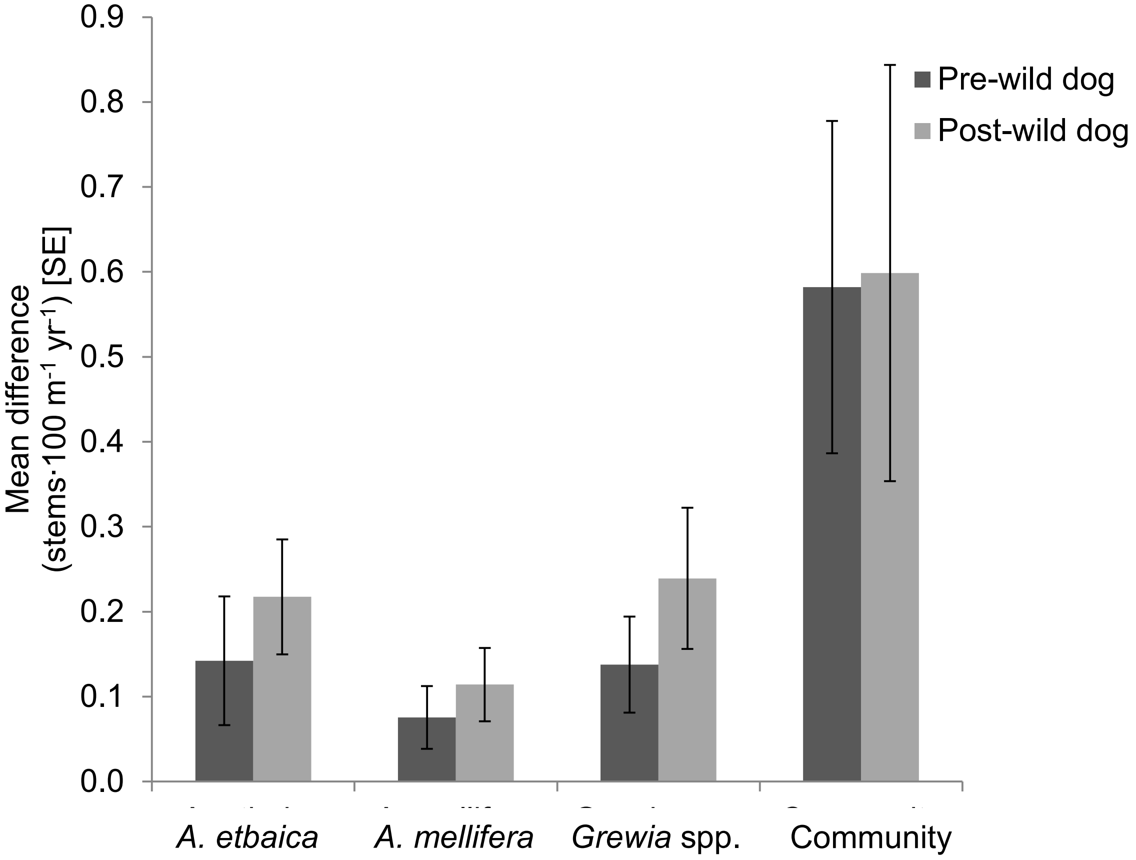


**Table 4.1 Model selection table for the effects of dik-dik density (DENSITY = individuals km$^{-2}$), rainfall (RAIN = mm 6 months$^{-1}$), the estimated consumption of dik-dik by wild dogs prior to dik-dik population surveys (EATEN = individuals km$^{-2}$) and an interaction between EATEN and DENSITY on dik-dik population growth (*r*) between surveys. *K* refers to the number of parameters in the model, *LL* is the log-likelihood.**

| Model | *K* | *LL* | AICc | ΔAICc | Akaike weight ($w_i$) |
|---|---|---|---|---|---|
| EATEN | 6 | -71.33 | 165.17 | 0.00 | 0.66 |
| RAIN | 6 | -72.76 | 168.02 | 2.85 | 0.16 |
| DENSITY | 6 | -73.04 | 168.57 | 3.41 | 0.12 |
| EATEN + RAIN | 7 | -70.18 | 170.36 | 5.20 | 0.05 |
| EATEN + DENSITY | 7 | -71.21 | 172.41 | 7.24 | 0.02 |
| DENSITY + RAIN | 7 | -75.13 | 180.25 | 15.09 | < 0.01 |
| EATEN + DENSITY + EATEN*DENSITY | 8 | -72.56 | 185.12 | 19.95 | < 0.01 |
| EATEN + DENSITY + RAIN | 8 | -73.57 | 187.14 | 21.98 | < 0.01 |
| EATEN + DENSITY + RAIN + EATEN*DENSITY | 9 | -71.88 | 197.76 | 32.59 | < 0.01 |

**Table 4.2 Model selection table for the effects of treatment (OPEN vs. TOTAL) and recovery (pre- vs. post-wild dog recovery) on the net difference in stem density (stems 100 m$^{-2}$ yr$^{-1}$). "Community" includes the aggregate response of 32 species of trees and woody plants. *K* refers to the number of parameters in the model, *LL* is the log-likelihood.**

| Species | Model | *K* | LL | AICc | ΔAICc | Akaike weight ($w_i$) |
|---|---|---|---|---|---|---|
| Community | Treatment + Recovery | 4 | -9.38 | 29.83 | 0.00 | 0.75 |
| | Treatment + Recovery + Treatment*Recovery | 5 | -9.38 | 33.75 | 3.92 | 0.11 |
| | Recovery | 3 | -13.21 | 34.12 | 4.29 | 0.09 |
| | Treatment | 3 | -13.93 | 35.58 | 5.75 | 0.04 |
| | Intercept-only | 2 | -16.43 | 37.66 | 7.83 | 0.01 |
| *A. etbaica* | Treatment + Recovery | 4 | 21.73 | -32.38 | 0.00 | 0.52 |
| | Treatment | 3 | 19.67 | -31.62 | 0.76 | 0.35 |
| | Treatment + Recovery + Treatment*Recovery | 5 | 22.29 | -29.58 | 2.80 | 0.13 |
| | Intercept-only | 2 | 11.76 | -18.73 | 13.66 | 0.00 |
| | Recovery | 3 | 12.56 | -17.41 | 14.97 | 0.00 |
| *A. mellifera* | Treatment + Recovery | 4 | 21.84 | -32.61 | 0.00 | 0.59 |
| | Treatment | 3 | 18.95 | -30.20 | 2.41 | 0.18 |
| | Treatment + Recovery + Treatment*Recovery | 5 | 21.99 | -28.98 | 3.63 | 0.10 |
| | Recovery | 3 | 18.22 | -28.72 | 3.89 | 0.08 |
| | Intercept-only | 2 | 16.19 | -27.57 | 5.04 | 0.05 |
| *Grewia* spp. | Treatment | 3 | 15.44 | -23.16 | 0.00 | 0.45 |
| | Treatment + Recovery | 4 | 17.10 | -23.12 | 0.04 | 0.44 |
| | Treatment + Recovery + Treatment*Recovery | 5 | 17.70 | -20.41 | 2.75 | 0.11 |
| | Intercept-only | 2 | 9.19 | -13.59 | 9.57 | 0.00 |
| | Recovery | 3 | 9.98 | -12.25 | 10.90 | 0.00 |

**Table 4.3 Changes in the metabolic load of mammalian browsers at Mpala Research Centre pre- (1999-2002) and post- (2008-2011) recovery of African wild dogs. Mean population densities were determined using distance sampling methods, described in the main text.**

| | | | Density (individuals · km$^{-2}$) | | Biomass density (kg · km$^{-2}$) | | Metabolic load (KJ · km$^{-2}$) | |
|---|---|---|---|---|---|---|---|---|
| Species | Mass (kg) | Residency | Pre- | Post- | Pre- | Post- | Pre- | Post- |
| Dik-dik | 5 | Resident | 139.00 | 109.00 | 694 | 369 | 93406 | 78359 |
| Steinbuck | 10 | Resident | 0.52 | 0.08* | 5 | 1 | 2574 | 767 |
| Thompson's gazelle | 25 | Resident | 0.00 | 0.04* | 0 | 4 | 0 | 2123 |
| Bushbuck | 30 | Resident | 0.20 | 0.10* | 6 | 3 | 2859 | 1719 |
| Impala | 40 | Resident | 20.30 | 23.30 | 812 | 744 | 104872 | 116037 |
| Grant's gazelle | 50 | Resident | 0.00 | 1.11 | 0 | 68 | 0 | 16895 |
| Eland | 340 | Resident | 0.37 | 0.12 | 126 | 133 | 26682 | 27733 |
| Giraffe | 750 | Migrant | 0.33 | 1.78 | 248 | 1170 | 43846 | 137118 |
| Elephant | 1725 | Migrant | 1.70 | 0.21 | 2933 | 1691 | 269153 | 179643 |
| All browsers | | | 162 | 137 | 4823 | 4547 | 543392 | 560395 |
| Resident-only | | | 160 | 135 | 1643 | 1686 | 230393 | 243634 |

* Due to low detection, these estimates are at the limit of resolution.

# Chapter 5: Conclusion and synthesis

## 5.1 Introduction

The focal phenomena that ecologists endeavor to explain are dynamic interactions. Arguably, this focus on the interaction separates ecology from natural history, in which focal phenomena often are descriptive and static. For example, natural history may describe the occurrence of a particular behavior in an animal, the size or distribution of a population, or the number of species in a particular area. Conversely, ecology seeks to explain and quantify variation in the descriptions of natural history – *Why* does this behavior occur? *Why* does the population of these species change between areas or over time? *Why* does this community have more or less species than another? Using testable hypotheses, these and other questions posed by ecologists generalize to the study of two forms of interaction: direct and indirect (Wootton 1994).

Direct interactions are defined as the effect of one individual, population, trophic level, or environmental factor on another individual, population, or trophic level. Examples include predation, herbivory, mutualism, parasitism, and interference competition (Wootton 1994). Quantifying a direct interaction typically involves manipulation of a single variable (e.g., individual, population, trophic level or environmental factor) from a pair-wise relationship. For example, the effects of herbivory may be quantified by measuring a decline in plant biomass following a rise in the biomass of herbivores (Belsky 1984, Schmitz 2010). Alternative explanations to the observed decline in plant biomass, like resource limitation or disease, also need to be tested to provide convincing evidence for the effects of herbivory (McNaughton 1983, 1986, Anderson et al. 2010). Because of the pair-wise nature of direct interactions, their quantification is tractable in most study systems  (Fretwell 1987, Wootton 1994).

Indirect interactions involve the cascading or ‘knock-on’ effects of two or more direct and independent interactions (Wootton 1994). Examples include trophic cascades, apparent competition, scramble competition, and indirect mutualisms. Evidence for an indirect interaction requires the documentation of at least two direct interactions in addition to the indirect interaction itself (Ohgushi et al. 2012). For example, scramble competition between species requires evidence of resource limitation of at least one of the focal populations (direct interaction 1), resource suppression by at least one of the populations of competitors (direct interaction 2), and a decline in abundance of the focal population caused by resource suppression from the competitor population (the indirect interaction) (Tilman 1977, Mac Nally 1983). Because evidence is needed for at least three interactions, indirect interactions are far less tractable than direct interactions in most study systems. Indeed, experimental methods often are needed to obtain the control and replication needed to demonstrate an indirect effect (Fretwell 1987, Wootton 1994, Underwood et al. 2000).

Experiments that quantify indirect interactions have been conducted largely in systems characterized by small-bodied and short-lived organisms that can persist in controlled environments (Gause 1969, Schmitz et al. 2000, Borer et al. 2005). Studies conducted in these systems are afforded high levels of replication, can control for both top-down and bottom-up forces in food chains, and enjoy multi-generational population dynamics over the duration of most academic research projects (e.g., a 2-4 year graduate degree program). The extent to which these findings generalize to larger-bodied organisms remains unclear, despite the obvious implications for our understanding of nature in general and wildlife conservation, specifically.

In systems dominated by large and long-lived species of plants and animals (e.g., trees and large mammals), indirect interactions manifest over expansive scales of time and space. Quantifying these interactions using experiments typically is not feasible for ethical and logistical reasons. For example, manipulation of nutrient densities and predator morphology have been used to evaluate the relative contribution of bottom-up and top-down forces in grass-grasshopper-spider mesocosms (Schmitz 2010), but these manipulations are unrealistic for researchers asking similar questions in systems characterized by aspen-elk-wolf interactions  (Terborgh et al. 2010; but see Sinclair et al. 2000, Hughes et al. 2013). Instead, researchers studying large and long-lived organisms typically rely on correlative approaches or 'natural experiments' (Hurlbert 1984, Underwood et al. 2000, Guthery et al. 2004, Oksanen 2004, Guthery 2007).

Correlative studies often suffer from confounding variation, which obfuscates the mechanistic pathways underlying interactions between organisms and their environment. For example, at the scale of individuals, studies quantifying habitat selection for large mammals typically relate animal locations (via GPS collars or direct observations) to GIS-derived environmental variables (Boyce et al. 2002). Examples of commonly-used predictor variables include elevation, land cover (e.g., urban areas, forest) or the location of other species (e.g., predators, conspecifics) (Johnson et al. 2004, Hebblewhite et al. 2008, Gervasi et al. 2013, Peters et al. 2013). However, many of these predictor variables cannot be manipulated to an extent that yields a perceptible change in habitat selection. Moreover, these predictor variables may not be the ultimate cause of habitat selection because they are confounded with other (unmeasured) factors responsible for driving habitat selection. For example, environmental variation associated with elevation (e.g., changes in plant communities, energetic costs of locomotion, water availability, distance to disturbed areas) are likely what an animal perceives and responds to, rather than distance above sea level *per se* (Hebblewhite et al. 2008). Consequently, finding novel ways to tease apart confounding variation in studies of habitat selection remains a promising avenue for ecological field studies (Hebblewhite and Haydon 2010).

At the population-level, key interactions like predation or herbivory typically are inferred from variation in the abundance of carnivores and herbivores, respectively (Underwood et al. 2000, Peckarsky et al. 2008). For example, the effects of predation are assessed by comparing herbivore biomass between areas with high and low carnivore abundance (Sinclair et al. 2003). The reasoning behind this approach is that more herbivores occur because there are fewer carnivores present to both consume them and suppress their population. However, variation in the abundance of both carnivores and herbivores is dependent on a host of other environmental factors. For example, drought, increased human hunting pressure, fire and wolf abundance all covaried in Yellowstone National Park, obfuscating the driver of elk population decline (Mech 2012, Winnie 2012). Such covariation associated with broad-scale, correlative studies undermines our ability to identify and quantify the causal interactions influencing individuals, populations, and communities.

When causation eludes inference in ecological studies of large mammals, our ability to use science as a tool to resolve controversy in the conservation and management of wildlife is diminished. For example, wolf restoration in the Rocky Mountains of North America has been linked to the recovery of woody plants via suppression of elk (Ripple and Larsen 2000, Ripple et al. 2001, Ripple and Beschta 2003). This hypothesis requires that elk be suppressed directly by wolves, and woody plants – in the absence of wolves - be directly suppressed by elk. For many ecologists, these data have not been presented in a convincing manner (e.g., Kauffman et al. 2010, Mech 2012, Winnie 2012, Kauffman et al. 2013), highlighting uncertainty over the claim that wolves have 'restored' the Greater Yellowstone Ecosystem (Middleton 2014). Lacking consensus from the scientific community, debate over wolf conservation continues be driven by belief rather than fact (Mech 2012). Moreover, uncertainty over the ecological effects of wolves in North America muddles our ability to predict the impact of future wolf restorations elsewhere (Williams et al. 2002, Phillips et al. 2003, Nilsen et al. 2007). This example highlights the consequences of the knowledge gap that persists because of the lack of experimentation in the ecology of large mammals. Thus, there is a compelling rationale to identify not just correlative associations in the spatial and temporal patterns of large mammal behavior, population dynamics and community structure, but the causal mechanisms underlying these patterns.

The goal of my dissertation research was to help fill this knowledge gap by combining focal experiments with correlative observations to quantify interactions involving large, terrestrial mammals. Specifically, I examined the effects of experimentally-controlled perceptions of risk on the movement patterns of dik-dik (Chapter 2), the synergy of plant defense and risk of predation to impala on tree communities (Chapter 3), and the effects of wild-dog recolonization on the density of dik-dik and the trees that they eat (Chapter 4). Below, I review the goal of these individual studies, their main findings, limitations, anticipated significance for ecology and conservation, and then provide a prospectus for future research in my study area. I end this chapter with a synthesis of the science of trophic cascades involving large carnivores (i.e., the focus of Chapters 3 and 4).

## 5.2 The landscape of fear for a dwarf antelope, *Madoqua guentheri*: Spatial responses to simulated cues of risk (Chapter 2).

Risk of predation can powerfully shape the physiology, behavior and demography of prey. The ‘landscape of fear’ conceptualizes the spatial distribution of these risk-effects, and has been demonstrated widely in a variety of ecosystems and taxa. Among the many studies that have examined the landscape of fear for ungulates, most have focused on large (>40 kg) and gregarious species. Much less is known about the effect of risk on smaller or territorial species. Using high-resolution GPS tracking (ca. 10 min relocation interval), I examined the spatial responses of Guenther’s dik-dik - a small (ca. 5 kg), monogamous, and territorial antelope - to simulated olfactory cues of risk (scentmarks) from wild predators (African wild dogs) and humans. In response to wild dog scentmarks, dik-dik movements were constrained, scentmarks were avoided, use of overstory cover decreased and movement pathways were more directed. Similar behaviors occurred in response to human scentmarks, with the exception that there was no change in use of cover relative to controls, and movement pathways became significantly more variable than expected. Total amount of movement did not vary among scentmark treatments. These results highlight how the traits of a diminutive antelope shaped its journey through the landscape of fear, and point to the need to broaden the scope of focal species used in field studies in ungulate ecology.

## 5.3 Large carnivores make savanna tree communities less thorny (Chapter 3).

Controversy surrounds the mechanisms underlying the indirect effect of carnivores on plants (i.e., trophic cascades). I hypothesized that risk avoidance influences impala habitat selection and the plant defenses mediate diet selection, such that well-defended trees should occur in relatively safe habitats while poorly-defended trees should be more abundant in risky areas. By combining a series of field experiments with GPS telemetry of an abundant antelope (impala) and one of its main predators (the African wild dog), I showed that the tree community shifted to dominance by a less thorny, poorly-defended species with increasing risk of predation to impala. These results indicate that plants can persist in landscapes characterized by intense herbivory, either by defending themselves or by thriving in risky areas where carnivores hunt.

## 5.4 Sequential top-down forcing does not trigger a trophic cascade following the recovery of a globally endangered carnivore in a savanna ecosystem (Chapter 4).

After an absence of 20 years, the globally endangered African wild dog recolonized the Laikipia Plateau in central Kenya in 2002. I hypothesized that the recolonization of wild dogs would trigger a trophic cascade via suppression of dik-dik. I tested the trophic cascade hypothesis using: (i) an 11-year time series on the abundance and distribution of wild dogs; (ii) surveys of dik-dik populations conducted pre-(1999-2002) and post-(2008-2013) wild dog recovery; and (iii) replicated herbivore exclosure experiments initiated in 1999 and in 2009. The abundance of dik-dik declined by 33% following the recovery of wild dogs; this decline could not be explained by factors other than predation by wild dogs. Dik-dik suppressed stem density for some tree species, but the strength of this effect did not differ between pre- and post-wild dog recovery. Consequently, and despite evidence for top-down forcing through two sequential trophic levels, the recovery of wild dogs did not reverberate from herbivores through plants to produce a trophic cascade. A diverse assemblage of herbivores, the social organization of dik-dik, and variation in rainfall may have nullified the indirect effect of wild dogs on trees. My results call into question the assumption that the restoration of large carnivores will necessarily have cascading effects on plant communities.

## 5.5 Limitations of study methods

Though I attempted to integrate experimental approaches with landscape-scale observations, three salient limitations are present in my research. First, replication of my experiments in areas varying in risk of predation or predator abundance would provide stronger evidence for top-down forcing. For example, the Risk Allocation Hypothesis predicts weaker risk effects in systems characterized by persistent risk of predation (Lima and Bednekoff 1999, Bednekoff and Lima 2011). Thus, in Chapter 2, the response of dik-dik to scentmarks may have been stronger in landscapes with fewer predators than occur at Mpala Research Center. Similarly, for Chapter 3, had I replicated my work in a less-risky landscape, I would expect to find that impala may spend more time in riparian areas, thereby homogenizing the distribution of *A. brevispica*. For Chapter 4, it would have helped to have a time series of dik-dik abundance and the effects of herbivory in a paired landscape where wild dogs were absent and where rainfall and/or herbivory by other ungulates matched conditions on MRC. Such an analysis would help to identify why the indirect effect of wild dogs on plants was buffered. While ideal, such a paired landscape would be extraordinarily difficult to locate in Laikipia without also introducing uncontrolled variation. Young et al. (2013) found that whole species assemblages in Laikipia are lost under different land-use regimes, such that maintaining a comparable herbivore density to that observed in Chapters 3 and 4, in the absence of carnivores, and yet consisting of the same plant communities is all but impossible.

Second, as is typical of many studies on large mammals, sample sizes within my experiments were limited. For example, it was extremely challenging to obtain GPS telemetry data from the $n = 15$ dik-dik used in Chapter 2. There is growing evidence that individuals of the same species may have different perceptions and responses to resources and risk (Bolnick et al. 2003, Gillies et al. 2006, Araujo et al. 2011, Avgar et al. 2013), and a greater sample size would have assisted me in identifying causes of intraspecific variation in movement patterns. The herbivore exclosure experiments featured in Chapters 3 and 4 ranged in sample size from 3 to 9 for a given treatment. Greater replication in this case would improve the statistical power of my analyses. For example, in Chapter 4, the $P$-value for changes in stem density in OPEN plots pre- and post- wild dog recovery was 0.084 ($n = 9$), even though the mean differences are quite large (Figure 4.7). Thus, it is likely that I would have found a significant ($P < 0.05$) association between wild dog biomass and tree abundance in OPEN plots with greater replication. However, this would not change the main conclusions of Chapter 4. In general, there are limited opportunities for replication and control in studies on large mammal ecology and researchers need to find creative approaches to ensure that inferences derived from field studies reflect the quality of data presented.

Third, the duration of my experiments may have effectively ‘attenuated’ effect sizes, particularly in Chapters 2 and 4. In Chapter 2, the response of dik-dik to scentmarks was only measured up to 48 h. This duration was chosen to minimize risk of introduced covariation in this field experiment (e.g., changes in weather, disturbances) but a longer duration may potentially have increased the effect of risk on movements. However, temporal variation in risk of predation can alter responses to risk (Lima and Bednekoff 1999, Bednekoff and Lima 2011), with longer exposure possibly decreasing the expression of anti-predator behavior. In Chapter 4, I did not find a significant effect of wild dogs on the effect of herbivory, even though I found a direct effect of wild dogs on dik-dik and of dik-dik on trees. Menge (1997) highlighted some early views of ecology which predicted that indirect effects will take longer to manifest than direct effects, though he did not find this to be the case for rocky intertidal systems. Still, it is possible that the continued suppression of dik-dik by wild dogs will eventually manifest as a trophic cascade. However, to detect this possibility would require additional measures of herbivory (exclosures) that are presently unavailable.

A fourth limitation of this study arose from the types of data made available through collaborations. A number of data sets used in my research were compiled for other research projects and made to fit within the predictions I was testing, particularly for Chapters 3 and 4. For example, use of wild dog GPS telemetry in Chapter 3 arose from collaboration with the Laikipia-Samburu Wild Dog Project. My preference would have been for a greater number of individuals to be collared within MRC, as well as more frequent GPS relocation intervals, and temporal overlap with collared impala. Given their propensity to kill impala, use of GPS data from leopards for Chapter 4 would also have been helpful had these data been available at the time of writing. Across the species range of leopards they generally prefer areas with dense woody cover, such that my conclusions regarding the effect of cover on the perceptions of risk for impala would likely remain intact had these data been available.

In addition to more data on carnivore movements, the herbivore exclosure experiments I used in Chapters 3 and 4 were not designed to test questions regarding top-down effects of predation risk to impala and consumption of dik-dik by wild dogs, respectively. Under ideal conditions, for example, the MESO vs. TOTAL analysis I performed in Chapter 4 to identify the effects of dik-dik *per se* on the plant community would also have been conducted prior to and following recolonization of wild dogs. Unfortunately, the pre-wild dog herbivore exclosure experiment only examined the effects of all or no ungulates. Still, if the effects of dik-dik are important relative to that of other herbivores, a MESO vs. TOTAL comparison should be similar to an OPEN vs. TOTAL comparison.

## 5.6 Prospectus for future research

There are four broad areas related to my field research that could provide productive inquiry for future research. First, individual ecology is a growing paradigm in ecology, and is related to heterogeneity of within-population specialization in resource use as a means of minimizing intra-specific competition (Lomnicki 1988). This specialization is an early step towards speciation, and so provides a powerful link between evolution and ecology. Currently, individual ecology focuses on how resource specialization can be quantified (Bolnick et al. 2003, Araujo et al. 2011). Missing from this paradigm is discussion about the specialization of anti-predator phenotypes in a population. Predation is seen as a pervasive force in selection, and so it follows that there must be strong selective pressure to enhance fitness by capitalizing on heterogeneity in predation risk (Schluter 2009, Ingram et al. 2012). Chapter 2 only touched on some potential ways in which dik-dik interact with their predators, but this study system may be ideal to test predictions over individual specialization in anti-predator behavior. Dik-dik face predation risk from a diversity of predators with different forms of hunting (stalking, coursing) and locomotion (terrestrial and aerial). Dik-dik are relatively easy to capture, track, manipulate and to record their behavior/survival. Examples of some key questions include: are some dik-dik ‘vigilance’ specialists and others ‘cryptic’ specialists? If there are different anti-predator phenotypes, what are trade-offs made in terms of costs and benefits of these phenotypes?

Second, Chapter 3 explored the interaction of predation risk to ungulates and plant defenses, in shaping a behaviorally-mediated trophic cascade. This cascade may potentially extend beyond the forage of impala. For example, heightened browsing by impala in safe areas may generate so called ‘browsing lawns’ of nutrient-dense re-growth that could facilitate other species, such as folivorous insects. Moreover, avoidance of palatable trees in risky areas could provide organisms that have a high-threshold of risk aversion with a ‘forage bank’. If so, carnivores may facilitate forage for herbivores like elephants and domestic livestock like goats and camels. Additionally, anecdotal observations suggest that some weavers (*Ploceus* spp.) prefer to nest in thornier trees. In creating thornier tree communities where risk of predation is lower, perhaps impala and carnivores are facilitating nesting habitat for these birds.

Third, impala use patches of open habitat to minimize risk of predation, but it is unclear how the spatial arrangement and density of these ‘safety hotspots’ affects impala movements. For example, how does persistence in a patch increase risk of predation? If persistence increases risk, then having a constellation of patches to move among may reduce risk, but this reduction would only manifest if patches were unoccupied by other prey. Impala appear to have non-overlapping home ranges that are suggestive of territoriality, and it is possible that this exclusivity in space use is related to risk-aversion. Territoriality in mammals is generally thought to be caused by defense of resources or mates, but impala at Mpala Research Center could be used to illustrate the potential role of ‘safety’ as a depletable resource that is actively defended.

## 5.7 Trophic cascades initiated by large carnivores: soft interactions or a law of nature?

Theories of evolution described by Jean-Baptise Lamarck – so called ‘soft-inheritance’- spurned a series of compelling and testable hypotheses long-since rebuked in the wake of evidence for natural selection (but see Bonduriansky 2012). An understated value of Lamarckism was not in its explanatory power, but in providing science with a testable and plausible alternative hypothesis for patterns of inheritance in nature. With the discovery of a genetic mechanism underlying evolution by natural selection, Lamarckism is now regarded as flawed. This genetic mechanism is so compelling that natural selection is now regarded by many scientists as a law of nature. The strength of inference inherent in this law has been derived from the repeated testing of multiple competing hypotheses, alongside experimental control and replication. Few laws are recognized in evolution or ecology (Lawton 1999; but see Turchin 2001); if and when additional laws are discovered, it will be because of an exhaustive effort to test competing hypotheses that explain the way nature works.

Recently, it has been suggested that trophic cascades are: “… a universal property of ecosystem functioning, a law of nature as essential and fundamental to ecology as natural selection is to evolution.” (Terborgh and Estes 2010: 354). Although the food-web model, of which trophic cascades are a part of, has long been argued as the central organizing theory of ecology (Fretwell 1987), the notion that trophic cascades are a law of nature overlooks critical gaps in both inductive and deductive reasoning. The inductive limitations of this statement arise because evidence for trophic cascades is primarily based on systems dominated by small (< 100 g) and typically aquatic organisms (see reviews in: Pace et al. 1999, Schmitz et al. 2000, Halaj and Wise 2001, Shurin et al. 2002, Borer et al. 2005, Preisser et al. 2005, Preisser and Orrock 2012). Extending the primacy of trophic cascades to all of nature is flawed without further evidence demonstrating their occurrence in systems dominated by larger-bodied bodied vertebrates. This is particularly true in speciose, terrestrial systems where reticulate food webs and donor control buffer the upward flow of energy through food chains, thus negating any would-be trophic cascades (Strong 1992b, Polis et al. 2000).

Inherent gaps in deductive reasoning in the statement by Terborgh and Estes (2010) arise from the correlative manner in which the trophic cascade hypothesis has been tested in systems dominated by large mammals. One of the best-known examples of such a gap is the putative effect of wolf reintroduction on the Greater Yellowstone Ecosystem. There, changes in the ecosystem that have been prominently attributed to wolves coincided with variation in the length of the growing season, greater human hunting effort, a drought, widespread fires, and the reintroduction of beavers by agency biologists (Kauffman et al. 2007, Kauffman et al. 2010, Mech 2012, Winnie 2012, Beschta and Ripple 2013, Kauffman et al. 2013). Consequently, it is impossible to isolate the effect of wolves amidst this confounding variation.

Equivocal evidence for the wolf-elk-aspen cascade in Yellowstone has recently permeated popular media outlets (Marris 2014, Middleton 2014, Ostlind and Wade 2014), but controversy surrounds other purported trophic cascades involving large carnivores. For example, land-use changes and abiotic gradients coincided with the exclusion of dingoes in Australia (Newsome et al. 2001, Allen et al. 2013), undermining claims that dingoes are top-down regulators of ecosystem function (Letnic et al. 2012). Environmental toxins and predation by sharks (Kuker and Barrett-Lennard 2010) muddle causation for the putative cascading effects of orcas on near shore ecosystems in the Eastern Pacific (Estes et al. 1998). Similarly, the cascading effects of otters on sea urchin and kelp communities (Estes and Palmisan 1974) may be of limited generality in the North Pacific, as no reciprocal response in the kelp community occurred in areas where otters are still absent (Foster 1990). These controversies reflect the challenge faced by ecologists in documenting trophic cascades over expansive scales of time and space. At least part of this challenge stems from the use of inconsistent standards of evidence to test the trophic cascade hypothesis. Thus, developing a rigorous test of the trophic cascade hypothesis in systems dominated by large carnivores has important consequences both for the way we understand nature and for the management and conservation of wildlife.

In this essay, I begin with a definition of trophic cascades and then evaluate how studies presented evidence for trophic cascades. I offer a roadmap for ways in which the exploration of trophic interactions involving large carnivores can potentially move forward in a more rigorous manner. I summarize this essay with a call for action by members of the scientific community – researchers, journal editors, review boards – to hold the trophic ecology of large mammals to the same standards of evidence that they hold any other discipline in ecology and therefore remove it from the dark shadows of a ‘soft’ interaction and towards the illumination of ecological generality.

### 5.7.1 Trophic cascades: logic and a definition

Although trophic cascades are an oft-studied and well-known process, the literature does not contain a clear, *a priori*, operational or standardized definition with which ecologist can test evidence against in field studies. It is perhaps because there is no broadly recognized definition of a 'trophic cascade' that ecologist have long debated the types of evidence needed for their discovery. Credit for the term 'trophic cascade' is given to Paine (1980), who discusses "…a cascade of effects" (pp 674), and after describing a series of results consistent with the trophic cascade hypothesis states that "Although the relationships are primarily inferential, all are realistic, and support the notion of a trophic cascade associated with a series of nested strong interactions" (pp 676). However, Paine (1980) does not offer an *a priori* definition of the term.

Fourteen years ago, Polis et al. (2000) published "When is a trophic cascade a trophic cascade" and highlighted a "…need for consensus in trophic ecology, beginning with a standard vocabulary and moving towards a standard criterion of importance." Polis et al. (2000) emphasized the differences between community- and species-level trophic cascades, at a point in the history of science when the mere existence of trophic cascades was being debated (see Persson 1999). According to Polis et al. (2000), species-level trophic cascades involve the positive, indirect effects of carnivores on a subset of plant species. Conversely, community-level trophic cascades involve the positive, indirect effects of carnivores on the biomass or abundance of the plant community in aggregate. Polis et al. (2000) argued cogently that Hairston et al. (1960) were describing a community-level trophic cascade in what would eventually be known as the 'Green World Hypothesis'. Perhaps surprisingly, Polis et al. (2000) did not define trophic cascades *a priori*, and only alluded to them as phenomenon consistent with the results of Hairston et al. (1960) and Oksanen et al. (1981), who themselves do not define a trophic cascade.

In a recent book bearing the title "Trophic Cascades", the closest statement to a definition in the suggestively-named chapter *Trophic Cascades: What they are, how they work and why they matter* was "Eliminating carnivores destabilizes ecosystems, setting off chain reactions that eventually cascade down the trophic ladder to the lowest rung. In 1980, Robert Paine coined the term *trophic cascade* to describe this process." (Estes and Terborgh 2010:2). Schmitz et al. (2004:153) defined trophic cascades as: "...the indirect effects of carnivores on plants mediated by herbivores…". However, this description by Schmitz et al. (2004) is not a definition *per se*, but a prediction from an undefined hypothesis. Moreover, this prediction cannot be extrapolated to 4-level trophic cascades (Oksanen et al. 1981), to cascades involving more than one carnivorous trophic level (Berger et al. 2008), or to bottom-up trophic cascades (Kagata and Ohgushi 2006).

Two definitions that most closely encapsulate operational definitions of trophic cascades are by Pace et al. (1999) and Persson (1999). Pace et al. (1999) state that trophic cascades are: "reciprocal predator–prey effects that alter the abundance, biomass, or productivity of a population, community, or trophic level across more than one link in a food web." (pp 483). However, by failing to explicitly define how 'more than one link' is organized topologically, the Pace et al. definition does not convey the directionality of population suppression. For instance, their definition could also describe apparent competition. Persson (1999) states that trophic cascades are the "propagation of indirect mutualisms between nonadjacent levels in a food chain." (pp 385). Persson's definition is perhaps the most succinct of those encountered; however, in four-level food chains, 'nonadjacent levels in a food chain' could also include both the suppression of the lowest trophic level and the facilitation of the penultimate trophic level; it is not clear which of these possibilities is being invoked. Moreover, trophic cascades represent a propagation of direct effects, rather than the less-straightforward propagation of 'indirect mutualisms'. In spite of the vague interpretations of the term 'trophic cascade', there are some common findings among the many studies that have claimed discovery of a trophic cascade.

The topology of direct and indirect interactions comprising trophic cascades generally includes the following three features: (i) interacting populations of at least three trophic levels; (ii) demonstrated, uni-directional forcing of populations through at least two sequential trophic levels (e.g., 'runaway consumption'); (iii) a positive correlation in the abundance of organisms from two different trophic levels that are separated by a single trophic level (the indirect effect). These features occur in classic trophic cascades described by Hairston et al. (1960), Paine (1980), Power (1990) and Carpenter et al. (1985), and in reviews by Schmitz et al. (2000), Halaj and Wise (2001), Shurin et al. (2002), Borer et al. (2005), Preisser et al. (2005), and Preisser and Orrock (2012). Moreover, these three features also occur in trophic cascades involving four-trophic levels as well as bottom-up and top-down cascades. Finally, these three features are inconsistent with the archetypal null-hypothesis for a trophic cascade – bottom-up regulation (Hunter and Price 1992, Strong 1992a) – thus permitting the evaluation of at least one exclusive and competing hypotheses. In sum, an operational and *a priori* definition for a trophic cascade is: *The interruption of suppression on an adjacent trophic level caused by suppression from a preceding trophic level, resulting in a sequence of alternating negative and positive correlations* *in abundance through the food chain*. Using this operational definition, I will next evaluate the manner in which trophic cascades have been sought in field studies involving large carnivores.

### 5.7.2 Standards of evidence used to identify the existence of trophic cascades: gold standards and weak inference

Across much of ecology, the gold standard for measuring the effect of one species on another is through a species removal (or addition) experiment. That is, removing one species from an area where at least two species co-occur, and then quantifying a change in abundance or behavior of the remaining species (or individuals) relative to pre-removal conditions and controls (Tilman 1977, Hurlbert 1984, Oksanen 2004). The logic and inference used in removal experiments can also be extended to the indirect interactions that characterize trophic cascades.

Under replicated and controlled conditions, researchers have quantified plant responses (i.e., changes in abundance, biomass, growth, or reproduction) in one- (plant-only), two- (plant and herbivore), and three-level (plant, herbivore and carnivore) food webs (Sinclair et al. 2000, Schmitz 2010). Using this approach, comparable response by plants in a one- and three-level food web, and suppression of plants in a two-level food web, is interpreted as evidence for a trophic cascade (Schmitz 2010). The strength of inference underlying this approach derives from the fact that each direct interaction (the direct effect of carnivores on herbivores, and of herbivores on plants) as well as the resultant indirect effect (the effect of carnivores on plants) are quantified independently. In addition to varying the length of food chains, research employing this experimental approach has addressed other factors such as productivity (bottom-up influences) and the role of species traits (plant defense, predator hunting mode, non-consumptive effects) to explain context-dependency in the strength of trophic cascades (Leibold 1989, Sinclair et al. 2000, Schmitz et al. 2004, Peckarsky et al. 2008, Ohgushi et al. 2012).

Efforts to adapt (or even approximate) this ‘gold standard’ have generally been disregarded by researchers working on trophic cascades involving large carnivores. For a number of reasons (logistics, ethics), quantifying trophic cascades in systems dominated by large carnivores requires broad-scale, correlative approaches over time and space. But unfortunately, causal mechanisms often are inferred or are not measured independently of covariation in other environmental factors. However difficult it may be to implement the gold standard approach, it does not follow that large mammal ecologists get a ‘free pass’ at weak inference. Ecologists must protect themselves from the allure of paternalism in their choice of hypotheses (Chamberlin 1931), and endeavor to present evidence in our discovery of trophic cascades. When evidence does not meet the standards to which other ecological investigations are held, ecologists should practice circumspection in their claims of discovery.

### 5.7.3 Case studies

In a recent review, Ripple et al. (2014) suggested that large carnivores have pervasive effects on ecosystems via trophic cascades, which justifies both a practical and moral imperative for their conservation. The authors focused on five carnivores, presumably because these examples most clearly exemplify the important roles played by large carnivores in triggering trophic cascades. I draw upon these five examples, along with other published examples, as case studies to illustrate irregularity in the rigor used to test the trophic cascade hypothesis. This irregularity includes markedly different assumptions relating to the existence of trophic cascades in general, and of trophic cascades initiated by the focal carnivore species, specifically.

#### 5.7.3.1 Approach 1: Carnivore occurrence and browsing pressure.

This approach quantifies height-class distributions of trees, and correlates them to the occurrence of carnivores over time (see "gray wolf" and "puma" Ripple et al. 2014:Fig 2, Ripple and Beschta 2005, 2006, 2008, Beschta and Ripple 2008) . Typically, three sources of data are used in this approach. First, temporal variation in the abundance or presence of carnivores is assessed often through unpublished reports in the gray literature. Second, the height-class distributions of trees in areas with and without current populations of large carnivores are collected. Third, a space-for-time substitution is employed, with the height-class distribution in areas with large carnivores interpreted as the historical height-class distribution for trees in the areas from which carnivores were extirpated. The reasoning behind this approach is that the missing height classes are indicative of a release of herbivore populations caused by the removal of the focal large carnivore.

The main limitation of this approach is that only a single trophic level is measured (e.g., height-class distributions of trees), resulting in at least three untested assumptions. First, in ascribing differences in height-class distributions to predation and herbivory, additional or alternative sources of variation in tree growth are assumed to be negligible (i.e., there are no controlled measures of tree consumption by the focal herbivores through exclosure plots or other means). Second, herbivores are assumed to be limited historically primarily by the focal species of carnivore and contemporarily only limited by forage resources. Third, this approach also assumes that plants are suppressed predominantly by herbivory, not disease or abiotic drivers of tree recruitment.

Missing from this approach are: (i) falsified alternative hypotheses for the observed patterns in height-class distributions, such as disease, fire, and resource limitation for plants and herbivores; (ii) correlations between the energetic demand of higher trophic levels to a proportional change in demographic performance and abundance of the adjacent, lower trophic level; and (iii) replicated observations among sites that vary in carnivore abundance or biomass.

This approach offers historical insight on wildlife management practices and potential changes to tree heights as result of human activity. Indeed, this approach has been broadly applied in a number of areas across North America where large carnivores, cervids and trees interact (reviewed in Beschta and Ripple 2009). However, greater emphasis should be placed on quantifying the dynamic interactions between each trophic level before this approach can be considered an empirical test of the trophic cascade hypothesis.

#### 5.7.3.2 Approach 2: Correlation between plant and carnivore abundance.

This approach associates historic variation in the abundance of carnivores with current and variation in plant abundance across space (see “dingo” Ripple et al. 2014:Fig 2). For example, Callan et al. (2013) assessed plant abundance in areas where wolves had occurred for long (8 - 10 years) and short (0 – 3 years) periods of time, and found that edible plants were more abundant in areas with long-term occupancy by wolves. These data led the authors to conclude (pp 8) “Our results provide compelling correlative evidence of top-down trophic effects generated by the recovery of Wisconsin’s wolf population.” In another series of examples, Letnic et al. (2009) and Letnic and Koch (2010) compared community composition on either side of a dingo exclusion fence that was established in the late 1880s, and concluded that dingoes indirectly regulate plant and animal communities.

Unlike many studies on trophic cascades involving large mammals, Letnic et al. (2009),Letnic and Koch (2010), and Callan et al. (2013) replicated their measurements in areas varying in carnivore abundance. For example, Callan et al. (2013) compared plant communities in 16 high and 16 low wolf-use areas. Letnic and Koch (2010) measured three pairs of sites established along a rainfall gradient, with one of each pair on either side of the exclusion fence. In addition, Callan et al. (2013) address the palatability of different plant types for the focal prey of wolves. The stronger correlation between wolf persistence and palatable plant abundance compared to unpalatable plants reinforces the case for a trophic cascade. The replication employed in Callan et al. (2013) and Letnic and Koch (2010) is a powerful step forward in our ability to disentangle contingency and covariation in studies involving large carnivores.

However, and as in Approach 1, Callan et al. (2013) infer mechanisms of top-down suppression by measuring a single trophic level. For example, Callan et al. (2013) do not provide evidence that herbivores (i.e., deer) are either less abundant or are foraging less in areas of high wolf persistence compared to areas with low persistence. Conceivably, wolves may persist for longer periods of time in areas with greater prey density and where herbivory may be intensified, though this possibility was not tested. In addition, Callan et al. (2013) do not quantify the effect of deer vs. other drivers of plant abundance in high and low wolf use areas (e.g., through herbivore exclosures). Finally, although it is not an exclusive limitation of Approach 2, alternative hypotheses (Newsome et al. 2001, Allen et al. 2013) to trophic cascades are not tested by Callan et al. (2013), Letnic et al. (2009) or Letnic and Koch (2010).

#### 5.7.3.3 Approach 3: Time-series of biomass for three or more trophic levels.

In one of the earliest published accounts of a trophic cascade involving large carnivores, McLaren and Peterson (1994) quantified long-term (36 - 40 years) covariation in wolves, moose and tree biomass accumulation in Isle Royale. Similarly, Brashares et al. (2010) used a long-term (32-year) data set of mammal monitoring in Ghana to track changes in large carnivores (lions and leopards), baboons and the prey of baboons (see "lions/leopards" Ripple et al. 2014:Fig 2). In both studies, proportional changes in abundance between species in adjacent trophic levels suggested top-down population forcing. For example, heightened abundance in basal trophic levels occurred when the abundance of large carnivores increased (McLaren and Peterson 1994, Brashares et al. 2010). Unlike the discrete representation of carnivore abundance used in Approaches 1 and 2, this approach emphasizes a continuous dependence between the abundance (or biomass) of species in adjacent trophic levels. Consequently, strong inferences can be made for top-down suppression, particularly by comparing areas where environmental variation and carnivore abundance vary independently over time.

#### 5.7.3.4 Approach 4: Comparison of time-series data from control and perturbed sites, with quantification of direct interactions.

This approach combines analyses on the direct interactions between two sequential trophic levels, as well as the indirect effect of the large carnivore on the basal trophic level. For example, Estes et al. (1998) relate the energetic demand of killer whales (*Oscines orca*) to vital rates and population change in sea otters (*Ephedra lustres*). The authors explore alternative explanations to killer whales that could drive changes in otter abundance, such as otter fertility, pollution and population redistribution. Estes et al. (1998) made use of natural variability in whale abundance to assess the indirect effects of whale predation on urchins (otter prey) and kelp (urchin prey). Similarly, Estes and Duggins (1995) exploited natural variation in sea otter abundance and recolonization events to measure the indirect effects of otters on kelp. Because recolonization events were both staggered in time and widely distributed, Estes and Duggins (1995) addressed previous criticism (Foster 1990) over the lack of generality from earlier studies on otters, urchins, and kelp (Estes and Palmisan 1974). These criticisms revolved around the potential for unmeasured environmental covariation to explain kelp abundance (Foster 1990, Underwood et al. 2000).

Another strategy used in Approach 4 is taken by Hebblewhite et al. (2005b), who took advantage of human-avoidance behavior by wolves to formulate a natural experiment. Areas where wolves were present were then compared to areas they avoided. Moreover, and unlike Approaches 1, 2 and 3, Hebblewhite et al. (2005b) quantified a demographic mechanism by which wolves suppress elk populations, which in turn led to heightened aspen growth. Similarly, Post et al. (1999) correlated the energetic demand of wolves (moose kill sites) with variation in biomass accumulation in trees over a 40 year period. Both of these studies explored alternative explanations for variation in prey abundance other than predation by wolves (e.g., diet quality [Hebblewhite et al. 2005b]), as well as alternative sources of variation in plant abundance (e.g., climate [Post et al. 1999]).

The major limitation of Approach 4, as demonstrated by Estes et al. (1998), Estes and Duggins (1995), Post et al. (1999), and Hebblewhite et al. (2005b) is the absence of experiments coupled with unmanipulated controls to reinforce the inferences made from correlative observations. Indeed, as Underwood et al. (2000) note: "Experimental removals of otters have not been done, even though there is overwhelming evidence that properly controlled experiments are necessary to prove any sound basis for unravelling the complexities of indirect interactions." (pp107). Similar concerns have been identified for studies conducted on wolves, ungulates and trees in North America (Mech 2012).

#### 5.7.3.5 Approach 5: Manipulating the length of food chains.

Perhaps surprisingly, I could only locate two experimental studies involving large, terrestrial carnivores which tested the trophic cascade hypothesis (Sinclair et al. 2000, Maron and Pearson 2011). Of even greater concern to the generality of the trophic cascade hypothesis was that both studies did not find evidence for an indirect effect of carnivores on the basal trophic level. An additional experiment, based in a marine system, builds a compelling case for the manner in trophic cascades triggered by large carnivores can be quantified in a rigorous manner (Hughes et al. 2013).

Sinclair et al. (2000), Maron and Pearson (2011) and Hughes et al. (2013) used exclusion fences (or cages) to control the length of food chains and then to isolate the strength of both direct and indirect interactions comprising trophic cascades. Sinclair et al. (2000) measured plant abundance in plots that excluded snowshoe hares (*Lepus Americanos*) and their predators (one-level food chain), allowed hares but excluded lynx (*Lynx Canadensis*) (two- level food chain), and in controls (three-level food chain). They found that while lynx suppressed hares, and hares suppressed woody plants, the abundance of woody plants was similar in areas with predators allowed or excluded. Maron and Pearson (2011) discovered rodents suppressed plants, but did so equally in plots with and without carnivores. Thus, neither Sinclair et al. (2000) nor Maron and Pearson (2011) found evidence for a trophic cascade, despite clear evidence for top-down forcing.

While both Sinclair et al. (2000) and Maron and Pearson (2011) used experimental manipulations to quantify direct and indirect interactions in naturally-occurring food chains, these studies had few, if any replications for their treatments nor do they extend their findings to the broader landscape. For example, though covering an area of 1 km$^2$ for each treatment, the exclosure plots used by Sinclair et al (2000) were unreplicated. The treatments in Maron and Pearson (2011) were 1 ha each and replicated four times. These two studies represent some of the greatest advances in experimental food-web ecology involving large carnivores, and yet one to four replications per treatment strongly limits capacity to meet the assumptions of randomization and statistical power (Hurlbert 1984, Oksanen 2004). Lastly, the results of the exclosure experiments provide exceptional insight on the mechanism of species interactions, but our understanding of large mammal food web ecology would be further aided if we knew the extent to which these mechanisms scale up to broader patterns across the landscape.

In one of the most insightful demonstrations of a trophic cascade involving a large carnivore, Hughes et al. (2013) linked the mechanistic patterns emerging from an experimental mesocosm and field experiment, with correlative measurements taken over an expansive area. This study is one of the first to bring together the broad-scale relevance of observation studies, with the strong inference that only an experimental approach can provide. This study is replicated, manipulates the length of the food chain, and uses continuous variation in carnivore abundance to quantify a proportional change in the abundance of lower trophic levels. While Hughes et al. (2013) set a comparatively high standard of evidence relative to previous work on trophic cascades, the results of this single study cannot be taken as evidence for a 'law of nature' (*sensu* Terborgh et al. 2010), especially in light of the results of experiments by Sinclair et al. (2000) and Maron and Pearson (2011).

### 5.7.4 Framework for quantifying trophic cascades involving large carnivores

In testing the trophic cascade hypothesis in systems dominated by large carnivores, ecologists need to bring together the inferential strength of experiments with the relevance of observational studies. The example of  Hughes et al. (2013) is one such study, but there are other examples in which the food web ecology (not trophic cascades *per se*) of large mammals has integrated expansive and mechanistic approaches. For example, Goheen and Palmer (2010)  bring together foraging experiments, herbivore exclosures and coarse-scale satellite imagery to quantify the mechanistic pathway by which large herbivores, soil nutrients and ant-plant mutualisms interact to change woody cover at expansive spatial scales. Consistent in these approaches is testing for multiple competing hypotheses for each of the interactions predicted to occur. In the case of a tri-trophic cascade initiated by a large carnivore, this means testing evidence for suppression of the herbivore by the carnivore, and of the plants by their herbivore and then for the positive effects of the carnivore on the plant (Figure 5.1).

While quantifying the effects of vagile herbivores on sessile plants is readily achieved through exclosure experiments, it is far more challenging to exclude large carnivores from an area while also allowing access by a population of herbivorous prey. Nonetheless, evidence for the potential suppression (not just consumption) of herbivores by large carnivores is needed to test the trophic cascade hypothesis. Evidence for suppression should not only include inverse correlations in abundance, but measures of demographic vital rates in the prey population. For example, Estes et al. (1998) and Hebblewhite et al. (2005b) measured the effect of large carnivore abundance on prey recruitment or adult survival to identify a demographic mechanism by which prey were suppressed. This demographic mechanism allows inference to carry from a correlative association between two populations, into a causal interaction. Studies only examining correlations between large carnivore abundance and plant abundance/biomass (e.g., Beschta and Ripple 2009, Callan et al. 2013) do not provide evidence that the putative change in the prey population is caused by the large carnivore. Indeed, just because prey are consumed by the carnivore it does not follow that the carnivore necessarily suppresses the population of its prey (Fretwell 1987).

An additional strategy to quantify suppression of prey is to correlate the energetic demand of the carnivore population to changes in prey abundance (e.g., Estes et al. 1998, Post et al. 1999, Hebblewhite et al. 2005b). Such an approach typically requires a time series of both carnivore and herbivore abundance and evidence of prey in the diet of the carnivore (e.g., kill sites). Finally, a critical and rigorous test for the suppression of herbivores by predators needs to include data on other drivers of prey abundance, such as resource limitation, disease, detectability by observers, and dispersion (Estes et al. 1998).

Evidence for suppression of plants by the herbivore should not only include inverse correlations in abundance, but a mechanistic response as well. One of the simplest means to quantify herbivory is through the use of herbivore exclosures: suppression is evident when plants inside an exclosure become more abundant (or have greater biomass) than those in control areas outside the exclosure. However, two critical pieces of information are also needed to build a case for the indirect effects of the carnivore on plants using herbivore exclosures. First, not all species of herbivore are equally vulnerable to predation (Sinclair et al. 2003). Thus, an herbivore exclosure treatment that removes both prey and non-prey herbivores masks the putative indirect effect of the carnivore on plants when those herbivores share resources ('reticulate food webs', *sensu* Polis and Strong 1996). Second, in most terrestrial systems, not all species of plants are equally vulnerable to herbivory. Aggregated measures of plant biomass in response to herbivore exclusion may combine plant species with different growth-defense trade-offs, thereby obfuscating trophic cascades (Leibold 1989, Schmitz 1994, Mooney et al. 2010). Feeding trials can be used to identify the preferred forage of the herbivorous prey, and an increased abundance of these preferred species inside an exclosure relative to controls is taken as evidence for suppression.

Evidence for the indirect effect of large carnivores on plants typically accrues from a positive correlation between plant and carnivore biomass. Key to this approach is that increased plant abundance actually reflects suppression of herbivory by the large carnivore, rather than more favorable abiotic conditions for plants or heightened plant defense. Thus, in the presence of carnivores, a weakening of herbivory, rather than heightened plant abundance *per se*, is an accurate representation of a trophic cascade. An ideal way to quantify the indirect effect of carnivores on plants is to establish herbivore exclosures in areas (or times) of high and low carnivore abundance. Thus, evidence needed to demonstrate a trophic cascade involving large carnivores needs to show the weakening of herbivory-effects on the plant community coincident with increased carnivore abundance, coupled with clear evidence for suppression of herbivores by carnivores and of plants by herbivores.

### 5.7.5 The special case of behaviorally-mediated trophic cascades

Much attention has recently been paid to the mechanism by which wolves are interacting with elk to enhance the abundance of woody plants in the Greater Yellowstone Ecosystem (Kauffman et al. 2010, Winnie 2012, Kauffman 2013, Middleton et al. 2013a, Middleton 2014). Two non-exclusive pathways have emerged – density mediation and behavioral mediation. Density-mediated trophic cascades (DMTCs) are the archetypal cascade described by Hairston et al. (1960), and relate to the numerical response of herbivores to carnivores. Behaviorally-mediated trophic cascades (BMTCs) involve non-lethal, anti-predator responses of herbivores to the risk predation. Such BMTCs are believed to have stronger effects on plant communities than DMTCs, particularly when anti-predator behavior manifests as risk-averse habitat selection (Preisser et al. 2005).

The framework for quantifying trophic cascades involving large carnivores (Figure 5.1) is identical for DMTCs and BMTCs in that evidence for the predicted direction and strength of interactions between trophic levels needs to be quantified independently. While DMTCs require evidence for a numerical response via a demographic mechanism, BMTCs require evidence that prey behavior is risk-averse and that risk aversion translates into a perceptible change in the plant community (Kauffman et al. 2010, Winnie 2012, Burkholder et al. 2013). Of these two requirements of the BMTC, researchers have struggled most with different ways to quantify perceptions of risk in large mammals. In particular, researchers attempting to quantify how risk shapes habitat selection should first identify if ‘risk’ entails areas where predators are most abundant (increased probability of encounters between carnivores and prey), where prey are least abundant (loss of dilution and the many-eyes effect), where probability of detecting a carnivore is lowest (increased probability of attack) or where probability of being captured upon encounter is lowest (Lima and Dill 1990). In the few systems where the spatial distribution of risk from large carnivores has been measured, these different types of ‘risk’ do not always occur in the same location (Hebblewhite et al. 2005a, Hopcraft et al. 2005, Kauffman et al. 2007). Thus, in testing for a BMTC, researchers must first identify which form of risk matters the most to herbivores, then whether risk aversion is taking place, and finally, whether or not risk aversion has a meaningful effect on plants.

### 5.7.6 When is a negative result not a negative result and why does it matter?

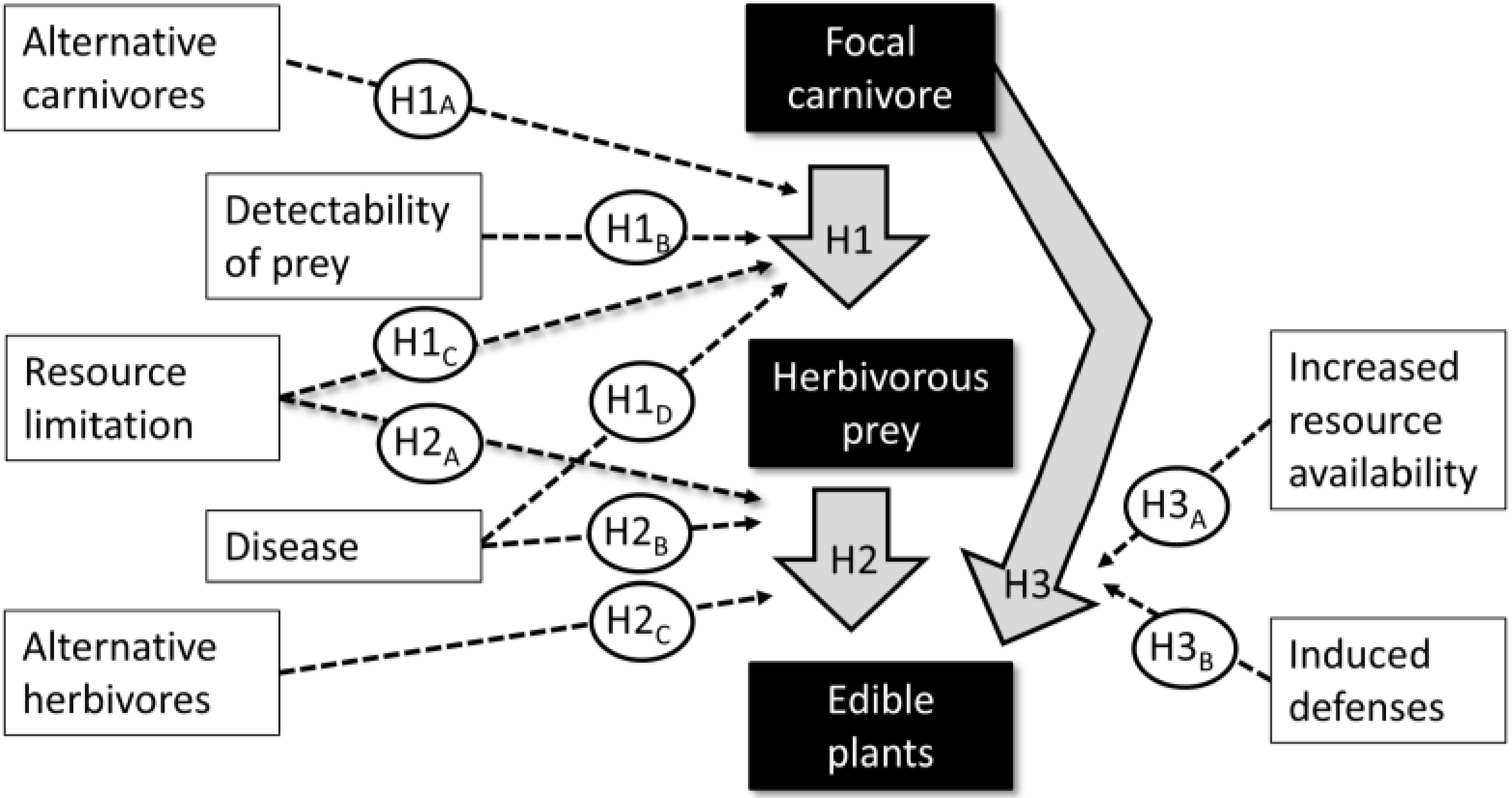
When tested properly, failure to find evidence in support of the trophic cascade hypothesis should not be viewed as a negative result. Indeed, a historic problem in the peer-reviewed system of communicating science is publication bias towards positive results and a great deal of commentary has been made about ways to address this issue (e.g., reviewed in Jennions and Moller 2002, Leimu and Koricheva 2004). However, and unlike many negative results, failure to find an indirect effect in a trophic cascade is consistent with a deep body of theoretical work describing the conditions when bottom-up regulation should occur most strongly (Fretwell 1977, Oksanen et al. 1981, Wootton 1994). There are food webs where indirect effects ought to occur and those where indirect effects are rare or intractable (Polis and Strong 1996) and large carnivores are candidate species for food webs where trophic cascades are rare. Donor control (plant defense, anti-predator behavior), reticulation (functional overlap within speciose trophic levels) and environmental heterogeneity (as experienced over the expansive spatial and temporal scales that large carnivores interact with their environment) are all predicted to diminish the strength of trophic cascades (Polis et al. 2000). Indeed, these features are characteristic of most large carnivore-mediated food webs in terrestrial biomes.

Perhaps more critical than the theoretical implications of trophic cascades in systems dominated by large carnivores, is the need to understand when and where conservation practice can deliver its stated promises. The purported generality of trophic cascades is being used to justify large carnivore restoration across the globe (Ripple et al. 2014). However, if this hypothesis is not upheld and the indirect effects of large carnivores are not realized, then conservationists risk alienating the local communities most affected by such restoration efforts while also endangering the very species they are trying to protect.

Consider the following thought experiment. First, assume that a trophic cascade has been triggered by the reintroduction of wolves to Yellowstone, as many have argued (Estes et al. 2011, Ripple and Beschta 2012b, Ripple et al. 2014). The conservation value of this cascade (Ripple and Beschta 2005), not species restoration itself, is essentially a ‘purchase’ of elk biomass in return for increased aspen growth. If the public supports this trophic exchange, it would presumably bolster efforts to conserve wolves. However, these trophic exchanges do not always favor conservation. In Ijara District of Kenya, less than 500 hirola (*Beatragus hunteri*) antelope co-occur alongside a diverse assemblage of browsers in an increasingly woody landscape. For the hirola, woody cover reduces the availability of forage and increases their risk of predation (A. Ali, unpublished data). If the trophic cascade hypothesis is a law of nature, as some suggest, then removing the large carnivores that suppress Ijara's browsers will increase suppression of woody cover and thus help hirola recover from the brink of extinction. Unfortunately, these large carnivores – cheetahs and wild dogs – are both listed as endangered by the IUCN. The criticality of the hirola's situation cannot be overstated, and a rationale calculus of conservation triage could permit extirpation of these endangered carnivores if it will save the hirola. Thus, the conservation value of a trophic exchange between trees and herbivores may be far murkier in Ijara than Yellowstone and overstating the generality of trophic cascades will not clarify the situation. Fortunately, a trophic cascade was not triggered by wild dogs in central Kenya (Chapter 4) and so their extirpation is unlikely to benefit the quality of habitat for hirola Eastern Kenya. There are a number of convincing moral and aesthetic reasons to conserve historical species assemblages, including large carnivores (Ripple et al. 2014); however, using trophic cascades as an omnibus justification for large carnivore recovery does not lead us to that objective.

Trophic cascades are a compelling explanation for the way nature works. It draws together aspects of ecology that many in the public and in the scientific community hold dear to their hearts – that things in nature interact and are connected with one another (Fretwell 1987). Another compelling feature of nature is its diversity of landscapes, species and behaviors. The checklists that accompany almost every field guide is testament to the desire of people to bear witness to this diversity. Prior to the modern evolutionary synthesis, historical explanations for the mechanisms by which species diversity has arisen were varied, and many remain controversial in some parts of the world today. Resolving that controversy, from creationism to Lamarckism and to natural selection, came about because of adherence by scientists to a rigorous and objective program to test multiple hypotheses. Unlike evolutionary biology, explanations for the mechanisms by which interactions arise in ecology are still emerging. Viewing trophic cascades as a paradigm, rather than a testable hypothesis, will at best keep ecology in the dark shadows of the ‘soft interaction’ and at worst, we risk losing the very diversity needed to appreciate the interactions in nature.

**Figure 5.1 Conceptual framework for evaluating multiple-competing hypotheses for a tri-trophic cascade involving large carnivores, herbivores and plants. Focal interactions must include evidence for: (H1) suppression of the herbivore by a carnivore; (H2) suppression of plants by the prey of the carnivore; (H3) increase plant abundance/biomass in the presence of the carnivore. Alternatives to H1 may include: ($H1_A$) suppression of herbivores by a non-focal carnivore, including humans; ($H1_B$) behavioural or environmental changes that lowered the detectability but not abundance of prey; ($H1_C$) food, water or other resource limitations that decreased herbivore abundance; ($H1_D$) disease or parasites that caused a decline in the abundance of herbivorous prey. Alternatives to H2 may include: ($H2_A$) water, light, nutrient or other resource limitations that decreased plant abundance; ($H2_B$) disease or parasites that caused a decline in the abundance/biomass of plants; ($H2_C$) increased herbivory from non-prey herbivores. Alternatives to H3 may include: ($H3_A$) heightened plant abundance occurred because of increased water, light, nutrient or other resources; ($H3_B$) herbivory-induced defenses in plants slowed rates of herbivory and increased plant abundance. Black boxes indicate focal trophic levels, gray arrows indicate focal interactions for the main hypotheses (H1, H2, H3) and dashed lines indicate potential alternative hypotheses for the focal interactions. Support for alternative hypotheses may coincide with support for H1, H2 or H3, weakening inferences that a trophic cascade has occurred.**


Alternative carnivores
H1A
Focal carnivore
Detectability of prey
H1B
H1
Resource limitation
H1C
H1D
H2A
Herbivorous prey
Increased resource availability
H3A
Disease
H2B
H2
H3
Alternative herbivores
H2C
H3B
Induced defenses
Edible plants

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