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Ng'weno C. Caroline., Predator-prey interactions and apparent competition following the restoration of lions to a human-occupied savanna., Ph.D., Program in Zoology, August, 2017.

Efforts to restore large carnivores often are conducted with an assumption of reciprocity, in which prey populations are expected to return to levels approximating those prior to carnivore extirpation. The extent to which this assumption is met depends on the intensity of predation, which in turn can be influenced by the magnitude of environmental change over the period of large-carnivore extirpation. To understand whether and the extent to which predation by lions underlies hartebeest declines, following lion restoration I monitored vital rates of hartebeest that were variably exposed to or protected from lions between August 2014 and December 2015. My findings showed that, lion exclusion shifted rates of population growth from negative to positive ($\lambda = 0.89 \pm 0.04$ versus 1.11 ± 0.11 for control and lion-exclusion zones, respectively) and, consistent with other studies on ungulate demography, adult survival was the most sensitive and elastic vital rate. Analysis of life table response experiments revealed that 32% of the variation in population growth was due to fecundity, which had the greatest proportional effects on λ. In addition, hartebeest selected open (grassland) areas more strongly where lions occurred, and avoided areas with dense tree cover. My work provides experimental evidence to support the hypothesis that hartebeest declines have been driven primarily by lion restoration, although I cannot eliminate the possibility that predation by spotted hyenas (*Crocuta crocuta*) additionally suppressed populations of hartebeest. Given that tree cover has increased across Laikipia over the past 50 years, I suggest that lion-driven declines of hartebeest have been exacerbated by landscape change. Chapter 2 addresses the vulnerability of an individual to predation depending on the availability of other prey items in the surrounding environment i.e. prey aggregations or 'neighborhoods'. I examined the influence of prey

neighborhood structure (i.e., the densities and identities of prey neighborhoods) on spatial variation in predation in a multi-prey, single predator system in an African savanna. I combined GPS tracking of lions (*Panthera leo*), kill-site surveys, and spatially-explicit density surfaces of five species of ungulates for which a significant level of predation was attributable to lions to quantify interspecific variation in patterns of mortality from predation for a multi-prey, single predator system in a semiarid savanna. My findings showed that, in addition to the dual influence of predator activity and vegetation, predation risk was attributable to the structure of prey neighborhoods for the majority of prey. Thus, along with traditionally-recognized components of predation (the rate of predator-prey encounters and prey catchability), I encourage ecologists to consider how prey neighborhood structure influences spatial variation in predation risk. Lastly, Chapter 3 explored whether glades (nutrient-rich hotspots created by abandoned cattle corrals) could be used to manipulate top-down control of hartebeest via their influence on the spatial distribution of zebra. Predator restorations often result in apparent competition, where co-occurring prey experience asymmetric predation pressure driven by predator preferences. In many rangeland ecosystems, livestock share the landscape with wildlife, including ungulates and the large carnivores that consume them. For example, recent declines of hartebeest (*Alcelaphus buselaphus*) populations in Laikipia, Kenya have coincided with recolonization by large carnivores, particularly lions (*Panthera leo*), over the past 20 years. Therefore, Three lines of evidence supported the hypothesis that hartebeest (an ungulate of conservation concern whose populations are declining) are suppressed via apparent competition. First, hartebeest exhibited an Allee effect where they were exposed to lions, but displayed negative density-dependent population growth where they were protected from lions. Second, spatial overlap between zebra (the primary prey of lions) and hartebeest further exacerbated lion predation on hartebeest. Finally,

hartebeest were killed selectively by lions, whereas zebra were killed by lions in proportion to their abundance. Also, zebra aggregated at glades, and survival of hartebeest increased when there was no glade within their home range, suggesting that corrals may be placed on the landscape to create refugia whereby hartebeest can escape top-down control. My findings demonstrate how informed placement of livestock corrals can be used to manipulate the spatial distribution of primary prey (zebra), thereby reducing apparent competition suffered by hartebeest. My work further demonstrates how integrating apparent competition theory with spatially-explicit data on predation can improve conservation efforts in multiple-use landscapes.

PREDATOR-PREY INTERACTIONS AND APPARENT COMPETITION FOLLOWING THE RESTORATION OF LIONS TO A HUMAN-OCCUPIED SAVANNA

By

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To my Son, Emmanuel Kimutai. You have made me stronger, better and more fulfilled than I could have ever imagined. I love you to the moon and back.

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Chapter 1

1.1 Introduction

Large-carnivore restoration often is expected to revert ecosystem properties to states approximating those prior to large-carnivore extirpation (Soulé et al. 2005; Estes et al. 2011; Ripple et al. 2014; Ford and Goheen 2015a). Carnivore restoration can be achieved through targeted reintroduction or translocation (Breitenmoser et al. 2001), or through natural recolonization of a historical geographic range in response to increased tolerance by local people (Hayward and Somers 2009; Woodroffe 2011; Chapron et al. 2014). When carnivores are restored following lengthy absences, ungulates and other prey may be naïve to the risk of predation, creating strong potential for declines of species of prey that already were rare before carnivore restoration. This phenomenon is particularly acute with secondary prey (i.e., rare species that are consumed opportunistically, and whose populations are therefore decoupled from those of carnivores; *sensu* Holt and Kotler 1987; DeCesare et al. 2010; Wittmer et al. 2013). Additionally, carnivore restoration may impact prey populations by inducing behavioral modifications (Brown et al. 1999; Preisser et al. 2005). For example, in the presence of large carnivores, ungulates minimize predation risk by selecting habitats to reduce their risk of detection, or by increasing vigilance (Lima 1999; Laundre et al. 2001; Caro 2005; Ford and Goheen 2015b; Donadio and Buskirk 2016), both of which can reduce food intake.

Effects of reintroduced or recolonizing carnivores on their ungulate prey range from pronounced impacts on prey numbers and behavior (e.g., Berger et al. 2001; Fortin et al. 2005; Ford et al. 2015a) to subtle or otherwise limited shifts in abundance, group size, or vigilance (e.g., Hunter and Skinner 1998; Davies et al. 2016; Moll et al. 2016). Such variable outcomes likely are a consequence of prey vulnerability and other system-specific details (Creel 2011; Gervasi et al.

2013). In African savannas, tree cover repeatedly has been demonstrated to affect predation risk, with high cover impeding detection and evasion of predators (Riginos and Grace 2008; Thaker et al. 2011; Ford et al. 2014; Riginos 2015). Therefore, tree cover may mediate the relative strength of top-down and bottom-up forcing of ungulate populations, and may be particularly influential in shaping recently restored predator-prey dynamics.

The Laikipia Plateau in central Kenya provides opportunity to examine ungulate responses to carnivore restoration. Following settlement by European ranchers in the early 1900s, livestock ranching and commercial sport-hunting were the predominant land uses in Laikipia (Denney 1972; Western and Henry 1979). During this period, livestock losses were reduced by lethal control (shooting and poisoning) of large carnivores (spotted hyenas [*Crocuta crocuta*], leopards [*Panthera pardus*], African wild dogs [*Lycaon pictus*], and especially lions [*P. leo*]). Consequently, large carnivores were greatly reduced in number, and lions were largely extirpated from most parts of Laikipia by the 1960s leading to increases in the abundance of their primary prey, plains zebra (*Equus quagga*; Denney 1972). In the 1950s (i.e., around the same time that lethal control of carnivores was highest), commercial ranchers began to suppress wildfire and prohibited local Maasai, Samburu, and Turkana tribes from controlled burning (Heady 1960; Sundaresan and Riginos 2010) thereby triggering increases in tree cover (Augustine and McNaughton 2004). During this time, some species of tree expanded into areas from which they had been absent previously (Heady 1960; Pratt and Gwynne 1977; Okello et al. 2001).

In the 1990s, lethal control of large carnivores abated as most commercial ranchers 1) adopted the use of predator-resistant enclosures (locally known as “bomas”) for corralling cattle at night (Ogada et al. 2003; Woodroffe et al. 2005; Frank 2008); 2) increasingly perceived competition between zebra and cattle (*Bos indicus*) for grass; and 3) began viewing ecotourism as a potential supplement to revenues from livestock. This period, therefore, marked the beginning of attempts to conserve large carnivores alongside livestock in the region, and commercial ranchers started to tolerate lions and other large carnivores on “pro-wildlife” properties (Georgiadis et al. 2007a). Because tourism offered financial incentive to conserve large carnivores despite livestock depredation, pro-wildlife properties tolerated the recolonization of lions across landscapes occupied by people and their livestock. Currently, lion numbers on pro-wildlife properties in Laikipia are estimated at 200-250, representing a density of 6 individuals/100 km^2 (Frank 2011). These densities are comparable to protected areas (e.g., Tsavo National Park, with 4 individuals/100 km^2 [Patterson et al. 2004]).

Following the recolonization of lions over the past 25 years in Laikipia, many species of wild ungulates on pro-wildlife properties have declined markedly (Georgiadis et al. 2007a), including hartebeest (*Alcelaphus buselaphus*), waterbuck (*Kobus ellipsiprymnus*), eland (*Taurotragus oryx*), and greater kudu (*Tragelaphus strepsiceros*). The rate and timing of these declines are similar across species, suggesting one or more common mechanisms of decline. Poaching in Laikipia is uncommon, particularly on pro-wildlife properties that maintain coordinated anti-poaching and security networks. Likewise, a 40-year time series exploring rainfall and density-dependent population regulation demonstrated that only zebra were regulated by rainfall and that only zebra and giraffes (*Giraffa camelopardalis*) exhibited density-dependence (Georgiadis et al. 2003, 2007a). Livestock populations on pro-wildlife properties have not increased over this time (Georgiadis 2011).

Georgiadis et al. (2007b) attempted to elucidate the causes of ungulate declines in Laikipia, addressing 10 alternatives, and focusing mostly on hartebeest. They found only predation to be consistent with all available information, but the precise mechanisms of hartebeest decline remain unconfirmed. To test the hypothesis that predation--and specifically, predation by lions--underlies declines of hartebeest, I used 6 years (2009-2015) of hartebeest sight-resight data to estimate population trends, age structure, and vital rates (survival of calves, subadults, and adult females, plus adult fecundity). I also quantified resource selection by hartebeest via resource selection functions (RSFs; Boyce and McDonald 1999). I sought to answer 2 questions: 1) How do lions influence growth and vital rates of hartebeest populations? and 2) Does risk of predation from lions alter habitat selection of hartebeest? I chose to focus on hartebeest vital rates and habitat selection for the following reasons. Hartebeest have exhibited the steepest proportional declines of any wild ungulate within Laikipia over the past 3 decades (Georgiadis et al. 2007a); additionally, hartebeest appear to be preferred prey of lions on at least some properties in Laikipia (Ng'weno et al., pers. obs.). So, if predation has driven declines of populations of wild ungulates, changes in population size, behavior, or both should be detected readily for hartebeest. Additionally, hartebeest are open-grassland specialists, for which I might expect the strongest interactions between risk of predation and habitat selection (see also Moll et al. 2016).

1.2 Materials and Methods

1.2.1 Study area

I conducted my study at Ol Pejeta Conservancy (OPC) in Laikipia County, Kenya, a 328-km^2 pro-wildlife property located on the equator (0º N, 36º56'E). *Acacia drepanolobium* and *Euclea divinorum* characterize the overstory of OPC. The conservancy receives approximately 900 mm rainfall annually (Birkett 2002). Within OPC, ca. 70 lions occur in 5 prides (OPC Ecological Monitoring Department, pers. comm.). Other large carnivores on OPC include spotted hyenas, leopards, cheetahs (*Acinonyx jubatus*), and African wild dogs. Other large mammals on OPC include elephants (*Loxodonta africana*), African buffalo (*Syncerus caffer*), black (*Diceros* *bicornis*) and white rhinoceros (*Ceratotherium simum*), Thomson's gazelle (*Eudorcas thomsonii*), Grant's gazelle (*Nanger granti*), impala (*Aepyceros melampus*), oryx (*Oryx gazella*), Grevy's zebra *(Equus grevyi*), waterbuck, eland, plains zebra, giraffes, and hartebeest.

Ol Pejeta Conservancy is comprised of 2 zones with different management regimes: 1) a 294-km^2 conservation area in which cattle production occurs alongside wildlife with the full complement of large carnivores; and 2) a 32-km^2 lion exclusion zone (hereafter "exclusion zone"), constructed with the intent of bolstering numbers of declining ungulates, primarily hartebeest. Stocking rates are maintained at equal densities of 20 cattle per km^2 in both zones. Prior to construction of the exclusion zone, lions (but not other large carnivores) were captured and translocated to the conservation area (hereafter "control zone"); in the rare instances that lion incursions occur, they are removed and translocated to the control zone within OPC or to other pro-wildlife ranches. The exclusion zone is adjacent to the conservation area, and is demarcated by a 3,200-m long, 2.5-m tall solar powered electrified (6,000-7,000-volt) fence with 9 strands spaced 0.2-m apart. The fence is fortified with chain-link 1.50 m above and 0.60 m beneath the ground. The 2 zones have comparable grass biomass (ca. 1,500 kg/ha) and water availability (OPC Ecological Monitoring Department, pers. comm.).

1.2.2 Data collection and analysis

1.2.2.1 Camera-trap surveys

In each of 4 years (2012-2015), I conducted camera-trap surveys to assess densities of large carnivores in control and exclusion zones. I divided OPC into 3 blocks (northern, southern, and eastern) of comparable area, overlaid a 2 x 2 km grid over each block, and sampled each block for 21 consecutive days between the months of October and December. A single camera trap (Reconyx Rapidfire RM45, Reconyx , Holmen, Wisconsin) was deployed at the center of each grid cell to ensure uniform distribution of sampling points. This yielded 1,512 camera-trap nights (72 traps x 21 days) per year. I deployed cameras within 50 meters from the centroid of each grid cell, typically near active game paths to maximize captures. I mounted cameras on trees or metal cages 3 m from game paths at 45 cm above the ground, and checked them every 7 days to ensure continuous operation. After 21 days, I removed cameras, downloaded images, and calculated density estimates for lions, spotted hyenas, and black-backed jackals (*Canis mesomelas*) according to Carbone et al. (2001). Leopards, cheetahs, and African wild dogs were photographed too infrequently to calculate densities. Densities of spotted hyenas within the exclusion zone were approximately 70% of the control zone; densities of black-backed jackals were not statistically distinguishable between zones (Supplementary Data S1; OPC Ecological Monitoring Department, pers. comm.).

1.2.2.2 Hartebeest and lion surveys

Hartebeest are pure grazers that form distinct herds; a strong dominance relationship between females defines the social organization of each herd (Kingdon 1982). They calve throughout the year in accord with rainfall variability. At OPC, hartebeest occur in herds of up to 15 individuals that defend small territories (< 5 km^2) from conspecifics. From 2009 to 2015, I conducted twice-monthly drive transects to quantify population densities of hartebeest in within my study area. Beginning in 2012, I included sight-resight methods on drive transects to estimate demographic rates and age structure of herds within both zones (Skalski et al. 2005; see also Supplementary Data S2). I conducted surveys with 2 observers and a driver from 0800 to 1100 hours ($n = 17$, mean distance per transect = 7.50 km ± 0.84 SE). Surveys of the exclusion zone took 1 day whereas the control zone was surveyed in 3 consecutive days. Upon sighting a herd, I approached from the downwind side to within a distance of about 150 m, and then would spent 10-15 min habituating the herd before gradually moving to ca. 70 m to avoid disturbing the animals. During these 2 stops, I estimated the bearing to the herd using hand-held compasses. I determined the radial distance from the point where the center of the group was initially sighted to the nearest meter using a laser rangefinder. Lastly, I marked the location of observations using hand-held GPS units. I used binoculars to clarify group size, and the sex and age classes of individuals within the herd. Individuals were categorized as 1 of 3 age classes using a suite of characteristics, including size, body shape, and horn shape and development (Andanje 2002; Supplementary Data S3): calves (0-12 months), subadults (13-23 months), and adults (≥ 24 months). Individuals were considered to belong to the same herd when the distance between them was less than 60 m. My methods adhered to ASM animal care and use guidelines (Sikes et al. 2016).

I estimated abundance of lions by radio-tracking 5 dominant lionesses from each of the 5 established prides within OPC, fitted with radio collars. Lions were captured and collared with the assistance of a Kenya Wildlife Service veterinary team using protocols described by Frank et al. (2003). Lions were darted from a parked field vehicle at a distance of 10 – 30 m with a 2mL dart containing a combination of ketamine (0.2 mg/kg), medetomidine (0.03 mg/kg) and atipamezole (0.33 mg/kg) using a CO_2 rifle (Dan-inject RSA, Skukuza, South Africa). Lions were then reversed and observed until they were able to walk and rejoined other pride members. From 2009-2011, Very High Frequency (VHF) collars (Telonics, Mesa, Arizona) were used and later replaced in 2012 with Global Positioning System (GPS) collars (Vectronics Aerospace GmbH, Berlin, Germany). Because lions live in stable social units (prides), collars allowed regular re-sighting of uncollared individuals within prides, allowing for weekly monitoring. We obtained additional data from sightings and photographs by safari guides and clients operating within the conservancy (see Supplementary Data S1). I estimated abundance of lions from weekly monitoring of known individuals, during which all lions were individually identified using whisker-spot patterns, scarring, and tooth breakage (Pennycuick and Rudnai 1970; Becker et al. 2013).

I fit generalized linear models (GLMs) to explain hartebeest densities in the control zone using the following predictor variables: 1) lion density, estimated by re-sighting of uniquely identifiable individuals from whisker spots (see below); 2) rainfall, collected from 10 stations distributed throughout OPC; and 3) population size of hartebeest in the control zone from the previous year. I constructed a suite of candidate models and calculated each model's AIC_c (Akaike Information Criterion, corrected for small sample sizes) and AIC_c weights (W_i) as a metric for strength of evidence to compare the performance of each model (Burnham and Anderson 2002). These statistical analyses were conducted in Program R version 3.2.3 (R Development Core Team 2015) using package MASS (Venables and Ripley 2002).

1.2.2.3 Demographic analysis

I calculated age-specific survival (calf survival [S_c], subadult survival [S_{sa}], and adult survival [S_{ad}]; Supplementary Data S4) from October (t) to September of each subsequent year (t + 1) for 288 individuals in 15 herds between 2012 and 2015 using the "survival" package in R (Therneau 2012). To calculate fecundity (F_a), I used estimates of the number of calves produced per year per adult female (calves/adult female * S_{ad}), and assumed an equal sex ratio of offspring following Sinclair et al. (2003). Female hartebeest are philopatric, and remain within the maternal herd for life (Gosling 1974). Males begin dispersing at about 20 months (Kingdon 1989). Hence, I was able to identify individuals from when they were first observed until they either recruited to the subadult age class or disappeared. I equated disappearance (lack of detection in 6 consecutive sight-resight surveys over the course of 3 months; see *Hartebeest surveys*) with mortality. Hartebeest have an 8-month gestation period, and gravid females were noticeable at 5 months with swollen bellies. I observed calves for 94.3% of gravid adult females in the control zone, 96.3% of gravid adult females in the exclusion zone (Supplementary Data S5).

I constructed 3 x 3 age-structured post-birth pulse matrix models to estimate population growth rate (λ) in each zone, and determined sensitivity and elasticity of λ to individual vital rates (Caswell 2001; Owen-Smith and Mason 2005). To discern vital rates with the greatest impact on differences in λ between control and exclusion zones, I performed a Life Table Response Experiment (LTRE; Caswell 2000; Maclean et al. 2011; Supplementary Data S6). I calculated 1) the difference in λ between the zones ($\Delta\lambda = \lambda_{\text{Exclusion}} - \lambda_{\text{Control}}$); and 2) contributions of each vital rate toward this difference for the period 2012–2015 using averaged estimates of vital rates. LTREs and other retrospective analyses identify the demographic variables that have, in the past, contributed most to observed variation among populations in λ (Caswell 2001).

1.2.2.4 Analysis of habitat selection

I quantified habitat selection using selectivity measures (Manley et al. 2002). I characterized habitat types based on tree cover according to GIS layers ground-truthed and digitized from a landsat ETM7 satellite image by Birkett (2002): 1) Dense bushland (>50% overstory cover dominated by *E. divinorium*); 2) Open bushland (10-30% overstory cover dominated by *A. drepanolobium*); and 3) Open grassland (mostly treeless areas, with understory cover dominated by *Themeda triandra*, *Pennisetum stramineum*, and *P. mezianum*). From studies in similar systems (e.g., Hopcraft et al. 2005, Valeix et al. 2009, Ford et al. 2014), I believed dense bushland, open bushland, and open grassland would be correlated with high, intermediate, and low levels of risk of predation, respectively. For each hartebeest herd, I constructed minimum convex polygons (MCP; Mohr 1947), with 95% of the locations to delineate habitat availability using ArcGIS 10.3 (ESRI, Redlands, California). I then generated random points and sampled availability using a 1:1 ratio of used to available locations within the MCP. For all used and random points, I measured habitat use and availability with a population level design in each zone (control zone: *n* = 1,806 used locations [herd sightings]; exclusion zone: *n* = 857 used locations; Boyce and McDonald 1999; Manly et al. 2002; Boyce 2006). I described habitat selection as differences in observed use to expected availability of habitat type using selection ratios, and tested preference or avoidance for each habitat using a log-likelihood chi-square test for overall habitat selection. Selection ratios greater than 1.0 indicated positive selection for a habitat type and ratio values less than 1.0 indicated a selection against habitat type. I used the adehabitatHR package in R to analyze habitat selection (Calenge 2014).

1.3 Results

From 2009 to 2015, population size of hartebeest in the exclusion zone increased while it declined in the control zone (Fig. 1), and the GLM containing only lion abundance was the most plausible model for population density of hartebeest in the control zone through time (Table 1). In both exclusion and control zones, survival of adults was higher than survival of subadults and calves (χ^2_2 = 77.3, $P < 0.001$; Fig. 2), which were statistically indistinguishable (exclusion zone: χ^2_1 = 2.2, $P = 0.134$; control zone: χ^2_1 = 0.2, $P = 0.696$). Except for survival of adults, all other vital rates were significantly higher in the exclusion zone than in the control zone (calf survival: χ^2_1 = 25.7, $P < 0.001$; subadult survival: χ^2_1 = 18.4, $P < 0.001$; adult survival: χ^2_1 = 2.9, $P = 0.09$; fecundity: $F_{1,10} = 0.16$, $P < 0.001$; Fig 2). Exclusion of lions bolstered population growth of hartebeest ($F_{1,\,4} = 12.87$, $P = 0.023$; control zone: $\lambda = 0.89 \pm 0.04$; exclusion zone: $\lambda = 1.11 \pm 0.11$), principally through fecundity and survival of adults but also through survival of calves and subadults (Fig. 3).

Habitat selection of hartebeest varied with the occurrence of lions (Fig. 4). In the presence of lions, hartebeest selected open grasslands (selection ratio = 1.50, 95% C.I.: 1.44-1.56) and avoided dense (selection ratio = 0.48, 95% C.I.: 0.40-0.56) and open (selection ratio = 0.69, 95% C.I.: 0.64-0.74) bushland. In contrast, there was weak evidence for selection for all 3 habitat types where lions were absent ($\chi^2_2 = 1.811$, $P = 0.404$).

1.4 Discussion

My work contributes to growing recognition that predation is a major factor in driving population dynamics and behavior of savanna ungulates, particularly numerically subordinate species (Owen-Smith et al. 2005; Thaker et al. 2011; Grange et al. 2015; Riginos 2015). Specifically, survival rates of hartebeest calves and subadults were suppressed by lion predation, and lions triggered stronger selection for open habitats characterized by higher visibility. At least with respect to hartebeest on Ol Pejeta Conservancy, my work affirms the inferences of Georgiadis et al. (2007b) with direct evidence implicating predation as the cause of decline, and significantly extends them through several key findings. First, I experimentally identified a demographic pathway (reduced fecundity) through which predation suppressed population growth of hartebeest. Second, I isolated the role of a recently recolonized large carnivore (lions, and perhaps spotted hyenas to a lesser extent) in ongoing declines and projected rates of population growth of hartebeest. Finally, I demonstrated large carnivore-mediated shifts in habitat selection, whereby hartebeest are more likely to use ostensibly risky habitats following lion exclusion.

Although Ol Pejeta Conservancy represents a single property within Laikipia County, I believe my findings are representative of many properties on which hartebeest and lions co-occur. Nonetheless, I cannot rule out other potential drivers, which may exacerbate or altogether replace predation in underlying region-wide population declines of hartebeest. Increasingly, wildlife in African savannas is being compressed into ever-dwindling areas; it is possible that the aggregations of wild ungulates on Ol Pejeta have concentrated hunting by lions and other predators into the few habitats suitable for hartebeest (see also Ali et al. 2016). Additionally, severity of droughts has increased in Laikipia since the mid-1970s (Ogalleh et al. 2012). On a neighboring property, rainfall and hartebeest activity are negatively correlated (Kimuyu et al. 2016), although the degree to which increasing drought has caused population declines of hartebeest is unknown. Finally, in addition to its potential role in increasing risk of predation, tree encroachment might reduce nutritive quality of grasses, thereby reducing recruitment of hartebeest and other ungulates (Riginos et al. 2015; Proffitt et al. 2016).

For large mammals, survival of adults typically has the largest potential effect on population growth (i.e., λ is highly sensitive to small changes in adult survival; Gaillard et al. 2000). Additionally, LTRE analysis revealed that lions impacted population growth of hartebeest through all 4 vital rates, in contrast to several studies on temperate ungulates in which predators typically influence population growth mainly by suppressing survival of calves (Eberhardt 1977, 2002; Gaillard et al. 1998, 2000; Gaillard and Yoccoz 2003; Owen-Smith and Mason 2005; Raithel et al. 2007). Notably, lions suppressed population growth by reducing fecundity, which may be attributable to effects of predation as a result of 2 pathways: predator-induced stress and predator-induced shifts toward less nutritious forage. Although it has not been documented in tropical ungulates, predator-induced stress has been demonstrated to reduce reproduction in elk (*Cervus elaphus*; Creel et al. 2007, 2009), snowshoe hares (*Lepus americanus*; Sheriff et al. 2010, 2015), and common voles (*Microtus arvalis*; Jochym and Halle 2013). For example, cow elk can enhance their survival by making reproductive or behavioral trade-offs in the presence of wolves (Creel et al. 2007). Similarly, predators may trigger shifts in forage selection that are accompanied by nutritional costs. Elsewhere in Laikipia, risk of predation from African wild dogs and leopards cause impala to forage on thornier, less-preferred trees (Ford et al. 2014; see also Fortin et al. 2005). Whether reduced fecundity of hartebeest is an outcome of lion-induced stress, lion-induced shifts in habitat, or both remains a hypothesis for testing in the future.

Animals must balance food availability and predation risk when selecting habitat, and bushland habitats appear riskier than open grassland for hartebeest. Elsewhere in sub-Saharan Africa, wooded areas provide more cover for lions and other large carnivores to hunt (Hopcraft et al. 2005; Thaker et al. 2011; Loarie et al. 2013; Ford et al. 2014). In my system, hartebeest shifted their activity toward areas with higher visibility (open grasslands) in the presence of lions, suggesting that perceived risk of predation is at least partly responsible for driving the distribution of hartebeest across landscapes (Lima and Dill 1990; see also Donadio and Buskirk 2016). To the extent that such non-consumptive effects translate to reduced survival, fecundity, or both for hartebeest, declining populations of hartebeest in Laikipia are likely the outcome of a combination of direct (density-mediated) and indirect (behaviorally mediated) effects of recolonizing lions. The relative impact of density- versus behaviorally mediated effects of lions and other predators on hartebeest declines represents another open question for future research.

Predator restoration can inject optimism into conservation efforts typically characterized by reactive, stopgap measures. Ecologists tend to treat predator restorations as “natural experiments”, a view that downplays changes in environmental conditions that may have occurred during predator extirpation. Through experiments in other systems, I know that predators can have variable effects at different times (Vaughn and Young 2010; Stier et al. 2013) and in different places (Paine 1966), so my ability to predict the impacts of their restoration should depend on environmental context (Agrawal et al. 2007; Gervasi et al. 2013; Middleton et al. 2013). Although my work points to lions in limiting contemporary populations of hartebeest, both species co-occurred for millennia in Laikipia, so it is unlikely that lions are solely responsible for continued declines of hartebeest at OPC and elsewhere in this region. Because hartebeest typically are open-grassland specialists, and because wooded areas in Laikipia have expanded with fire suppression since the 1950s, I suggest that hartebeest (and possibly other ungulates comprising secondary prey for lions) have declined because of intensified predation. I suspect that this intensified predation itself is a combination of recent recolonization of a large carnivore (lions) to a bushier landscape in which hartebeest are rendered more vulnerable than they have been historically, and possibly because lions increasingly are excluded from pastoral land (Oriol-Cotterill et al. 2015). Consequently, I recommend that wildlife managers incorporate range restoration (e.g., prescribed fire, manual bush clearing, and other practices that promote grass growth) into efforts to conserve lions and their native prey in landscapes that have been impacted by human activities.

1.6 References

AGRAWAL, A. A., ET AL. 2007. Fılling key gaps in population and community ecology. Frontier in Ecology and the Environment 5:145-152.

ALI, A.H., A.T. FORD, J.S. EVANS, D. MALLON, M.M. HAYES, J. KING, R.AMIN, AND J.R. GOHEEN. 2016. Resource selection and landscape change reveal mechanisms suppressing population recovery for the world's most endangered antelope. Journal of Applied Ecology, online in advance of print.

ANDANJE, S. A. 2002. Factors limiting the abundance and distribution of hirola (*Beatragus hunteri*) in Kenya [Thesis]. Newcastle University, United Kingdom.

AUGUSTINE, D. J., AND S. J. MCNAUGHTON. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. Journal of Applied Ecology 41:45-58.

BECKER, M. S., F. G. R. WATSON, E. DROGE, K. LEIGH, R.S. CARLSON, AND A. A. CARLSON. 2013. Estimating past and future male loss in three Zambian lion populations. Journal of Wildlife Management 77:128-142.

BERGER, J., J. E. SWENSON, AND I.-L. PERSSON. 2001. Recolonizing carnivores and naïve prey: conservation lessons from pleistocene extinctions. Science 291:1036-1039.

BIRKETT, A. 2002. The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. African Journal of Ecology 40:276-282.

BOYCE, M. S. 2006. Scale for resource selection functions. Diversity and Distributions 12:269-276.

BOYCE, M. S., AND L. L. MCDONALD. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14(7):268-272.

BREITENMOSER, U., C. BREITENMOSER, L. N. CARBYN, AND S. M. FUNK. 2001. Assessment of carnivore reintroductions. Pp. 241-281 in Carnivore conservation (Gittlemen, J. L., S. M. Funk, D. MacDonald, and R. K. Wayne, eds.). Cambridge University Press, Cambridge.

BROWN, J. S., J. W. LAUNDRE, AND M. GURUNG. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385-399.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York, USA.

CALENGE, C. 2014. Compana {adehabitat}: compositional analysis of habitat use. http://www.inside-r.org/packages/cran/adehabitat/docs/compana. Accessed 14 March 2015.

CARBONE, C., ET AL. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. Animal Conservation 4:75–79.

CARO, T. M. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago.

CASWELL, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81:619-627.

CASWELL, H. 2001. Matrix population models. Sinauer Associates, Massachusetts, USA.

CHAPRON, G., ET AL. 2014. Recovery of large carnivores in Europe's modern human dominated landscapes. Science 346:1517-1519.

CREEL, S. 2011. Toward a predictive theory of risk effects: hypotheses for prey attributes and compensatory mortality. Ecology 92:2190-2195.

CREEL, S., J. A. WINNIE., AND D. CHRISTIANSON. 2009. Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. Proceedings of the National Academy Science USA 106:12388-12393.

CREEL, S., D. CHRISTIANSON, S. LILEY, AND J. A. WINNIE. 2007. Predation risk affects reproductive physiology and demography of elk. Science 315:960.

DAVIES, A. B., C. J. TAMBLING, G. I. H. KERLEY, AND G. P. ASNER. 2016. Limited spatial response to direct predation risk by African herbivores following predator reintroduction. Ecology and Evolution (6) 16: 5728-5748

DECESARE, N. J., M. HEBBLEWHITE, H. S. ROBINSON, AND M. MUSIANI. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. Animal Conservation 13:353-362.

DENNEY, R. N. 1972. Relationships of wildlife to livestock on some developed ranches on the Laikipia Plateau, Kenya. Journal of Range Management 25:415-425.

DONADIO, E., AND S. W. BUSKIRK. 2016. Linking predation risk, ungulate antipredator responses, and patterns of vegetation in the high Andes. Journal of Mammalogy 97:966-977.

EBERHARDT, L. L. 1977. Optimal policies for conservation of large mammals with special reference to marine ecosystems. Environmental Conservation 4:205-212.

EBERHARDT, L. L. 2002. A paradigm for population analysis of long–lived vertebrates. Ecology 83:2841-2854.

ENVIRONMENTAL SYSTEMS RESOURCE INSTITUTE (ESRI). 2013. ArcMap 10.3: Professional GIS software for geospatial processing. Redlands, California. http://desktop.arcgis.com/en/arcmap/.

ESTES, J. A., ET AL. 2011. Trophic downgrading of planet Earth. Science 333:301-306.

FORD, A. T., AND J. R. GOHEEN. 2015a. Trophic cascades by large carnivores: a case for strong inference and mechanism. Trends in Ecology and Evolution 30:725-735.

FORD, A. T., AND J. R. GOHEEN. 2015b. An experimental study on risk effects in a dwarf antelope. Journal of Mammalogy 96:918-926.

FORD, A. T., ET AL. 2014. Large carnivores make savanna tree communities less thorny. Science 346:346-349.

FORTIN, D., H. L. BEYER, M. S. BOYCE, D. W. SMITH, T. DUCHESNE, AND J. S. MAO. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320-1330.

FRANK, L. 2011. Living with lions: lessons from Laikipia. In Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem (Georgiadis, N. J. ed.). Smithsonian Institution press, Washington DC, USA,

FRANK, D. A. 2008. Evidence for top predator control of a grazing ecosystem. Oikos 117:1718–1724.

FRANK, L. G., D. SIMPSON, AND R. WOODROFFE. 2003. Foot snares: an effective method for capturing African lions. Wildlife Society Bulletin 31:309-314.

GAILLARD, J. M., A. LOISON, C. TOIGO, M. FESTA-BIANCHET, AND N. G. YOCCOZ. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367-393.

GAILLARD, J.-M., AND N .G. YOCCOZ. 2003. Temporal variation in survival of mammals: a case of environmental canalization. Ecology 84:3294-3306.

GAILLARD, J.-M., M. FESTA-BIANCHET, AND N. G. YOCCOZ. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58-63.

GEORGIADIS, N. J. 2011. Introduction: Conserving wildlife in Kenya’s Ewaso landscape. Smithsonian Contributions to Zoology 632:1-10.

GEORGIADIS, N. J., G. OJWANG’, J. G. N. OLWERO, AND S. S. ROMAÑACH. 2007a. Savanna herbivore dynamics in a livestock-dominated landscape I: I. Dependencedependence on land use, rainfall, density, and time. Biological Conservation 137:461-472.

GEORGIADIS, N. J., I. FESTUS, J. G. NASSER, AND S. STEPHANIE. 2007b. Savanna herbivore dynamics in a livestock-dominated landscape II: Ecologicalecological, conservation, and management implications of predator restoration. Biological Conservation 137:473-483.

GEORGIADIS, N. J., M. HACK, AND K. TURPIN. 2003. The influence of rainfall on zebra population dynamics: implications for management. Journal of Applied Ecology 40:125-136.

GERVASI, V. H. SAND, B. ZIMMERMAN, J. MATTISSON, P. WABAKKEN, AND J. D. C. LINNELL. 2013. Decomposing risk: landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. Ecological Applications 23:1722–1734.

GOSLING, L. M. 1974. The social behavior of Coke's hartebeest (*Alcelaphus huselaphus cokei)*. Pp. 488-511 in Ac behavior of ungulates and its relation to management (V. Geist and F. R. Walther, eds.). International Union for the Conservation of Nature, Morges, Switzerland.

GRANGE, S., ET AL. 2015. Demography of plains zebra (*Equus quagga*) under heavy predation. Population Ecology 57:201-214.

HAYWARD, M. W., AND J. M. SOMERS. 2009. Reintroduction of top-order predators. Wiley-Blackwell, Oxford, UK.

HEADY, H. F. 1960. Range Management in East Africa. Department of Agriculture illus. 125. Govt. Printer, Nairobi, Kenya.

HOLT, R. D., AND B. P. KOTLER. 1987. Short-term apparent competition. The American Naturalist 130:412-430.

HOPCRAFT, J. G. C., A. R. E. SINCLAIR, AND C. PACKER. 2005. Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology 74:559-566.

HUNTER, L.T.B. AND J.D. SKINNER. 1998. Vigilance in African ungulates: the role of predation pressure. Behaviour 135:195–211.

JOCHYM, M., AND S. HALLE. 2013. Influence of predation risk on recruitment and litter intervals in common voles (*Microtus arvalis*). Canadian Journal of Zoology 91:281-286.

KIMUYU, D.M., K.E. VEBLEN, C. RIGINOS, R.M. CHIRA, J.M. GITHAIGA, AND T.P. YOUNG. 2016. Influence of cattle on grazing and browsing wildlife varies with season and presence of megaherbivores. Ecological Applications, online in advance of print.

KINGDON, J. 1982. East African Mammals. Vol. 3c. New York Academic Press, USA.

KINGDON, J. 1989. East African mammals: An Atlas of Evolution in Africa, Part D (Bovids). Vol. 3d. University of Chicago Press, Chicago.

LAUNDRÉ, J. W., L. HERNÁNDEZ, AND K. B. ALTENDORF. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Canadian Journal of Zoology 79:1401-1409.

LIMA, S. L., AND L. M. DILL. 1990. Behavioural decisions made under the risk of predation: A a review and prospectus. Canadian Journal of Zoology 68:619-640.

LIMA, S. L., AND P. A. BEDNEKO. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. The American Naturalist 153 (2):649-659.

LOARIE, S. R., C. J. TAMBLING, AND G. P. ASNER. 2013. Lion hunting behaviour and vegetation structure in an African savanna. Animal Behaviour 85: 899–906.

MACLEAN, J. E., J. R. GOHEEN, D. F. DOAK, T. M. PALMER, AND T. P. YOUNG. 2011. Cryptic herbivores mediate the strength and form of ungulate impacts on a long-lived savanna tree. Ecology 92:1626-1636.

MANLY, B. F. J., L. L. MCDONALD, D. L. THOMAS, T. L. MCDONALD, AND W. P. WALLACE. 2002. Resource selection by animals: statistical design and analysis for field studies. 2nd ed. Kluwer Academic Publishers, Dordrecht, Netherlands.

MIDDLETON, A. D. ET AL. 2013. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. Ecology Letters 16:1023–1030.

MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223-249.

MOLL, R., A. K. KILLION, R. A. MONTGOMERY, C. J. TAMBLING, AND M. W. HAYWARD. 2016. Spatial patterns of African ungulate aggregation reveal complex but limited risk effects from reintroduced carnivores. Ecology 7:1123-1134.

OGADA, M. O., R. WOODROFFE, N. O. OGUGE, AND L. G. FRANK. 2003. Limiting depredation by African carnivores: the role of livestock husbandry. Conservation Biology 17:1521-1530.

OGALLEH S.A., C. VOGL R, J. EITZINGER, AND M. HAUSER. 2012. Local perceptions and responses to climate change and variability: the case of Laikipia District, Kenya. Sustainability 4:3302-3325.

OKELLO, B. D., T. G. O'CONNOR, AND T. P. YOUNG. 2001. Growth, biomass estimates, and charcoal production of *Acacia drepanolobiu*m in Laikipia, Kenya. Ecological Management 142:143-153.

ORIOL-COTTERILL, A., M. VALEIX, L.G. FRANK, C. RIGINOS, AND D.W. MACDONALD. 2015 Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. Oikos 124:1263-1273.

OWEN-SMITH, N, AND D. R. MASON. 2005. Comparative changes in adult vs. juvenile survival affecting population trends of African ungulates. Journal of Animal Ecology 74(4):762-773.

OWEN-SMITH, N., D. R. MASON, AND J. O. OGUTU. 2005. Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. Journal of Animal Ecology 74:774-788.

PAINE, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65-75.

PATTERSON, B. D., KASIKI, S. M., D. SELEMPO, AND R. W. KAYS. 2004. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. Biological Conservation 119:507-516.

PENNYCUICK C. J., AND J. RUDNAI. 1970. A method of identifying individual lions (*Panthera leo)* with an analysis of the reliability of identification. Journal of Zoology (London) 160:497-508.

PRATT, D. J., AND M. D. GWYNNE. 1977. Rangeland management and ecology in East Africa. Hodder and Stoughton, London.

PREISSER, E. L., D. I. BOLNICK, AND M. F. BENARD. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86:501-509.

PROFFITT, K., M. HEBBLEWHITE, W. PETERS, N. HUPP, AND J. SHAMHART. 2016. Linking landscape-scale differences in forage to ungulate nutritional ecology. Ecological Applications 26: 2156-2174.

R DEVELOPMENT CORE TEAM. 2015. R: A a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org. Accessed November 2015

RAITHEL, R. D., M. J. KAUFFMAN, AND D. H. PLETSCHER. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795-803.

RIGINOS, C. 2015. Climate and the landscape of fear in an African savanna. Journal of Animal Ecology 84:124-133.

RIGINOS, C., AND J. B. GRACE. 2008. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. Ecology 89:2228-2238.

RIPPLE, W. J., ET AL. 2014. Status and Ecological effects of the world's largest carnivores. Science 343:301-306.

SHERIFF, M. J., C. J. KREBS, AND R. BOONSTRA. 2010. The ghosts of predators past: population cycles and the role of maternal programming under fluctuating predation risk. Ecology 91:2983-2994.

SHERIFF, M. J., E. K. MCMAHON, C. J. KREBS, AND R. BOONSTRA. 2015. Predator-induced maternal stress and population demography in snowshoe hares: The more severe the risk, the longer the generational effect. Journal of Zoology 296(4):305-310.

SIKES, R. S., AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

SINCLAIR, A. R. E., S. MDUMA, AND J. S. BRASHARES. 2003. Patterns of predation in a diverse predator-prey system. Nature 425:288-290.

SKALSKI, J. R., K. E. RYDING, AND J. J. MILLSPAUGH. 2005. Wildlife Demography. Elsevier Press, Amsterdam, Netherlands.

SOULÉ M. E., J. A. ESTES, B. MILLER, AND D. L. HONNOLD. 2005. Strongly interacting species: conservation policy, management and ethics. Bioscience 55:168-76.

STIER, A.C., S.W. GEANGE, K. M. HANSON, AND B. M BOLKER. 2013. Predator density and timing of arrival affect reef fish community assembly. Ecology 94:1057-1068.

SUNDARESAN, S. R., AND C. RIGINOS. 2010. Lessons learned from biodiversity conservation in the private lands of Laikipia, Kenya. Great Plains Research 20:17-27.

THAKER, M., A. T. VANAK, C. R. OWEN, M. B. OGDEN, S. M. NIEMANN, AND R. SLOTOW. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. Ecology 92:398-407.

THERNEAU, T. 2012. {survival}: a package for survival analysis in R. http://www.CRAN.Rproject.org/package=survival>. Accessed November 2015

VALEIX, M., ET AL. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology 90:23-30.

VENABLES, W. N., AND B. D. RIPLEY. 2002. Modern Applied Statistics with S. Springer Verlag, New York.

WESTERN, D., AND W. HENRY. 1979. Economics and conservation in Third World national parks. BioScience 29:414–418.

WITTMER, H. U., R. SERROUYA, L. M. ELBROCH, AND A. J. MARSHALL. 2013. Conservation strategies affected by apparent competition. Conservation Biology 27:254-260.

WOODROFFE, R. 2011. Demography of a recovering African wild dog (*Lycaon pictus*) population. Journal of Mammalogy 92 (2):305-315.

WOODROFFE, R., AND L. G. FRANK. 2005. Lethal control of African lions: local and regional population impacts. Animal Conservation 8:91-98.

Tables

Table 1: A priori models (Generalized Linear Model, Gaussian family) for factors influencing hartebeest (*Alcelaphus buselaphus*) population densities at Ol Pejeta Conservancy, Kenya (2009-2015).

Selected models	k	ΔAICc	W_i	R^2
Lion numbers†	2	0.00	0.97	0.73
Hartebeest density (t-1)	2	7.94	0.02	0.15
Rainfall	2	8.73	0.01	0.05
Lion numbers + Rainfall	3	13.63	0.00	0.68
Lion numbers + Hartebeest density (t-1)	3	13.93	0.00	0.66
Rainfall + Hartebeest density (t-1)	3	16.60	0.00	0.51

† AICc = 66.49

Figures

Figure 1: Observed time-series of counts of hartebeest (Alcelaphus buselaphus) on Ol Pejeta Conservancy, Kenya (2009 - 2015). Error bars represent 95% confidence intervals (CI) based on standard errors calculated through variance estimators in Skalski et al. (2005).

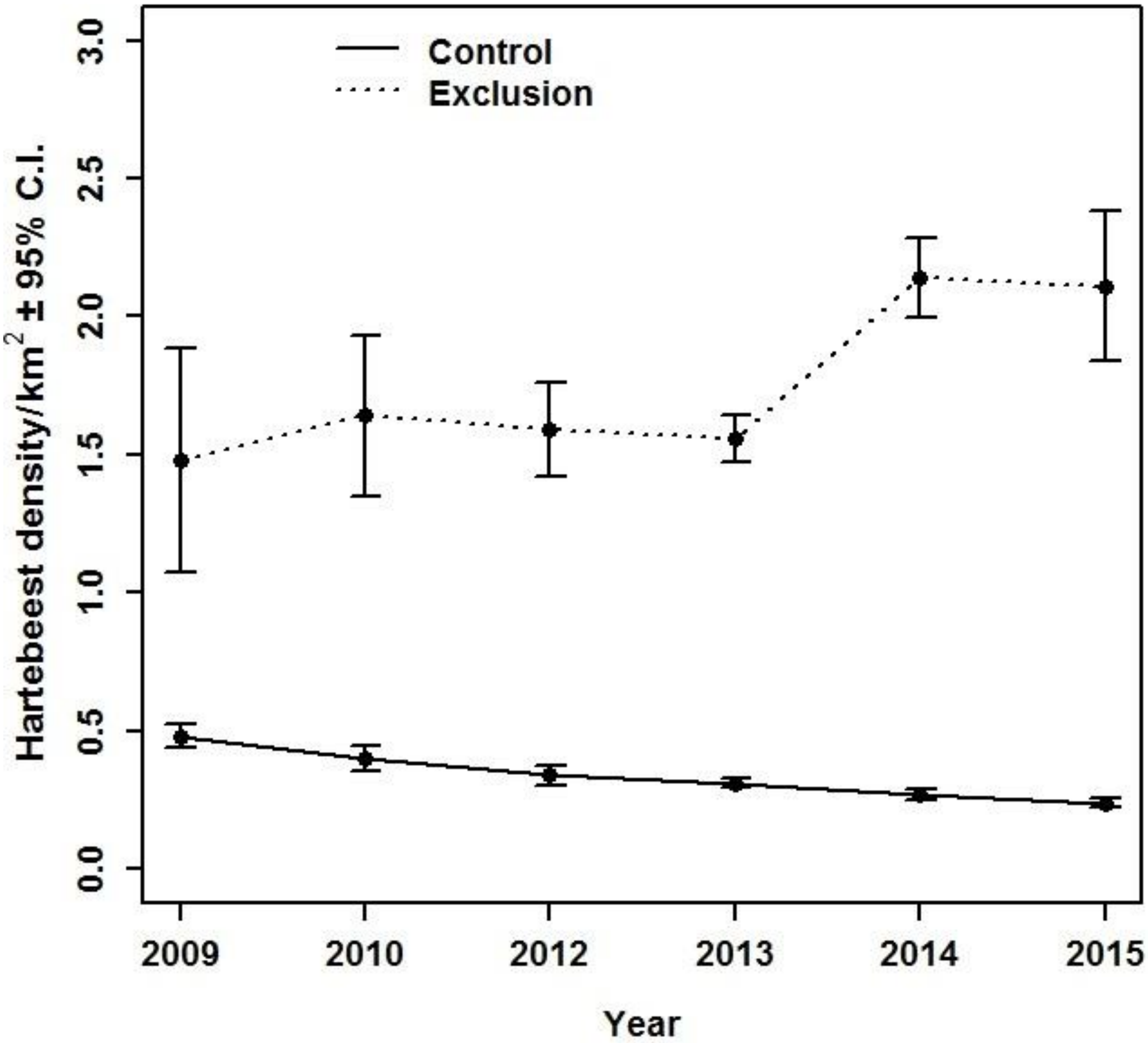


Figure 2: Survival rates (mean + S.E.) of 3 age classes of hartebeest (*Alcelaphus buselaphus*) within control and lion (Panthera leo) exclusion zones at Ol Pejeta Conservancy, Kenya (2009 - 2015).

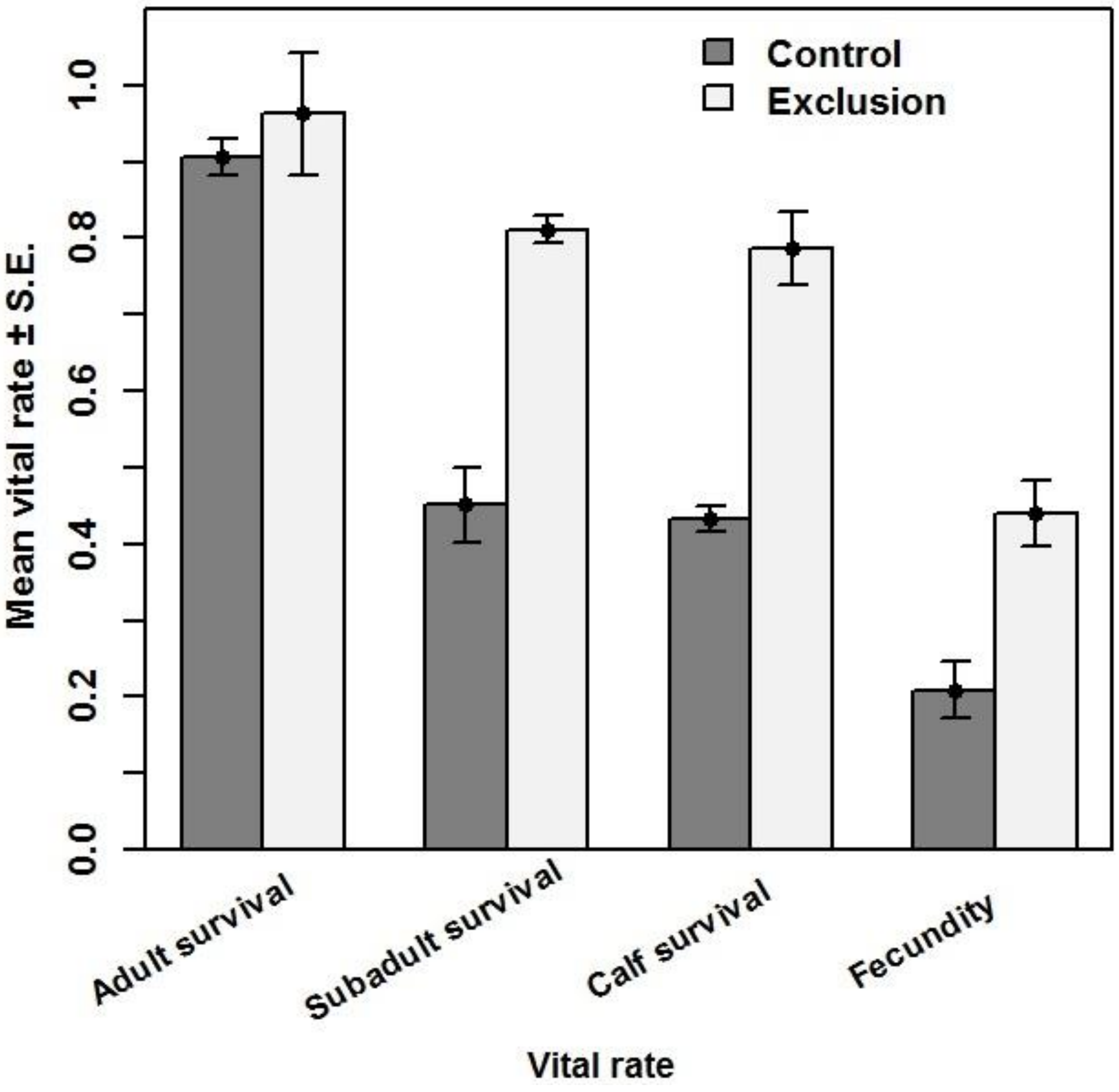


Figure 3: Life table response experiment (LTRE) showing demographic sensitivity and percentage contribution of vital rates (2012 – 2015) to change in population growth (λ) in hartebeest (*Alcephalus busephalus*) in paired exclusion versus control zones.

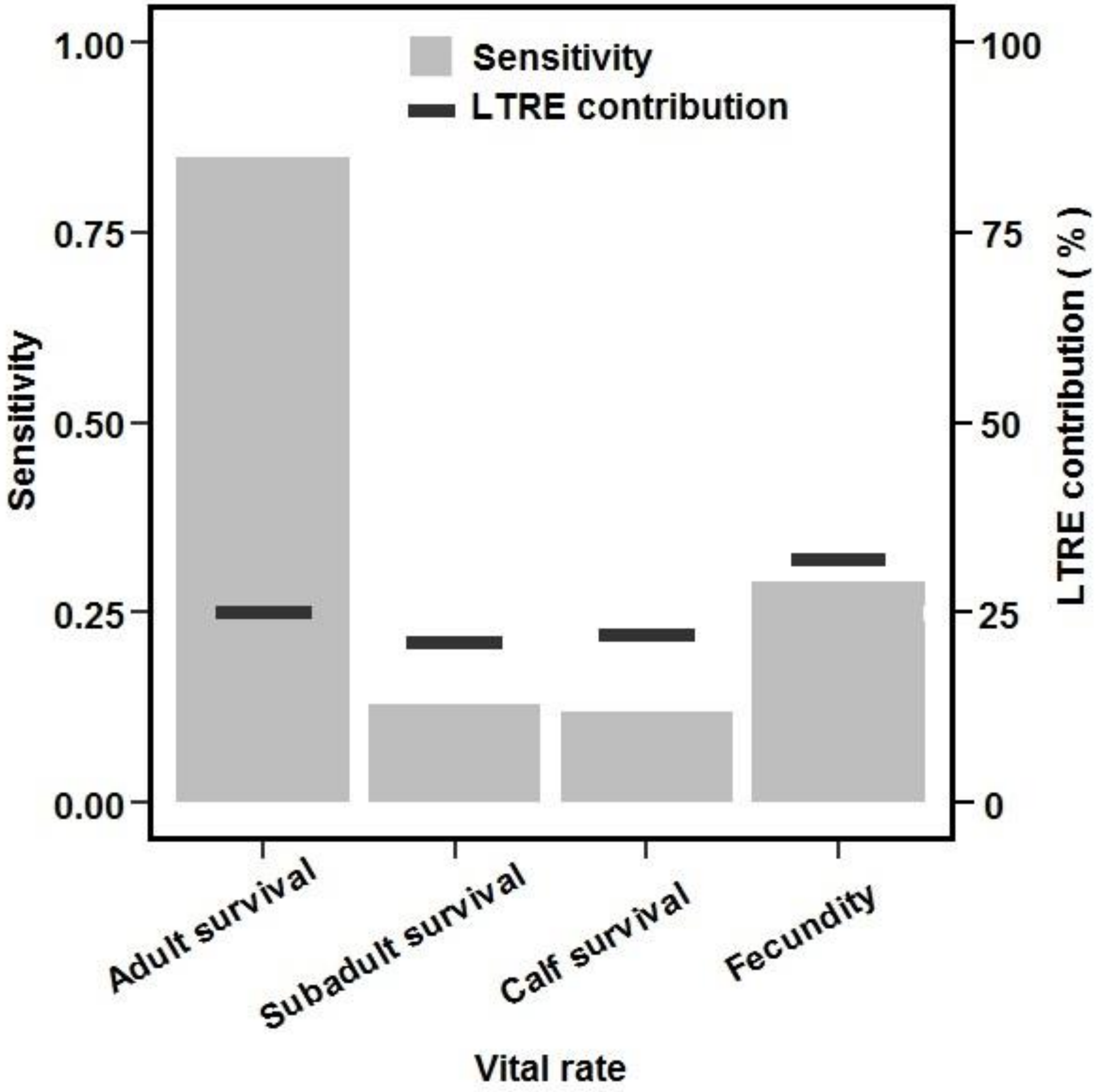
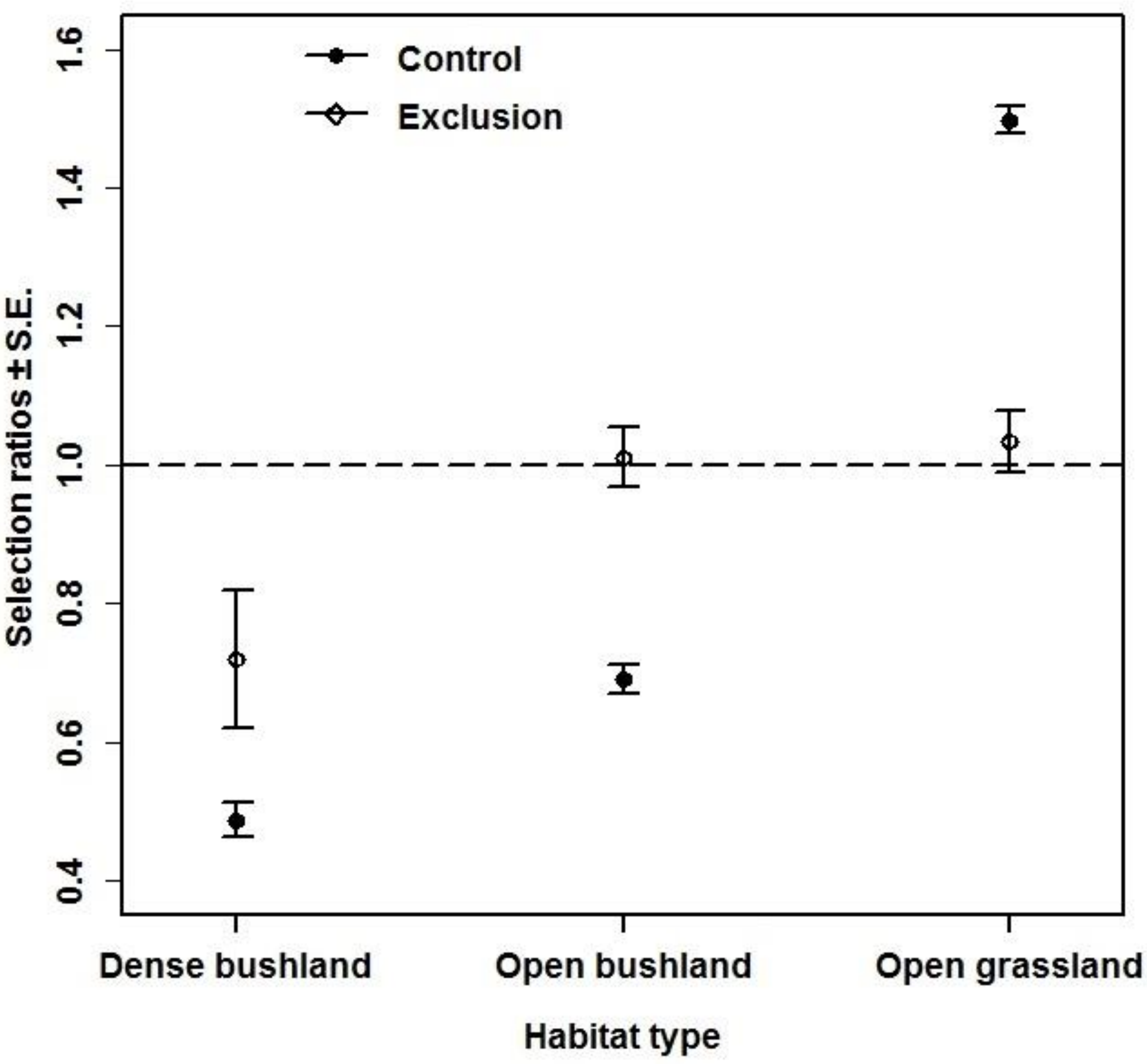


Figure 4: Selection ratios for hartebeest (*Alcephalus busephalus*) in 3 habitat types with standard error of the selection ratio. Selection is estimated from hartebeest locations at Ol Pejeta Conservancy, Kenya (2009 - 2015). Selection ratios > 1 indica preference, whereas < 1 indicate avoidance. Error bar indicate 95% confidence intervals



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Chapter 2

Prey neighborhoods and catchability shape risk of predation in a multi-prey savanna ecosystem

2.1 Introduction

Predation is one of nature's greatest biological forces, altering the abundance and behavior of prey, with cascading effects for community structure and ecosystem function (Paine 1966; Peckarsky *et al.* 2008; Hawlena & Schmitz 2010; Estes *et al*. 2011; Letnic *et al.* 2012; Breviglieri *et al.* 2017). Central to my understanding of predator-prey interactions is the heterogeneous distribution of prey, in which prey aggregations are assumed to confer net fitness benefits that exceed the costs of competition and advantages of a solitary lifestyle (Pulliam & Caraco 1984; Sridhar *et al.* 2009; Stensland *et al.* 2003). The benefits of prey aggregation include heightened vigilance and detection of predators (Lima 1995; Hunter & Skinner 1998; Brown 1999; Ward *et al.* 2011), predator confusion, (Olson *et al.* 2013), collective defense, (Bertram 1978; Krause & Ruxton 2002), and risk dilution (Hamilton 1971; Dehn 1990; Caro & Girling 2005; Schmitt *et al.* 2014). The costs of prey aggregation include greater potential for resource competition and disease transmission (Griffiths & Richardson 2006).

The costs and benefits of prey aggregations have largely been examined through the lens of single-species groups, which have examined optimal group sizes and shapes to provide safety, reduce vigilance, and maximize foraging rates (Hamilton 1971; Lehtonen & Jaatinen 2016). In addition to single-species groups, there is some research suggesting that multi-species aggregations also could change species-specific vulnerability of individuals to predation (Stensland *et al.* 2003; Goodale *et al*. 2017). For example, sticklebacks and minnows often occur together in streams and have a shared predator (i.e., yellow perch). Because sticklebacks reduce their risk of predation with bony, protective plates, minnows prefer to associate with conspecifics over sticklebacks, whereas sticklebacks preferentially associate with minnows when predation risk is high (Mathis & Chivers 2003). Similarly, Grant's gazelle manage risk of cheetah predation by associating with smaller and more vulnerable Thomson's gazelles (Fitzgibbon 1990), and predation risk to zebra is lower in association with wildebeest, the most common prey of lions (Sinclair 1985). Collectively, these studies suggest that benefits of aggregation may not be shared equally among individuals, if prey traits influence predator preferences.

In addition to any effects of aggregation, predation risk also should be an outcome of predator-prey encounter rates and the probability of death, given an encounter (hereafter "catchability"; Lima and Dill 1990; see also Creel *et al.* 2017; Moll *et al.* 2017). If predators concentrate their hunting activity in places and times where prey are abundant (Palomares et al. 2001; Balme et al. 2007; Valeix et al. 2009a), the density and composition of prey neighborhoods may interact with encounter rates and catchability such that both components work in opposition: prey aggregation could simultaneously increase encounter rates between predators and prey while decreasing catchability via some combination of enhanced detection of predators, more effective defense against predators, and risk dilution (Caro & Girling 2005). On the other hand, predators might forego high encounter rates to maximize catchability, if they choose to hunt in areas where prey are rendered more vulnerable (Hopcraft *et al*. 2005; Kauffman *et al*. 2007; Laundre 2010).

Over the past decade, several influential studies conducted in African savannas have attempted to distinguish the former scenario—in which predators attempt to maximize encounters by hunting where prey are most abundant—from the latter, in which predators attempt to maximize catchability (Hopcraft *et al*. 2005; Valeix, *et al*. 2009b; Thaker *et al*. 2011; Davies *et al*. 2016). Consequently, knowledge gaps exist with regard to how prey aggregations enhance or dampen risk of predation to individuals (see Hebblewhite *et al*. 2005; Atwood *et al*. 2009; and Gervasi *et al*. 2013 for examples from northern latitudes). This is especially true in the case of multi-species groups of ungulates, in which the species that comprise aggregations vary in baseline levels of vigilance, ability to detect predators, and other traits and behaviors that should affect their vulnerability (Creel *et al*. 2014; Schmitt *et al*. 2014). In particular, variation in body size within multi-species groups has the potential to shape outcomes of predator-prey interactions, because smaller species often are at greater risk of predation than larger species (Sinclair *et al*. 2003; Hopcraft *et al*. 2010).

I examined the effect of prey neighborhoods alongside the effects predator activity (a proxy for predator-prey encounter rates) and vegetation (which may conceal predators and increase catchability, given an encounter [Hopcraft *et al*. 2005]), on patterns of mortality from predation for a multi-prey system in a semiarid savanna. I tested three groups of hypotheses to explain the location and species identity of kills made by lions (1) the Prey Neighborhood Hypothesis; (2) the Prey Catchability Hypothesis; and (3) the Predator-Prey Encounter Hypothesis, in addition to interactions between #2 and #3.

I tested five possible pathways through which the Prey Neighborhood Hypothesis could operate:

> Hypothesis 1A. *Prey Neighborhood—Conspecific Density*. Risk of predation to a focal species is a function of conspecific density, such that per capita risk of predation (Ford *et al.* 2014; Ali *et al.* 2017) is diluted with increasing density of conspecific.
>
> Hypothesis 1B. *Prey Neighborhood—Total Prey Density*. Risk of predation to a focal species is a function of the total density of prey in the neighborhood, such that their combined density—but not their identity—influences risk of predation (Fortin *et al.* 2009).

Hypothesis 1C. *Prey Neighborhood—Body-Size-Mediated Risk Dilution*. Risk of predation to a focal species is diluted through association with smaller-bodied heterospecific, which may be more vulnerable to predation (Sinclair *et al.* 2003; Whelan 2003; Owen-Smith & Mills 2008; Hopcraft *et al.* 2010; Preisser & Orrock 2012; Owen-Smith 2015).

Hypothesis 1D. *Prey Neighborhood—Body-Size-Mediated Apparent Competition*. Risk of predation to a focal species is enhanced through association with larger-bodied heterospecific (i.e., short-term apparent competition; Holt & Kotler 1987), which may be less vulnerable to predation (Brown & Mitchell 1989; Sinclair *et al.* 2003; Owen-Smith & Mills 2008; Hopcraft *et al.* 2010; Preisser & Orrock 2012; Owen-Smith 2015).

Hypothesis 1E. *Prey Neighborhood—Zebra-Mediated Apparent Competition*. Risk of predation to a focal species is enhanced through association with plains zebra, the most abundant wild ungulate in my study system (Georgiadis *et al.* 2007), and the most common prey of lions (Frank 2008).

Additionally, I tested the following hypotheses:

Hypothesis 2. *Prey Catchability.* Risk of predation to a focal species increases in areas with high vegetative cover (Hopcraft *et al.* 2005; Thaker *et al.* 2011; Valeix *et al.* 2011; Loarie *et al.* 2013; Ford *et al.* 2014) regardless of conspecific or heterospecific density.

Hypothesis 3A. *Predator-Prey Encounters*. Risk of predation to a focal species is correlated positively with lion activity (Fischhoff *et al.* 2007; Thaker *et al.* 2010), regardless of conspecific or heterospecific density.

Hypothesis 3B. *Predator-Prey Encounters x Prey Catchability*. Risk of predation to a focal species arises from a combination of lion activity and high vegetative cover (Tambling *et al.* 2010; Loarie *et al.* 2013), regardless of conspecific or heterospecific density.

2.2 Materials and methods

2.2.1 Study area

I conducted my study at Ol Pejeta Conservancy, a 364 km^2 semiarid savanna (N0°.00' – S0°.02'; E36°.44' – 36°.59') in Laikipia County, Kenya. Mean annual rainfall across the property is 900 mm, with marked inter-annual variation (Birkett 2002; Wahungu *et al.* 2011). Ol Pejeta is characterized by a discontinuous overstory of *Acacia drepanolobium* and *Euclea divinorium*; the property is managed jointly for wildlife conservation and cattle (*Bos indicus*) production. Approximately 70 lions occur in five prides, and are responsible for a significant level of predation on the most common large (≥30 kg) ungulates, which account for 78% of the large ungulates on Ol Pejeta: buffalo (*Syncerus caffer*), hartebeest (*Alcephalus busephalus*), impala (*Aepyceros melampus)*, warthog (*Phacochoerus aethiopicus*), and plains zebra (*Equus quagga*, hereafter simply "zebra"; Fig. S1). Other large carnivores include African wild dogs (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), leopards (*Panthera pardus*), and spotted hyena (*Crocuta crocuta*). In addition to the aforementioned species, less-common ungulates at Ol Pejeta Conservancy include black (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*), eland (*Tragelaphus oryx*), elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Nanger granti*), Grevy's zebra (*Equus grevyi*), oryx (*Oryx beisa*), Thomson's gazelle (*Eudorcas thomsonii*), and waterbuck (*Kobus ellipsiprymnus*).

2.2.2 Data collection and analysis

2.2.2.1 Lion capture and kill site surveys

Between March and May 2014, and with the assistance of a Kenya Wildlife Service veterinary team, I captured and immobilized five female lions from different prides representing 55 individuals (see methods in Frank *et al.* 2003). Lions were darted using a CO_2 rifle (Dan-inject

RSA, Skukuza, South Africa) from a parked field vehicle at 10-30 m with a combination of ketamine (0.2 mg/kg) and medetomidine (0.03 mg/kg). Immobilized individuals were fitted with Global Positioning System (GPS) collars (Vectronic Aerospace GmbH, Berlin, Germany) before reversal with atipamezole (0.33 mg/kg). Following reversal, individuals were observed until they rejoined other pride members. Once per week between March 2014 and December 2015, I used hand-held telemetry receivers (R-1000, Communication Specialists, Orange, California) to download location data via UHF bi-directional radio link.

GPS collars were programmed to record locations every hour between 1800 and 0700 hours (when lions are most active) plus a fix at 1200 hours; thus, all collars made 15 daily fix attempts during the study period. Because lions live in stable social units (prides), collars permitted me both to locate kills made by prides and to quantify activity of prides, which I equated with the probability of encountering lions from the perspective of their ungulate prey (uncollared members of the pride were within 100 m of the collared individual for >95% of data downloads). Collectively, these five prides represented 79% of the lion population at Ol Pejeta Conservancy. I located lion kills by identifying GPS clusters using an algorithm adapted from Knopff *et al.* (2009). I defined a cluster as ≥2 successive GPS relocations occurring within 100 m of each other. From previous work on hunting behavior of lions (Tambling *et al.* 2010), I assumed that clusters were indicative either of ambush locations or kill sites (collectively, "potential kill sites"). I visited potential kill sites within 3-4 days of downloading location data, and searched for evidence of kills within a 50-m radius from the cluster centroid for a maximum of 30 min. Based on lion claw and bite marks on carcasses, and lion tracks, scat, and hair, I classified potential kill sites as kill sites (i.e., instances in which carcasses both were found and were verified to be kills by lions; n = 246), or non-kills (i.e. instances in which no carcasses were found [n = 99] at potential kill sites, or in which sign of other large carnivores occurred, such that I could not distinguish lion kills from scavenging by lions; n = 23).

To quantify predator-prey encounters, I used GPS tracking to estimate a lion's utilization distribution (UD's), which I equated with a pride's UD. I assumed that UD's represented the probability of an encounter between a lion and potential prey. I constructed 246 kill-site specific UD's, each a single month prior to the date at which a kill occurred, for the pride responsible for the kill. I then used kernel density estimation with least squares cross validation and a smoothing factor of 1000 using R package 'adehabitatHR' version 1.8.18 (Seaman & Powell 1996; Calenge 2006).

2.2.2.2 Densities, resource selection, and predation risk for lion prey

I estimated population density (individuals/km^2) for five species of ungulates killed frequently by lions (FIG. S1) and for which I detected $\geq$27 kill sites. Collectively, these five species (hereafter "lion prey") accounted for 94% of the lion kills that I detected from GPS clusters. To quantify prey neighborhoods, I conducted a series of quarterly, vehicle-based drive transects between August 2014 and December 2015 (n = 6 sampling periods). I systematically drove 12 (4-13 km) transects at 10-15 km/h, based on a predetermined, random starting point within the study area. The same 12 transects were driven each quarter; a total of 3 days were dedicated to each sampling period. All counts were conducted between 0700 and 1100 hours by three trained observers. One observer was responsible for driving and maintaining the route via GPS, while the other two observers recorded species, herd size, sighting distance, and bearing to all lion prey. I measured sighting distance using laser rangefinders and recorded bearings using a compass. I estimated densities and effective strip width (ESW) for detection functions for each species of lion prey in each survey using the R package 'distance' version 0.9.7. (Miller *et al.* 2017).

Using the following procedure, I generated spatially-explicit density surfaces for each of the five species of lion prey from each of the six surveys using resource selection functions (RSFs). First, I compared used points – where an animal was sighted – to 'available points' located near the transect. All available points were constrained to a buffer representing the prey species and survey-specific ESW. Second, I used generalized linear mixed-effect models to estimate species x survey-specific RSF coefficients. I tested for selection of three continuous variables known to influence the abundance and distribution of lion prey on the landscape: (1) NDVI (a metric associated with visibility, see below); (2) distance to glades (nutrient-rich grazing lawns derived from livestock corrals [Augustine *et al.* 2003; Porensky & Veblen 2015]); and (3) distance to water sources. Transect was included in models as a random effect. I used Akaike's Information Criterion corrected for small sample sizes (AICc) to evaluate support for competing models, then averaged parameter estimates for all models for a species with ΔAICc ≤ 2 (Burnham & Anderson 2002). I performed model selection and averaging using the R package 'MuMIn' version 1.15.6. (Barton 2016). Third, I projected the RSF in each 30×30 m grid cell across my study area. I selected this grid-cell size as in attempt to balance trade-offs between spatial autocorrelation in resource selection (and resultant density estimates), numbers of cells within a pride's home range, and spatial scale over which heterogeneity in ungulate density arose (Valeix *et al.* 2012; Everatt *et al.* 2015; Dröge *et al.* 2017). I rescaled each RSFs to create continuous surfaces ranging between 0 (strongest avoidance) and 1 (strongest selection), which I split into five bins of equal width following Morris *et al.* (2016). The first bin corresponded to the lowest probability of selection (0.00-0.20) and the fifth bin corresponded to the highest probability of selection (0.81-1.00). Finally, I combined species x survey-specific densities with species x survey-specific RSFs to create a spatially-explicit density surface for each species of lion prey at each survey. For similar approaches to estimating population densities from RSFs, see Boyce & McDonald (1999).

I validated the RSF-generated estimates of prey density using camera traps. For 21 days in July 2014 and 2015 and for 21 days in October 2014 and 2015, I overlaid camera traps (Reconyx Rapidfire RM45; Reconyx, Holmen, Wisconsin) on a 2×2 km grid within my study area. I deployed 72 camera traps (one at the center of each grid cell) for a total of 1512 camera-trap days. Cameras were mounted on trees or metal cages at 1 m above the ground. Only images showing clearly discernible individuals were analyzed. Images of the same species at the same site were deemed independent when >30 minutes elapsed between "captures"; I used the maximum number of individuals in an image within a 30 minute window as the number of "captures" (Rovero *et al.* 2005; Ohashi *et al.* 2013; Tambling *et al.* 2015). I then correlated the number of individuals "captured" from independent events in July and October 2014 and 2015 with population densities estimated at each 30×30 m cells associated with each camera trap, from species x survey-specific RSFs from August and November 2014 and 2015. The estimates of lion-prey density and number of individuals from camera traps were positively and significantly correlated across species (Pearson's $r = 0.92$, 0.96, 0.84, 0.69 and 0.95 for buffalo, hartebeest, impala, warthog, and zebra, respectively; $P < 0.01$ for all correlations).

2.2.2.3 Resource selection functions for kill sites

I measured visibility as a surrogate for prey catchability. Visibility is associated inversely with predation risk for lions elsewhere in sub-Saharan Africa (Hopcraft *et al.* 2005; Thaker *et al.* 2011; Valeix *et al.* 2011; see also Ford *et al.* 2014; Riginos 2015). To measure visibility, I used the normalized difference vegetation index (NDVI) from a Rapideye satellite image (5 m resolution, Digital Globe, Longmont, CO, USA) acquired in May 2013 (Pettorelli *et al.* 2005; Bro-Jørgensen *et al.* 2008). I validated the relationship between NDVI and visibility by groundtruthing with the following procedure. First, I created circular plots with radii of 50-m around each of the 246 kill sites. At the center of each circular plot, I used a laser rangefinder to measure distance to the nearest obstruction (branches, leaves, thick grass) at a height of 96 cm (average shoulder height for lions) at 72° intervals (Ford *et al.* 2014). For each kill site, I averaged the five visibility measurements, and correlated this value to the NDVI value at the center of each circular plot. Average visibility and NDVI were correlated negatively (Pearson's $r = -0.42$, $P < 0.01$), demonstrating that satellite-derived estimates of visibility are reflective of actual visibility. I constructed kill occurrence RSFs (*sensu* Ford *et al.* 2014; Ali *et al.* 2017) for each species of lion prey. Kill occurrence RSFs quantify the risk of mortality from lion predation as a function of eight predictor variables, framed as non-mutually exclusive hypotheses: conspecific density, total prey density, density of smaller-bodied heterospecifics, density of larger-bodied heterospecifics, zebra density, visibility, and lion activity (Table 1).

To create kill occurrence RSFs, I employed a use-availability design (Manly *et al.* 2002). First, I defined "use" as kill-site locations within pride home ranges (95% UD), and defined "availability" as random points within pride home ranges, subject to the constraint that random points could not fall within 500 m of used points (Gervasi *et al.* 2013; Thaker *et al.* 2010; Thaker *et al.* 2011). For each used location, I generated five available locations in ArcGIS. For kill sites that did not coincide with the timing of my drive transects (n = 235 out of 246 kill sites), I computed weighted averages for pairs of species x survey-specific density estimates associated with each kill (30×30-m cells). For each pair of drive transects associated with these 235 kill sites, I allocated proportionally more weight to the density estimates coinciding more closely with the date at which a kill occurred. I then extracted corresponding, weighted estimates of lion-prey density for each used or available location. Then, I developed generalized linear models to represent Hypotheses 1-3, calculated AICc values and AICc weights (W_i) using the R package 'MumIn' version 1.15.6 (Barton 2016), and used these as metrics for strength of evidence to compare the performance of competing models (Burnham and Anderson 2002). Finally, I averaged species-specific estimates of parameters in models with ΔAICc ≤ 2. All analyses were conducted in R version 3.4.0 (R Development Core Team, 2017).

2.3 Results

I recorded 17,788 GPS relocations from collared lionesses (average 4,447 locations ± 31 SEM per individual). Average home range size for prides per season; wet season averaged 79.3 Km^2 ± 18.3 SEM, while dry season averaged 69.4 Km^2 ± 20.1 SEM. From August 2014-December 2015, I located 246 kill sites of which 231 were the aforementioned five species of lion prey (Table S1).

Conspecific density did not predict kill occurrence for any prey species (Fig. 1). Density of heterospecifics predicted kill occurrence for buffalo, hartebeest, and warthogs. As zebra increased in abundance, buffalo were killed less frequently ($\beta = -1.33 \pm 1.23$, $P < 0.05$; Table 2, Figs. 1a and 1b). Conversely, hartebeest were killed more frequently as zebra abundance increased ($\beta = 2.86 \pm 1.67$, $P < 0.001$; Table 2; Figs. 1b and 2b). As total prey density increased, risk of predation to warthog decreased ($\beta = -0.78 \pm 1.14$, $P = 0.18$; Table 2; Figs. 1d and 2c).

Some combination of visibility, lion activity, and their interaction predicted kill occurrence for all five species of lion prey, although model fit was poor for impala (Table 1; Figs. 1 and 2). Areas characterized by low visibility exhibited relatively high occurrence of hartebeest kills ($\beta = -15.46 \pm 13.51$, $P < 0.05$; Figs. 1b and 2b). In contrast, warthog tended to be killed more frequently in open areas ($\beta = 4.19 \pm 4.50$, $P = 0.07$; Figs. 1c and 2c). Except in the case of warthog, lion activity was an important predictor for kill occurrence of all species of lion prey (Table 1; Figs. 1 and 2).

The interaction between visibility and lion activity approached statistical significance for hartebeest (β = -24.29 ± 24.30, $P = 0.08$; Fig. 1b). In areas of high lion activity, the occurrence of hartebeest kills increased with increasing visibility (Fig. 2b). The interaction between visibility and lion activity was statistically significant for zebra (β = -12.36 ± 11.35, $P < 0.05$; Fig. 1e), with risk of predation declining gradually in areas of high lion activity with increasing visibility (Fig. 2d). In areas of low lion activity (lion UD = 5%), kill occurrence for both hartebeest and zebra decreased steeply with increasing visibility (Figs. 2b and 2d).

2.4 Discussion

For each ungulate in this multi-prey system, I found support for a combination of prey neighborhoods, prey catchability, and predator-prey encounters in driving landscape-level patterns of predation risk. Prey neighborhoods altered risk of predation for individuals of three of the five focal species of lion prey (buffalo, hartebeest, and warthog), via diverse pathways. Buffalo reduced predation risk by associating with zebra, and warthog reduced predation risk by associating with all other lion prey, supporting the hypothesis that mixed-species aggregations dilute risk for some species (Sinclair 1985; Fitzgibbon 1990; Stensland *et al.* 2003; Mathis & Chivers 2003; Schmitt *et al*. 2014; Sutton *et al.* 2015). On the other hand, predation risk for hartebeest was elevated in association with zebra, implying that apparent competition with zebra may negatively impact hartebeest (DeCesare *et al.* 2010; Ng'weno *et al.* 2017). My work provides a complementary approach to a series of studies (Kauffman *et al*. 2007; Valeix *et al.* 2009b; Anderson *et al.* 2010; Thaker *et al*. 2011; Creel *et al.* 2014; Ford *et al*. 2014; Anderson *et al.* 2016; Gallagher *et al*. 2017) in which one or more species of ungulates adjust their behavior in response to perceived risk of predation, often quantified as a function of habitat or landscape features. While prey aggregations sometimes are envisaged as a response to perceived risk (e.g., Creel et al. 2014, Moll et al. 2016), they themselves may amplify or dilute the risk of predation experienced by individuals. In sum, the costs or benefits of multi-species aggregations hinge on the composition of prey neighborhoods within which individuals are embedded.

In addition to that of prey neighborhoods, my work supports the influence of prey catchability and predator-prey encounters in driving landscape-level patterns of predation (see also Hopcraft *et al.* 2005; Thaker *et al.* 2011; Valeix *et al.* 2011; Loarie *et al.* 2013; Ford *et al.* 2014). The majority of species of lion prey incurred more mortality in areas where lion activity was high (although this relationship was weak for impala, likely because most impala are killed by predators other than lions [Fig. S1]). Where lions were less active, kills of hartebeest and zebra were unlikely in all but the most densely-vegetated areas characterized by low visibility. Where lion activity was high, risk of predation to zebra declined steadily with increasing visibility, whereas risk of predation to hartebeest increased with increasing visibility. Despite supporting a growing population of lions in Laikipia (Georgiadis et al. 2007), this result implies that zebra are less catchable by lions, less preferred by lions, or both relative to hartebeest, thereby creating a situation in which apparent competition may arise between a numerically-dominant ungulate (zebra) and a rarer, more vulnerable one (hartebeest).

Neighborhood effects should be widespread in multi-prey systems where species differ in their vulnerability to predation, and are expected to occur through at least two pathways. First, neighborhood effects may emerge when predators concentrate hunting in areas of high abundances of their primary prey, and consume other (secondary) prey by virtue of their proximity to primary prey. Such short-term apparent competition (i.e., “associational susceptibility” [White and

Whitham 2000] or “shared doom” [Wahl and Hay 1995]) characterized prey neighborhoods of hartebeest, which incurred higher risk of predation in association with zebra. Second, and conversely, association with a diversity of prey may distract predators from consuming particular species, thereby reducing predation on that species (Whelan *et al.* 2003; Hughes 2012). Such an associational refuge conferred safety to buffalo in association with zebra, and warthogs in association with all other lion prey.

A major challenge for future study is to understand the scale-dependence over which prey neighborhoods are perceived by lions, as scale-dependent neighborhood effects have been noted elsewhere (e.g., Emerson *et al.* 2012; Champagne *et al.* 2016). I estimated but did not directly assess the distribution of lion prey across a 364 km^2 savanna ecosystem, based on resource selection functions for each species of lion prey. I restricted prey neighborhoods to 900 m^2 grid cells, which I selected as a compromise between the size of pride home ranges, the number of cells in which kill sites occurred, and the area over which prey aggregations arose. This spatial scale was sufficiently resolute to detect neighborhood effects in 3 of the 5 species of lion prey in my system. In a recent meta-analysis of plant-herbivore interactions, decreasing spatial scale (plot size) has increased the strength of neighborhood effects, regardless of the direction of the effect (Champagne *et al.* 2016). I cannot rule out the possibility that, had I attempted to quantify prey neighborhoods at spatial scales finer than 900 m^2, I would have detected neighborhood effects in risk of mortality for impala and zebra. At least with respect to predation by lions *per se*, I believe this scenario to be unlikely for two reasons. First, predation on impala is distributed relatively evenly among lions, leopards, and cheetahs (Fig. S1), and impala are rarely targeted by lions elsewhere (Ford *et al.* 2014; Davies *et al*. 2016). Therefore, while impala may confer increased vigilance and early detection in mixed-species aggregations, their own mortality likely is less sensitive to predation by lions than more commonly consumed ungulates. Second, zebra are more than twice as abundant as buffalo and warthog, and are an order of magnitude more abundant than hartebeest at Ol Pejeta (Table S1). Prey neighborhoods should more strongly influence the consumption of rarer (secondary) prey in association with more common species of prey, rather than the other way around (see also Root 1973).

Although they exhibit a rich intellectual history in the study of plant-herbivore interactions (e.g., Root 1973; Callaway 1995; Brooker *et al.* 2008; Barbosa *et al.* 2009) and pest control (e.g., Root and Karieva 1984; Kromp 1999; Landis *et al.* 2000; Zehnder *et al*. 2007), neighborhood effects are less widely appreciated in predator-prey systems, particularly those dominated by large mammals. In conjunction with classic components of predation (predator-prey encounter rates and catchability), I have demonstrated the importance of prey neighborhoods in influencing risk of predation in a multi-prey, single predator savanna ecosystem. I encourage ecologists working on predator-prey interactions in multi-prey systems to consider the potential for prey neighborhoods to shape risk of predation across expansive landscapes.

2.6 References

Anderson, T.M., Hopcraft, J.G.C., Eby, S., Ritchie, M., Grace, J. B., & Olff, H. (2010). Landscape-scale analyses suggest both nutrient and antipredator advantages to serengeti herbivore hotspots. *Ecology,* 91, 1519–1529.

Anderson, T.M., White, S., Davis, B., Erhardt, R., Palmer, M., Swanson, A., Kosmala, M. & Packer, C. (2016). The spatial distribution of African savannah herbivores: Species associations and habitat occupancy in a landscape context. *Philos. Trans. R. Soc. Lond. Biol. Sci.*, 371, 20150314.

Ali, A.T., Ford, A., Evans, J., Mallon, D., Hayes, M., King, J., Amin, R. & Goheen, J.R. (2017). Resource selection and landscape change reveal mechanisms suppressing population recovery for the world's most endangered antelope. *J. Appl. Ecol.*, URL http://dx.doi.org/10.1111/1365-2664.12856.

Atwood, T.C., Gese, E.M. & Kunkel, K. (2009). Spatial Partitioning of Predation Risk in a Multiple Predator–Multiple Prey System. *J. Wildl. Manage*., 73, 876–884.

Augustine, D.J., McNaughton, S.J. & Frank, D.A. (2003). Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecol. Appl.*, 13, 1325–1337.

Balme, G., Hunter, L. & Slotow, R. (2007). Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Anim. Behav.,* 74, 589–598.

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A. & Szendrei, Z. (2009). Associational resistance and associational susceptibility: Having right or wrong neighbors. *Annu. Rev. Ecol. Evol. Syst.,* 40, 1–20.

Barton, K. (2016). MuMIn: Multi-Model Inference. R package version 1.15.6. URL: https://CRAN.R-project.org/package=MuMIn.

Bertram, B.C.R. (1978). Living in groups: predators and prey. In *Behavioural Ecology*. (eds Krebs, J.R. & Davies, N.B.). Blackwell Scientific Press, Oxford, pp. 64–96.

Birkett, A. (2002). The impact of giraffe, rhino & elephant on the habitat of a black rhino sanctuary in Kenya. *Afr. J. Ecol.*, 40, 276–282.

Boyce, M.S. & McDonald, L.L. (1999). Relating populations to habitats using resource selection functions. *Trends Ecol. Evol.*, 14, 268–272.

Breviglieri, C.P.B, Oliveira, P.S. & Romero, G.Q. (2017). Fear mediates trophic cascades: non-consumptive effects of predators drive aquatic ecosystem function. *Am. Nat.*, 189, 490–500.

Bro-Jørgensen, J., Brown, M.E. & Pettorelli, N. (2008). Using the satellite-derived normalized difference vegetation index (NDVI) to explain ranging patterns in a lek-breeding antelope: The importance of scale. *Oecologia*, 158, 177–182.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G. et al., (2008). Facilitation in plant communities: The past, the present, and the future. *J. Ecol.,* 96, 18–34.

Brown, J.S. (1999). Vigilance, patch use and habitat selection: foraging under predation risk. *Evol. Ecol. Res.*, 1, 49–71.

Brown, J. S. & Mitchell, W. A. (1989). Diet selection on depletable resources. Oikos, 54, 33–43.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York.

Calenge, C. (2006). The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model*., 197, 516–519.

Callaway, R.M. (1995). Positive interactions among plants. *Bot. Rev*., 61–306-349.

Caro, T. & Girling, S. (2005). *Antipredator defenses in birds and mammals*. University of Chicago Press, Chicago.

Champagne, E., Tremblay, J. & Côté, S. D. (2016). Spatial extent of neighboring plants influences the strength of associational effects on mammal herbivory. *Ecosphere*, 7, e01371-n/a.

Creel, S., Droge, E., M'soka, J., Smit, D., Becker, M., Christianson, D. & Schuette, P. (2017). The relationship between direct predation and antipredator responses: a test with multiple predators and multiple prey. *Ecology*, 98, 2081–2092.

Creel, S., Schuette, P. & Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behav. Ecol.*, 25, 773–784.

Davies, A., Tambling, C.J., Kerley, G. & Asner, G. (2016). Limited spatial response to direct predation risk by African herbivores following predator reintroduction. *Ecol. Evol*, 6, 5728–5748.

DeCesare, N.J., Hebblewhite, M., Robinson, H.S. & Musiani, M. (2010). Endangered, apparently: the role of apparent competition in endangered species conservation. *Anim. Conserv.*, 13, 353–362.

Dehn, M.M. (1990). Vigilance for predators: detection and dilution effects. *Behav. Ecol. Sociobiol.*, 26, 337–342.

Dröge, E., Creel, S., Becker, M. & M'soka, J. (2017). Spatial and temporal avoidance of risk within a large carnivore guild. *Ecol. Evol*, 7, 189–199.

Emerson, S.E., Brown, J.S., Whelan, C.J. & Schmidt, K. A. (2012). Scale-dependent neighborhood effects: Shared doom and associational refuge. *Oecologia*, 168, 659–670.

ESRI. (2011). ArcGIS desktop: release 10. Environmental systems research institute, Redlands, California.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. *et al.* (2011). Trophic downgrading of planet earth. *Science*, 333, 301–306.

Fischhoff, I.R., Sundaresan, S.R., Cordingley, J., & Rubenstein, D.I. (2007). Habitat use and movements of plains zebra in response to predation danger from lions. *Behav Ecol.*, 18, 726–729.

Fitzgibbon, C. (1990). Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. *Anim. Behav.*, 39, 1116–1126.

Ford, A.T., Goheen, J.R., Otieno, T.O., Bidner, L., Isbell, L.A., Palmer, T.M. *et al.* (2014). Large carnivores make savanna tree communities less thorny. *Science*, 346, 346–349.

Fortin, D. & Fortin, M.E. (2009). Group-size-dependent association between food profitability, predation risk and distribution of free-ranging bison. *Anim. Behav.*, 78, 887–892.

Frank, D.A. (2008). Evidence for top predator control of a grazing ecosystem. *Oikos*, 117, 1718–1724.

Frank, L.G., Simpson, D. & Woodroffe, R. (2003). Foot snares: an effective method for capturing African lions. *Wildl. Soc. Bull.*, 31, 309–314.

Gallagher, A., Creel, S., Wilson, R.P. & Cooke, S.J. (2017). Energy landscapes and the landscape of fear. *Trends Ecol. Evol.*, 32, 88–96.

Georgiadis, N.J., Olwero, J.G.N., Ojwang', G. & Romañach, S.S. (2007). Savanna herbivore dynamics in a livestock-dominated landscape: I. dependence on land use, rainfall, density, and time. *Biol. Conserv.*, 137, 461–472.

Gervasi, V., Sand, H., Zimmermann, B., Mattisson, J., Wabakken, P. & Linnell, J. (2013). Decomposing risk: Landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. *Ecol. Appl.*, 23, 1722–1734.

Goodale, E., Beauchamp, G. & Ruxton, G.D. (2017). *Mixed-Species Groups of Animals: Behavior, Community Structure, and Conservation*. Academic Press, US.

Goodale, E., Beauchamp, G., Magrath, R.D., Nieh, J.C. & Ruxton, G.D. (2010). Interspecific information transfer influences animal community structure. *Trends Ecol. Evol.*, 25, 354–361.

Gregory, S.D., & Courchamp, F. (2010). Safety in numbers: extinction arising from predator-driven Allee effects. *J. Anim. Ecol.*, 79, 511–514.

Griffiths, C. & Richardson, C. (2006). Chemically induced predator avoidance behaviour in the burrowing bivalve *Macoma balthica*. *Exper. Marine. Bio. Ecol.*, 331, 91–98.

Hamilton, W.D. (1971). Geometry for the selfish herd. *J. Theor. Biol.*, 31, 295–311.

Hawlena, D. & Schmitz, O.J. (2010). Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *Proc. Natl. Acad. Sci. USA.*, 107, 15503– 15507.

Hebblewhite, M., Merrill, E.H. & McDonald, T.L. (2005). Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. *Oikos*, 111, 101–111.

Holt, R.D. (1977). Predation, apparent competition, and the structure of prey communities. *Theor. Popul. Biol.*, 12, 197–229.

Holt, R.D. & Kotler, B.P. (1987). Short-term apparent competition. *Am. Nat., 130*, 412–430.

Hopcraft, J.G., Olff, H. & Sinclair, A.R.E. (2010). Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends Ecol. Evol.*, 25, 119–128.

Hopcraft, J.G., Sinclair, A.R.E. & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *J. Anim. Ecol.*, 74, 559–566.

Hughes, N.K., Kelley, J.L., Banks, P.B. & Grether, G. (2012). Dangerous liaisons: The predation risks of receiving social signals. *Ecol. Lett.*, 15, 1326–1339.

Hunter, L. & Skinner, J.D. (1998). Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour,* 135, 195–211.

Johnson, C.J., Parker, K.L., Heard, D.C. & Gillingham, M.P. (2002). Movement parameters of ungulates and scale-specific responses to the environment. *J. Anim. Ecol*., 71, 225–235.

Kauffman, M.J., Varley, N., Smith, D.W., Stahler, D.R., MacNulty, D.R. & Boyce, M.S. (2007). Landscape heterogeneity shapes predation in a newly restored predator prey system. *Ecol. Lett.*, 10, 690–700.

Knopff, K.H., Knopff, A.A., Warren, M.B. & Boyce, M.S. (2009). Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. *J. Wildl. Manage.*, 73, 586–597.

Krause, J. & Ruxton, G.D. (2002). *Living in groups*. Oxford University Press, New York.

Kromp, B. (1999). Carabid beetles in sustainable agriculture: A review on pest control efficacy, cultivation impacts and enhancement. *Agric. Ecosyst. Environ.*, 74, 187–228.

Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.*, 45, 175–201.

Laundre, J.W. (2010). Behavioral response races, predator-prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. *Ecology*, 91, 2995–3007.

Lehtonen, J. & Jaatinen, K. (2016). Safety in numbers: the dilution effect and other drivers of group life in the face of danger. *Behav. Ecol. Sociobiol*., 70, 449–458.

Letnic, M., Ritchie, E.G. & Dickman, C.R. (2012). Top predators as biodiversity regulators: the dingo *Canis lupus din*go as a case study. *Biol. Rev.*, 87, 390–413.

Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, 68, 619–640.

Lima, S.L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Anim. Behav.*, 49, 11–20.

Loarie, S., Tambling, C.J. & Asner, G. (2013). Lion hunting behaviour and vegetation structure in an African savanna. *Anim. Behav.*, 85, 899–906.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Wallace, W.P. (2002). *Resource selection by animals: statistical design and analysis for field studies*, 2nd edn. Kluwer Academic Publishers, Dordrecht, Netherlands.

Mathis, A. & Chivers, P. (2003). Overriding the oddity effect in mixed-species aggregations: group choice by armored and nonarmored prey. *Behav. Ecol.*, 14, 334–339.

Miller, D.L. (2017). Distance Sampling Detection Function and Abundance Estimation. R package version 0.9.7. URL: https://CRAN.R-project.org/package=Distance.

Moll, R.J, Killion, A., Montgomery, R., Tambling, C.J. & Hayward, M.W. (2016). Spatial patterns of African ungulate aggregation reveal complex but limited risk effects from reintroduced carnivores. *Ecology*, 97, 1123–1134.

Moll, R.J., Redilla, K.M., Mudumba, T., Muneza, A.B., Gray, S.M., Abade, L. *et al*. (2017). The many faces of fear: A synthesis of the methodological variation in characterizing predation risk. *J. Anim. Ecol.*, 86, 749–765.

Morris, L.M., Proffitt, K.M. & Blackburn, J.K. (2016). Mapping resource selection functions in wildlife studies: Concerns and recommendations. *Appl. Geogr.*, 76, 173–183.

Ng'weno, C.C., Maiyo, N.J., Ali, A.H., Kibungei, A.K. & Goheen, J.R. (2017). Lions influence the decline and habitat shift of hartebeest in a semiarid savanna. *J. Mammal.*, 98, 1078–1087.

Ohashi, H., Saito, M., Horie, R., Tsunoda, H., Noba, H., Ishii, H. *et al.* (2013). Differences in the activity pattern of the wild boar *Sus scrofa* related to human disturbance. *Eur. J. Wildl. Res.*, 59, 167–177.

Olson, R.S., Hintze, A., Dyer, F.C., Knoester, D.B. & Adami, C. (2013). Predator confusion is sufficient to evolve swarming behaviour. *J. R. Soc. Interface.*, 10, 20130305–20130305.

Owen-Smith, N. & Mills, M. (2008). Predator-prey size relationships in an African large-mammal food web. *J Anim. Ecol.*, 77, 173–183.

Paine, R. (1966). Food Web Complexity and Species Diversity. *Am. Nat.*, 100, 65–75.

Palomares, F., Delibes, E., Revilla, J., Calzada, J. & Fedriani, M. (2001). Spatial ecology of Iberian lynx and abundance of European rabbits in southwestern Spain. *Wildlife Monogr.*, 148, 1–36.

Peckarsky, B.L., Abrams, P.A., Bolnick, D.I., Dill, L.M., Grabowski, J.H., Luttbeg, B. *et al.* (2008). Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology*, 89, 2416–2425.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J., Tucker, C.J. & Stenseth, N.C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. & Evol.*, 20, 503–510.

Porensky, L.M. & Veblen, K.E. (2015). Generation of ecosystem hotspots using short-term cattle corrals in an African savanna. *Rangeland Ecol. Manage.*, 68, 131–141.

Preisser, E.L. & Orrock, J.L. (2012). The allometry of fear: interspecific relationships between body size and response to predation risk. *Ecosphere*, 3, 77.

Pulliam, R.H. & Caraco, T. (1984). Living in groups: is there an optimal group size? In *Behavioral ecology: an evolutionary approach*, 2nd edn. (eds Krebs, J.R. & Davies, N.B.). Sinauer, Sunderland, Mass, pp. 122–147.

R Development Core Team. (2017). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.r-project.org/.

Riginos, C. (2015). Climate and the landscape of fear in an African savanna. *J. Anim. Ecol.*, 84, 124–133.

Root, R.B. (1973). Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards, *Brassica oleracea*. *Ecol. Monogr.*, 43, 95–124.

Root, R.B. & Kareiva, P. M. (1984). The search for resources by cabbage butterflies (*Pieris rapae*): Ecological consequences and adaptive significance of markovian movements in a patchy environment. *Ecology,* 65, 147–165.

Rostro-García, S., Kamler, J. & Hunter, L. (2015). To Kill, Stay or Flee: The Effects of Lions and Landscape Factors on Habitat and Kill Site Selection of Cheetahs in South Africa. *PLoS ONE*, 10 (2), e0117743.

Rovero, F., Jones, T. & Sanderson, J. (2005). Notes on Abbott's duiker (*Cephalophus spadix True* 1890) and other forest antelope of Mwanihana Forest, Udzungwa Mountains, Tanzania, as revealed by camera trapping and direct observations. *Trop. Zoo.*, 18, 13–23.

Schmitt, M.H., Stears, K. & Shrader, A.M. (2016). Zebra reduce predation risk in mixed-species herds by eavesdropping on cues from giraffe. *Behav. Ecol.*, 27, 1073–1077.

Schmitt, M.H., Stears, K., Wilmers, C. & Shrader, A.M. (2014). Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds. *Anim. Behav.*, 96, 151–158.

Schmitz, O.J. (2010). *Resolving Ecosystem Complexity*. Princeton University Press, Princeton, N.J.

Seaman, D.E. & Powell, R.A. (1996). Accuracy of kernel estimators for animal home range analysis. *Ecology*, 77, 2075–2085.

Sinclair, A.R.E. (1985). Does interspecific competition or predation shape the African ungulate community? *J. Anim. Ecol.*, 54, 899–918.

Sinclair, A.R.E., Mduma, S. & Brashares, J.S. (2003). Patterns of predation in a diverse predator-prey system. *Nature*, 425, 288–290.

Sridhar, H., Beauchamp, G. & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? a large-scale synthesis. *Anim. Behav.*, 78, 337–347.

Stensland, E., Angerbjorn, A. & Berggren, P. (2003). Mixed species groups in mammals. *Mamm. Rev.*, 33, 205–223.

Sutton, G., Hoskins, A. & Arnould, J. (2015). Benefits of Group Foraging Depend on Prey Type in a Small Marine Predator, the Little Penguin. *PLoS ONE*, 10, e0144297.

Tambling, C.J., Cameron, E.Z., Du Toit, J.T. & Getz, W.M. (2010). Methods for locating African lion kills using global positioning system movement data. *J. Wildl. Manage.*, 74, 549–556.

Tambling, C.J., Druce, D.J., Hayward, M.W., Castley, J.G., Adendorff J. & Kerley, G.I.H. (2012). Spatial and temporal changes in group dynamics and range use enable antipredator responses in African buffalo. *Ecol.*, 93, 1297–1304.

Tambling, C.J., Minnie, L., Meyer, J., Freeman, E.W., Santymire, R.M., Adendorff, J. *et al.* (2015). Temporal shifts in activity of prey following large predator reintroductions. *Behav. Ecol. Sociobiol.*, 69, 1153–1161.

Thaker, M., Vanak, A., Owen, C., Ogden, M. & Slotow, R. (2010). Group Dynamics of Zebra and Wildebeest in a Woodland Savanna: Effects of Predation Risk and Habitat Density. *PLoS ONE*, 5, e12758.

Thaker, M., Vanak, A., Owen, C., Ogden, M., Niemann, S. & Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, 92, 398–407.

Valeix, M., Chamaillé-Jammes, S., Loveridge, A.J., Davidson, Z., Hunt, J.E., Madzikanda, H. *et al.* (2011). Understanding patch departure rules for large carnivores: lion movements support a patch-disturbance hypothesis. *Am. Nat.*, 178, 269–275.

Valeix, M., Fritz, H., Loveridge, A.J., Davidson, Z., Hunt, J.E., Murindagomo, F. *et al.* (2009a). Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behav. Ecol. Sociobiol.*, 63(10), 1483–1494.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. *et al.* (2009b). Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology*, 90, 23–30.

Valeix, M., Hemson, G., Loveridge, A. J., Mills, G. & Macdonald, D. W. (2012). Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *J. Appl. Ecol.,* 49, 73–81.

Wahl, M. & Hay, M. E. (1995). Associational resistance and shared doom: Effects of epibiosis on herbivory. *Oecologia,* 102, 329–340.

Wahungu, G.M., Mureu, L.K., Kimuyu, D.M., Birkett, A., Macharia, P.G. & Burton, J. (2011). Survival, recruitment and dynamics of *Acacia drepanolobium Sjostedt* seedlings at Ol Pejeta Conservancy, Kenya, between 1999 and 2009. *Afr. J. Ecol.*, 49, 227–233.

Ward, A.J.W., Herbert-Read, J.E., Sumpter, D.J.T. & Krause, J. (2011). Fast and accurate decisions through collective vigilance in fish shoals. *Proc. Natl. Acad. Sci. USA.*, 108, 2312–2315.

Whelan, C.J., Brown, J.S., & Maina, G. (2003). Search biases, frequency-dependent predation. *Evol. Ecol. Res*., *5*, 329–343.

White, J.A. & Whitham, T. G. (2000). Associational susceptibility of cottonwood to a box elder herbivore. *Ecology,* 81, 1795–1803.

Zehnder, G., Gurr, G. M., Kühne, S., Wade, M. R., Wratten, S. D. & Wyss, E. (2007). *Arthropod pest management in organic crops*. United States: Palo Alto, United States of America: Annual Reviews.

Tables

Table 1: Summary of hypotheses and predictors used to evaluate drivers of predation risk at Ol Pejeta Conservancy, in Laikipia County, Kenya.

Hypothesis	Predictor variable
H1A Conspecific Density	Conspecific density [individuals/km^2] (i.e., estimated density of a focal species of lion prey).
H1B Total Prey Density	Total density of prey in the neighborhood [individuals/km^2] (i.e., the summed estimated densities of all five species of lion prey).
H1C Body-size-Mediated Risk Dilution	Smaller-bodied heterospecific density [individuals/km^2], (i.e., lion prey smaller than the focal species), aggregated into a single predictor. Because they are the largest species of lion prey, this hypothesis is redundant with 1B for buffalo.
HID Body-size-Mediated Apparent Competition	Larger-bodied heterospecific density [individuals/km^2], (i.e., lion prey larger than the focal species), aggregated into a single predictor. Because they are the smallest species of lion prey, this hypothesis is redundant with 1B for impala.
H1E Zebra-Mediated Apparent Competition or Risk Dilution	Zebra density [individuals/km^2], (i.e., the primary prey for lions within the study area).
2 Prey Catchability	Habitat structure consisting of visibility term (1- NDVI).
3A Predator-Prey Encounters	Lion activity (95% utilization distribution).
3B Prey Catchability x Predator-Prey Encounters	Interaction between visibility and lion activity.

Table 2: Results of model selection for hypotheses on species-specific resource selection functions for kill occurrence at Ol Pejeta Conservancy. Shaded cells indicate models within 2 AIC units.

Hypothesis	buffalo	hartebeest	impala	warthog	zebra
H1A Conspecific Density	3.96	9.90	6.22	3.27	47.34
H1B Total Prey Density	3.96	11.76	5.42	1.74	47.32
H1C Body-size-Mediated Risk Dilution	2.62	7.10	-	3.11	47.02
HID Body-size-Mediated Apparent Competition	-	13.89	5.40	3.36	47.08
H1E Zebra-Mediated Apparent Competition or Risk Dilution	0.00	1.32	6.20	3.26	-
H2 Prey Catchability	4.74	0.00	4.55	0.00	32.92
H3A Predator-Prey Encounters	0.92	13.19	0.00	3.55	20.92
H3B Prey Catchability * Predator-Prey Encounters	4.70	0.60	1.54	3.66	0.00

Note: ("-") means not included in the model, i.e. terms identical to hypothesis being tested; (*) means interaction, i.e. 2 terms; "smaller" and "larger" means all species smaller or larger than the focal species respectively.

Figures

Figure 1: Standardized coefficients (β ± SEM) from kill-site resource selection functions with the strongest support for (a) buffalo; (b) hartebeest; (c) impala; (d) warthog; and (e) zebra. Error bars represent standard errors. A positive coefficient for lion utilization indicates higher risk of predation when and where lion utilization is high. A positive coefficient for visibility indicates higher risk of predation in the open (i.e., where NDVI is low) and vice versa.

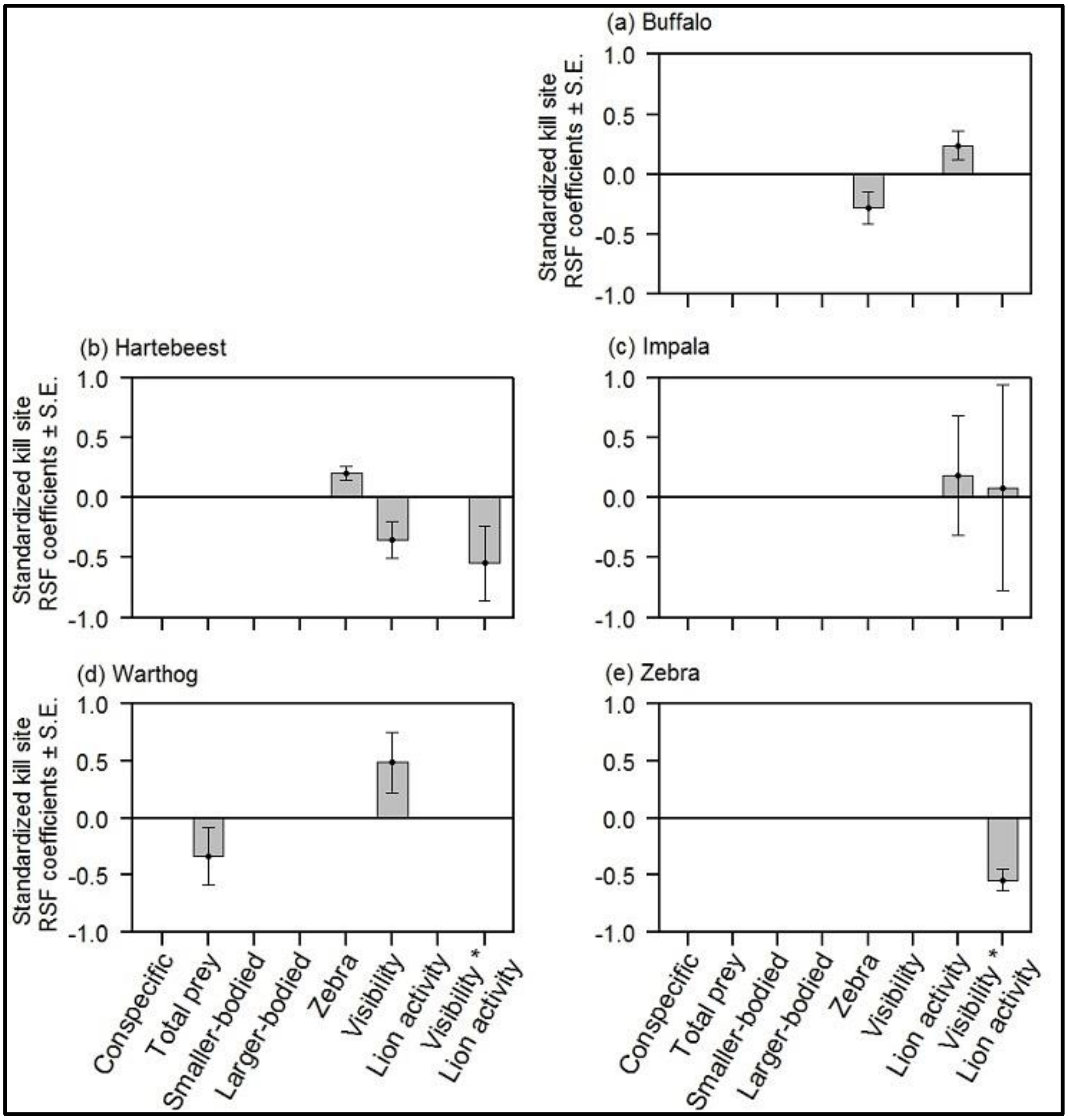


Figure 2: Graphical predictions from kill-site resource selection functions for four species of lion prey. The effect of visibility on the predicted probability of kill occurrence differs across levels of lion utilization and vice versa i.e. probability of kill occurrence changes with one-unit change of visibility while holding lion utilization constant at different levels (minimum = 0.05 and maximum = 0.95), while holding visibility constant at different values of lion utilization.

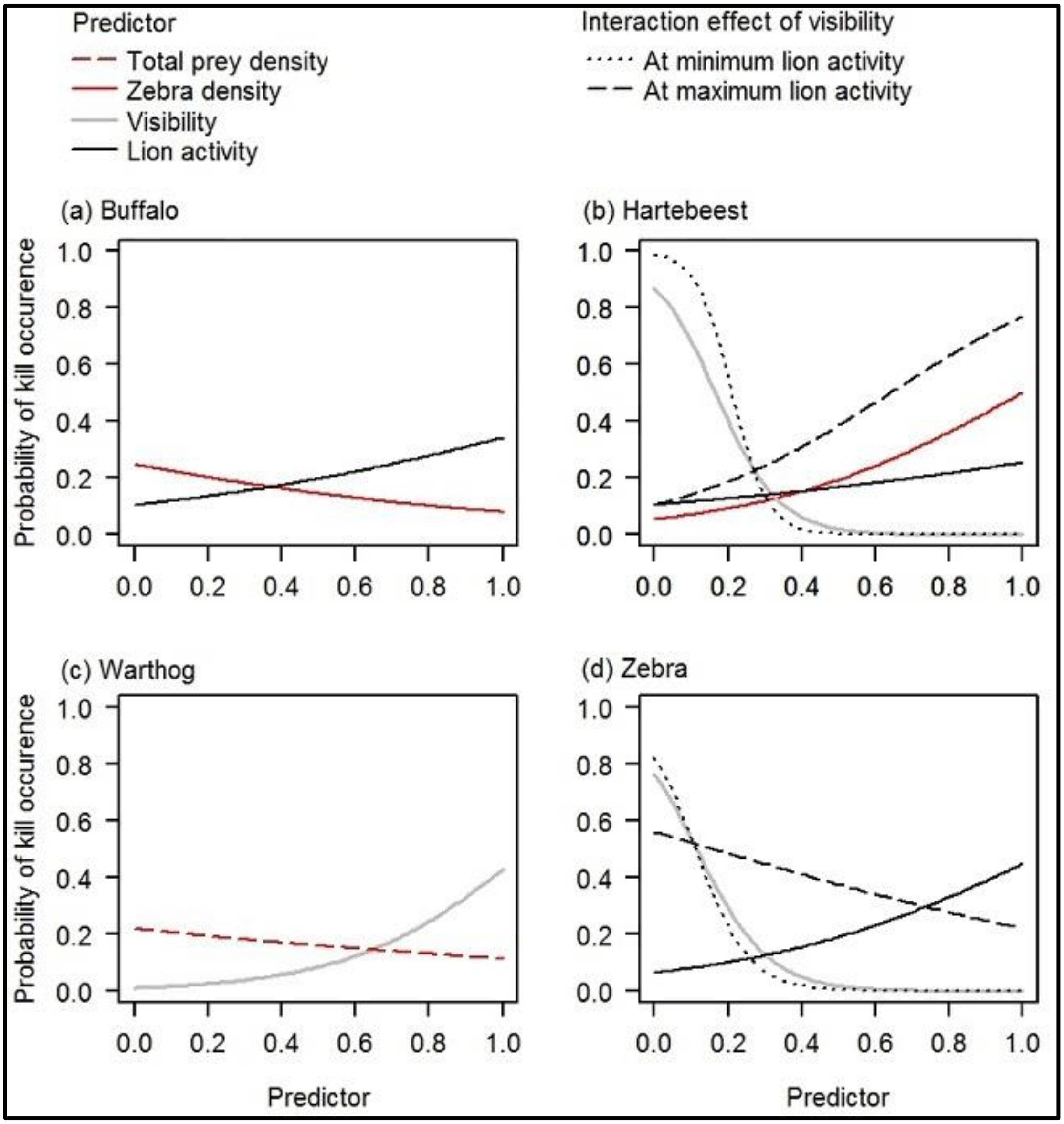
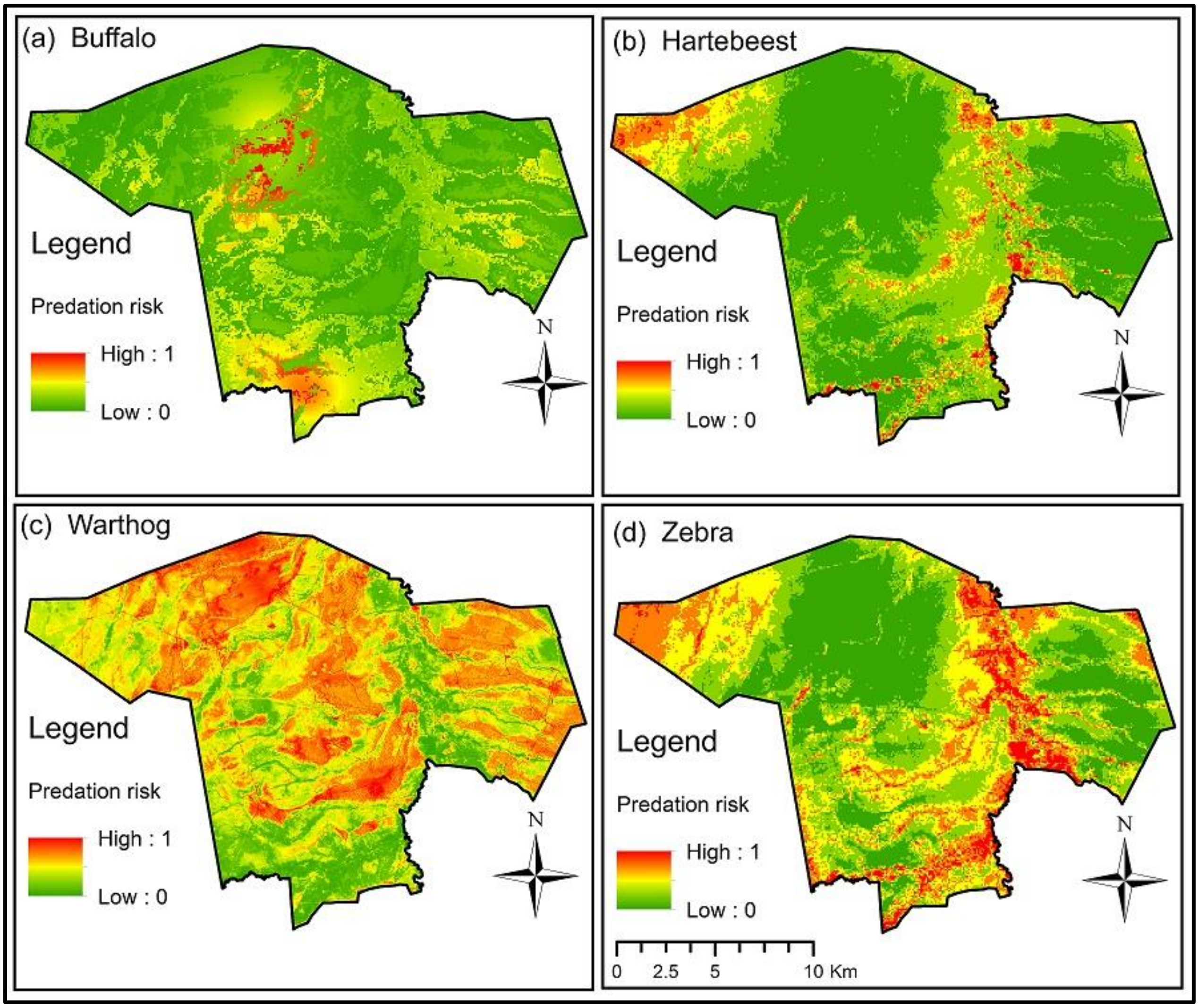


Figure 3: Risk of predation based on model-averaged coefficients from resource selection functions of kill occurrence. From top left to bottom right: (a) buffalo (b) hartebeest (c) warthog and (d) zebra. The boundary for Ol Pejeta Conservancy boundary is shown as a thick black line. Predation risk transitions from high (red) to low (green) risk.



Chapter 3

Apparent competition in a pastoral savanna: can predation pressure on secondary prey be manipulated via livestock production?

3.1 Introduction

Ecosystems devoid of large predators have become the new normal. Through predator restoration, conservation biologists attempt not only to return predators to ecosystems, but to restore ecosystem function and patterns of biodiversity (Terborgh *et al.* 1999; Sinclair *et al*. 2003; Ripple *et al.* 2014; Chapron *et al.* 2014). In the aftermath of predator restorations, however, the prey on which predators depend often exhibit stark changes in their numbers and their behavior. As a result, the composition of post-restoration communities may bear only slight resemblance to that of communities prior to predator extirpation (Lovari *et al.* 2009; DeCesare *et al.* 2010). Differences in predator-extirpated versus predator-restored communities often are attributed to apparent competition, in which predator preferences lead to differences in the degree to which primary and secondary species of prey are suppressed by predation (Holt 1977; Holt & Kotler 1987; see DeCesare *et al.* 2010 for a review of cases in which apparent competition presents challenges for conservation).

Regardless of the mechanism by which predator preferences arise, they typically result in secondary prey incurring greater risk of predation when they are in proximity to primary prey (Holt & Kotler 1987). Secondary prey may decline while primary prey subsidize predators, so that predator populations are decoupled from those of their secondary prey (e.g., Roemer *et al.* 2002; Angulo *et al.* 2007; Sundararaj *et al.* 2012; Hervieux *et al.* 2014). Population growth of secondary prey then decreases, creating potential for predators to drive secondary prey locally extinct (Schmidt 2004; McLellan *et al.* 2010). The likelihood of apparent competition generating these predator-mediated Allee effects is greatest when predator numbers do not change with secondary prey abundance, and are heightened further when predators have been restored after lengthy periods of extirpation over which environmental conditions have changed (Ford & Goheen 2015). Against the backdrop of such a shifting environment, effects of predator restorations often are stronger than expected, presenting a conservation challenge to species of secondary prey that already were rare before predator restoration.

The factors that drive predator preferences—and thus predispose secondary prey to high rates of predation—include differential resilience of primary versus secondary prey to predation, and differential space use between primary and secondary prey (DeCesare *et al.* 2010; Wittmer *et al.* 2013). This second feature of predator-prey dynamics affects the degree of spatial separation between primary and secondary prey, and may result in "gradients of consumption" (in which risk of predation varies directionally; Orrock *et al.* 2008), thereby creating refuges and reducing encounter rates between predators and secondary prey. In giving secondary prey a potential foothold for positive population growth, refuges are one of the few ways empirically demonstrated to negate predation-mediated Allee effects in nature (Sinclair *et al.* 1998), thereby providing a potential tool to ameliorate apparent competition.

For at least three reasons, African savannas hold promise and conservation importance to test whether and how spatial refugia might be used to reduce apparent competition stemming from predator restoration. First, these ecosystems house a staggering abundance and diversity of large ungulates and the predators that eat them (Craigie *et a*l. 2010). Almost invariably, communities of savanna ungulates are dominated by a single species that reaches sufficiently high abundances to escape control by predators, yet typically constitutes the primary prey for predators. In contrast, less abundant species (i.e., secondary prey) tend to be suppressed by predators, thus creating potential for apparent competition (Sinclair 1985; Harrington *et al.* 1999; McLoughlin & Owen-Smith 2003; Georgiadis *et al.* 2003; Owen-Smith *et al.* 2005; Georgiadis *et al.* 2007; Chirima *et al.* 2013). Second, pastoralism occurs alongside wildlife in many African savannas, and landscapes in these human-occupied systems bear the imprint of livestock production in the form of glades: nutrient-rich hotspots derived from abandoned boma ("boma" refer to actively used corral) that attract wild ungulates (Augustine & McNaughton 2006; Porensky & Veblen 2015). Finally, because livelihoods based purely on livestock production are becoming less profitable (Campos *et al.* 2016; Nadal-Romero *et al.* 2016), a changing mindset—to balance pastoralism with tourism, and potentially wildlife conservation—is gaining traction in many areas (Prins & Grootenhuis 2000; Odadi *et al.* 2011). Viewing large predators consistently ranks as a top priority among tourists, leading to financial benefits in ecotourism ventures (Lindsey *et al.* 2007). So, restoring large predators along with diverse assemblage of wild ungulates may hold the key to future economic prosperity in these regions (Cousins *et al.* 2008; Stein *et al.* 2010).

I sought to test the hypothesis of apparent competition in Laikipia County, Kenya, where multiple species of wild ungulates—most notably hartebeest (*Alcelaphus buselaphus*)—have experienced recent declines following lion (*Panthera leo*) restoration (Georgiadis 2007; Ng'weno *et al.* 2017). Restoration of lions has resulted from greater tolerance by ranch managers following decades of control via shooting and poisoning (Georgiadis *et al.* 2007). In contrast to hartebeest and other declining species, populations of plains zebra (*Equus quagga*; "zebra")—the most common wild ungulate and the primary prey for lions—increased during the same period by 200% (Georgiadis 2007; Georgiadis 2011). Zebra populations fluctuate in response to rainfall, but have not decreased with recovering lion numbers (Georgiadis *et al.* 2003). In contrast, the impact of lion predation is sufficiently strong to shift population growth of hartebeest from positive to negative (Ng'weno *et al.* 2017).

I used an understanding of predator-prey dynamics to conceptualize conservation efforts to enhance both wildlife-livestock coexistence and tourism economies. Under the hypothesis of apparent competition, I expected hartebeest herds in proximity to zebra to incur higher rates of predation. Because zebra but not hartebeest are attracted to glades in the study system (Porensky & Veblen 2015) and elsewhere in East Africa (Veblen & Young 2010; Augustine *et al*. 2011), I sought to quantify how spatial separation between primary (zebra) and secondary (hartebeest) prey, driven by glade location, ameliorated any apparent competition between zebra and hartebeest. Specifically, I predicted that (1) hartebeest herds occurring in areas of overlap and high zebra density would incur greater risk of predation from lions; and (2) hartebeest survival would increase when there no glades within their home range.

3.2 Materials and methods

3.2.1 Study area

I conducted my work in Laikipia County, Kenya, at Ol Pejeta Conservancy, (N0° 00' – S0° 02'; E36° 44' – 36° 59'). The property is a 364-km^2 semiarid savanna managed jointly for wildlife conservation and ~ 6000 Boran cattle (*Bos indicus*) production, with annual rainfall of 900 mm (Wahungu *et al.* 2011). Ol Pejeta is characterized by a wooded grassland dominated by *Acacia drepanolobium*. The understory is dominated by the grasses *Themeda triandra*, *Pennisetum straminiem*, *P. mezianum* and *Brachiaria lachnatha*. The most common ungulate at Ol Pejeta is plains zebra (individuals/km^2 = 11.55 ± 1.22 SEM); other wild ungulates include buffalo (*Syncerus cafer*), eland (*Taurotragus oryx*), elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Nanger granti*), Grevy's zebra (*Equus grevyi*), hartebeest, oryx (*Oryx gazella*), plains zebra, and steinbuck (*Rhaphicerus campestris*). In addition to lions, large carnivores include cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), and spotted hyena (*Crocuta crocuta*).

3.2.2 Data collection and analysis

3.2.2.1 Hartebeest population growth, selectivity indices, and spatial overlap between hartebeest and zebra

From 2009 to 2015, I estimated hartebeest population growth and sizes within two zones under different management regimes: (1) a 294 km^2 area in which cattle production occurs alongside wildlife with the full complement of large carnivores (hereafter “control”); and (2) a 32 km^2 lion exclusion zone (hereafter "exclusion"), constructed with the intent of boosting numbers of declining ungulates, primarily hartebeest. The exclusion zone is lion proof, such that it is demarcated from adjacent control zone by 3200-m long, 2.5-m tall solar powered electrified (6000-7000-volt) fence with nine strands spaced 0.2-m apart. The fence is fortified with chain-link 1.50 m above and 0.60 m beneath the ground. This elaborate fence prevents lion incursion into the zone. Stocking rates are maintained at equal densities of 20 cattle per km^2 in both zones. I conducted twice-monthly drive transects for hartebeest in both zones between 2009-2015. During each sampling period, I systematically drove 17 (4-13 km) transects, based on a predetermined random starting point within the study system. I conducted surveys from 0800-1100 hours and for each transect, I drove the vehicle along the transect at a maximum speed of 10-15 km/h with two trained observers. At each hartebeest sighting, observers recorded the herd size and the distance and angle to the herd with binoculars and laser rangefinder following standard distance sampling methods (Buckland *et al*. 2015). Typically, apparent competition is characterized by one or more species of secondary prey that exhibit an Allee effect (i.e., inverse density-dependence; Allee *et al*. 1949;

Courchamp *et al*. 1999; Stephens *et al*. 1999). To test for an Allee effect, I calculated the instantaneous rates of increase (r) for each zone (control and exclusion) as:

$$r = \frac{N_{i+1} - N_i}{t_{i+1} - t_i}$$

Where *N* is the estimate of population size from the i^{th} survey at time *t* (Sinclair *et al.* 1998). For hartebeest populations in both zones, I plotted population size against rate of increase, and determined goodness-of-fit of curves from regression analysis (Zar 2010).

Additionally, between 2012-2015, I conducted quarterly vehicle-based drive transects to determine abundance of 11 species of ungulates killed and consumed by lions (hereafter "lion prey"), within the study system. I systematically drove 12 (4-13 km) transects based on a predetermined, random starting point within the study area. I conducted all quarterly counts on the same transects between 0700 and 1100 hours with two trained observers. For each survey, 1 drove the vehicle-based drive transects at a maximum speed of 10-15 km/h, while two observers recorded species, herd size, sighting distance, and bearing to all lion prey sighted along the predetermined set of vehicle based line transects. Distance to lion prey were measured using a laser rangefinder and transect bearing was determined using a compass. (see also Fischhoff *et al.* 2007). To evaluate whether lions killed prey in accordance to their availability, I fit 5 female lions with Global Positioning System (GPS) collars (Vectronic Aerospace GmbH, Berlin, Germany) between March and May 2014. All procedures were conducted with a veterinary team under the authority of the Kenya Wildlife Service. I located lion kills by identifying GPS clusters using an algorithm adapted from Knopff *et al.* (2009). I defined a cluster as ≥2 successive GPS relocations occurring within 100 m of each other. Between August 2014 and December 2015, I identified n = 246 instances in which carcasses both were found and were verified to be kills by lions. I then used Jacobs' index

(Jacobs 1974; Hayward & Kerley 2005) to quantify seasonal selectivity for each of 11 species of lion prey:

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

Where *r* is the proportion of the total number of kills attributed to a particular species and *p* is the proportional abundance of that species of the total prey population. Jacobs's index is bounded between -1 (highly avoided) and 1 (highly selected). Selectivity indices were calculated for each of the 11 species of lion prey, using lion prey kill data from GPS clusters and lion prey abundance data collected between August 2014 and December 2015.

To quantify impact of zebra density on hartebeest predation by lions, using the following procedure, I generated zebra spatially-explicit density surface using resource selection function (RSF) in a use-available design (Manly *et al*. 2002). First. I constructed a minimum convex polygon around all zebra herd locations (used) and I generated an equal number of random locations (available, n=2450) within zebra MCP to achieve a 1:1 ratio of used to available locations. Second, I considered three variables: (1) categorical habitat types (which coincided with woody cover); (2) distance to glades (nutrient-rich grazing lawns derived from livestock corrals; (Augustine & McNaughton 2006; Porensky and Veblen 2015); and (3) distance to water sources. I used a Rapideye satellite image (Digital Globe, Longmont, Co, USA) from May 2013, with a spatial resolution of 5-m to create a map of habitat type categories, which coincided with woody cover. I performed an unsupervised classification through isoclustering and maximum likelihood to group pixels with similar spectral reflectance. I then characterized habitat types according to Wahungu *et al.* (2011): 1) Dense bushland (>50% overstory cover dominated by *E. divinorium*); 2) Open bushland (10-30% overstory cover dominated by *A. drepanolobium*); and 3) Open grassland (mostly treeless areas, with understory cover dominated by *Themeda triandra*, *Pennisetum stramineum*, and *P. mezianum*). I performed all image processing using ERDAS Imagine, version 14 (Hexagonal Geospatial, Madison, Alabama) and ArcGIS version 10.3 (ESRI, Redlands, California). Following assignment of pixels to habitat categories, I ground-truthed and classified pixel groups using 50-100 points in each habitat category. Using the Euclidian distance tool in ArcGIS version 10.3, I extracted distance to the nearest glade and water source to used and available locations restricted within zebra MCP. I also attached categorical habitat types to the used and available locations using spatial join tool in ArcGIS 10.3. I then used Pearson's correlation to assess for collinearity between independent variables and none of the variables were correlated ($r > 0.50$ or $r < -0.50$).

Third, I used logistic regression to estimate RSF coefficients, with selection for or avoidance of a resource indicated by coefficients > 1 and < 1, respectively (Manly *et al*. 2002). Fourth, I used the resultant coefficients to generate a zebra RSF and rescaled to create continuous surfaces ranging between 0 (strongest avoidance) and 1 (strongest selection), which I split into 5 bins of equal width following Morris *et al*. (2016). The first bin corresponded to the lowest probability of zebra selection (0.00-0.20) and the fifth bin corresponded to the highest probability of zebra selection (0.81-1.00). To create a zebra spatially-explicit density surface, I extracted estimated zebra density to each of the corresponding five zebra RSF bins. Fifth, I superimposed hartebeest kill locations obtained from GPS cluster (n=27) and glade locations (n=37) to the spatially-explicit zebra density surface. Lastly, I extracted the corresponding zebra density to each hartebeest kill location and used chi-squared test to assess for difference in proportion of hartebeest kills that occurred within highest and lowest zebra density areas within my study area.

3.2.2.2 Survivorship and refugia analysis

Beginning 2012-2015, I calculated hartebeest survival rate with the biological year starting 1 October and ending 31 September of each subsequent year. I conducted twice-monthly sight-resight drive surveys along the hartebeest transects described above to monitor survival of 179 matured individuals that occurred within 11 herds in the control zone. Hartebeest exhibit high site fidelity, so this enabled us to use unique marks (i.e., ear nicks, horn size and shape and scars) to monitor survival rate through repeated surveys (see also Ng'weno *et al.* 2017). Survival rates were calculated using the R package 'survival' version 2.41-3 (Therneau 2017).

Over the course of approximately three years, abandoned boma sites transition into glades and become attractive to zebra because of high biomass of *Cynodon and Pennisetum* grasses (Veblen & Young 2010, Porensky 2011). I therefore selected and restricted my analysis to glades; ≥3 years of age, 17.2 ± 0.8 m SEM in diameter, and used by approximately 200 cattle (see Porensky *et al.* 2015). To assess the influence of a refugia on hartebeest survival rate, I used hartebeest (n=1462 herd locations) data collected from twice-monthly surveys (2009-2015). I constructed 95% isopleths using kernel density estimation (KDE) to create utilization distributions (UD's), with least squares cross validation and a smoothing factor of 1000 using R package 'adehabitatHR' version 1.8.18 (Seaman & Powell 1996; Powell 2000; Calenge 2006). I then, overlaid glades (n = 37), on hartebeest home ranges, and determined whether glades occurred within their home range [95% isopleths]. Previous studies suggest that glade edge effects rarely exceed as far as 200 m (Young *et al.* 1995; Muchiru *et al.* 2008; Porensky 2011). Therefore, herds falling ≥ 600 m from the center of existing glade to home range boundary were considered to have no glade in their home range. To assess statistical support of my hypothesis concerning effects of glades on hartebeest survival, I fit a Cox proportional hazards model (Cox PH model; Cox 1972) containing frailty models (Rondeau *et al.* 2003) using R package 'frailtypack' version 2.12-3 (Rondeau *et al.* 2012). I used "herd" to which individual hartebeest belonged as random effect (the frailty) and glade as a predictor. All analyses were undertaken in R version 3.4.0 (R Development Core Team, 2017).

3.3 Results

Hartebeest population growth in the control zone shows evidence of an Allee effect (Fig.1a) driven by type 2 predator response, such that rates of population change increased with population size, unlike in the exclusion zone (Fig. 1.b). Hartebeest numbers were significantly negatively correlated with lion numbers (Fig. S1; $r = -0.88$, $t_5 = -4.13$, $P = 0.009$), indicating a direct predation effect. Of the 11-species utilized by lions, zebra was the species most frequently preyed upon (40% of kills, n = 109) followed by warthog (14.5%; n = 39), buffalo and impala (both 13%; n = 35,) and hartebeest (11%; n = 31). Further, my analyses show that lions consume hartebeest disproportionately to their abundance (Fig. 2), whereas buffalo, eland, and zebra are killed in proportion to their abundance in the wet season and waterbuck and zebra are killed in proportion to their abundance in the dry season.

As predicted from the apparent competition hypothesis, the number of hartebeest kill sites was higher than expected in areas of high zebra density than elsewhere ($\lambda^2_4 = 42$, $P < 0.001$, $n = 27$; Fig. 3). Additionally, zebras selected areas with glades ($\beta = 1.02 \pm$ CI 0.69, $Z = 2.88$, $P = 0.003$; Fig 3). Lastly, hartebeest survival significantly increased when there was no glade within their home range ($\lambda^2_1= 10.50$, $P < 0.001$; Fig. 4).

3.4 Discussion

Empirical evidence for apparent competition has been increasingly reported for a variety of taxa (Holt & Kotler 1987; Holt & Lawton 1994; Holt 1977). For example, in large mammals, apparent competition has been implicated in limiting the recovery of Sierra Nevada bighorn sheep (*Ovis canadensis*), DeCesare *et al.* 2010, and mountain caribou (*Rangifer tarandus*), (McLellan *et al.* 2010). My findings provide three lines of evidence supporting apparent competition, in the East African savanna: i). I show evidence of predator-mediated Allee effect, such that hartebeest (secondary prey) declined in an inversely density-dependent manner. ii) Type 2 predator response, in which lions continue to exploit hartebeest even when they occur in low numbers, and iii) Spatial overlap between zebra and hartebeest exacerbates lion predation on hartebeest (Fig 3), potentially limiting recovery of the latter. My findings support the hypothesis that predation can disproportionately affect secondary prey populations when generalist predators (i.e. lions) are numerically linked to more abundant primary prey (Sinclair *et al.* 1998; McLellan *et al.* 2010; DeCesare *et al.* 2010).

Spatial separation can reduce encounter rates between predators and secondary prey (see Palmer *et al.* 2003; Forrester & Steele 2004; Orrock *et al.* 2008). Similarly, my data indicate that higher survival of hartebeest occur in presence of refuge (Fig. 4.). Consistently, zebras, unlike hartebeest, are attracted to glades because of high biomass of *Cynodon and Pennisetum* grasses (Veblen & Young 2010; Porensky 2011), so that glades offer a promising approach to creating refuges for secondary prey (hartebeest): positioning livestock corrals to steer lions away from hartebeest. This should give secondary prey a potential foothold for positive population growth, in as much as refuges are one of the few ways empirically demonstrated to negate Allee effects in nature (Sinclair *et al.* 1998).

Apparent competition has been implicated in the declines of many species of conservation concern. For example, moose (*Alces alces*), have an indirect adverse effect on caribou (*Rangifer tarandus*) via a wolf (*Canis lupus*)-mediated-apparent competition interaction. However, the majority of studies investigating apparent competition have involved North American cervids: elk (*Cervus elaphus*), moose (*Alces alces*), and caribou (*Rangifer tarandus*) in response to wolf (*Canis lupus*) reintroductions (Fortin *et al.* 2005; Berger & Gese 2007; DeCesare et al. 2010). However, considering the high diversity of species in Africa, there is a dearth of research on apparent competition in the system. Therefore, my work provides a novel demonstration of how apparent competition== a pervasive outcome in large mammal communities characterized by a diversity of prey--can be managed by controlled grazing of livestock. Such efforts to reverse ongoing declines of diminishing African savanna wild ungulates through strategic livestock management may be critical to the coexistence of large predators and livestock on multiple-use lands. Therefore, I recommend that management plans should consider the innovative spatial distributions of primary prey in relation to their predators as a way to reduce the potential for apparent competition.

3.6 References

Allee, W.C., Park. O., Emerson, A.E., Part, T. & Schmidt, K.P. (1949) Principles of animal ecology. Saunders, Philadelphia.

Angulo, E., Roemer, G., Berec, L., Gascoigne, J. & Courchamp, F. (2007) Double llee effects and Extinction in the Island Fox. *Conservation Biology*, **21**, 1082–1091.

Augustine, D. & McNaughton, S. (2006) Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems*, **9**, 1242–1256.

Augustine, D.J., Veblen, K.E., Goheen, J.R., Riginos, C., Young, T.P. (2011) Pathways for positive cattle-wildlife interactions in semi-arid rangelands. *Conserving wildlife in African landscapes: Kenya's Ewaso ecosystem* (ed. N., Georgiadis), pp. 55–71. Smithsonian Institution Scholarly Press, Washington, D.C..

Berger, K.M. & Gese, E.M. (2007) Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology*, **76**, 1075–1085.

Buckland, S.T., Rexstad, E., Marques, T.A. & Oedekoven, C.S. (2015). Distance sampling: methods and applications. Springer, Heidelberg.

Campos, P., Ovando, P., Mesa, B. & Oviedo, J. (2016) Environmental income of livestock grazing on privately-owned Silvopastoral farms in Andalusia, Spain. *Land Degradation & Development*. DOI:10.1002/ldr.2529.

Calenge, C. (2006) "adehabitat": R package for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.

Chapron, G., *et al.* (2014) Recovery of large carnivores in Europe's modern human dominated landscapes. *Science*, **346**, 1517–1519.

Chirima, G., Owen-Smith, N., Erasmus, B. & Parrini, F. (2012) Distributional niche of relatively rare sable antelope in a South African savanna: habitat versus biotic relationships. *Ecography*, **36**, 68–79.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999) Inverse density-dependence and the Allee effect. *Trends in Ecology & Evolution*, **14**, 405–410.

Cousins, J.A., Sadler, J.P. & Evans, J. (2008) Exploring the role of private wildlife ranching as a conservation tool in South Africa: stakeholder perspectives. *Ecology and Society*, **13**, 43.

Cox, D.R. (1972) Regression models and life-tables. *Journal of the Royal Statistical Society, Series B (Methodological)*, **34**, 187–220.

Craigie, I., Baillie, J., Balmford, A., Carbone, C., Collen, B., Green, R. & Hutton, J. (2010) Large mammal population declines in Africa's protected areas. *Biological Conservation*, **143**, 2221–2228.

DeCesare, N., Hebblewhite, M., Robinson, H. & Musiani, M. (2010) Endangered, apparently: the role of apparent competition in endangered species conservation. *Animal Conservation*, **13**, 353–362.

ESRI. (2011) ArcGIS Desktop: Release 10. Environmental systems research institute, Redlands, California.

Fischhoff, I.R., Sundaresan, S.R. Cordingley, J., Rubenstein, D.I. (2007) Habitat use and movements of plains zebra in response to predation danger from lions. *Behavioral Ecology,* **18**, 726–729.

Ford, A. & Goheen, J.R. (2015) Trophic Cascades by Large Carnivores: A Case for Strong Inference and Mechanism. *Trends in Ecology & Evolution*, **30**, 725–735.

Forrester, G.E. & Steele. M.A. (2004) Prey refuges, and the spatial scaling of density-dependent prey mortality. *Ecology*, **85**, 1332–1342.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, **86**, 1320–1330.

Georgiadis, N.J. (2011) Introduction: Conserving wildlife in Kenya's Ewaso landscape. *Smithsonian Contributions to Zoology*, **632**, 1–10

Georgiadis, N.J., Olwero, J.G., Ojwang', G. & Romañach, S. (2007) Savanna herbivore dynamics in a livestock-dominated landscape: I. Dependence on land use, rainfall, density, and time. *Biological Conservation*, **137**, 461–472.

Georgiadis, N.J., Hack M. & Turpin. K. (2003) The influence of rainfall on zebra population dynamics: implications for management. *Journal of Applied Ecology,* **40**, 125–136.

Harrington, R., Owen-Smith, N., Viljoen, P., Biggs, H., Mason, D. & Funston, P. (1999) Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biological Conservation*, **90**, 69–78.

Hayward, M.W. & Kerley, G.H. (2005) Prey preferences of the lion (*Panthera leo*). *Journal of Zoology*, **267**, 309–322.

Hervieux, D., Hebbelwhite, M., Stepnisky, D., Bacon, M. & Boulin, S. (2014) Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus caribou*) in Alberta. *Canadian Journal of Zoology*, **92**, 1029–1037.

Holt, R.D. (1977) Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, **12**, 197–229.

Holt, R.D. & Kotler. B.P. (1987) Short-term apparent competition. *The American Naturalist*, **130**, 412–430.

Holt, R.D. & Lawton, J.H. (1994) The ecological consequences of shared natural enemies. *Annual Review of Ecology & Systematics*, **25**, 495–520.

Jacobs, J. (1974) Quantitative measurement of food selection. *Oecologia*, **14**, 413–417.

Knopff, K.H., Knopff, A.A., Warren, M.B. & Boyce, M.S. (2009) Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. *Journal of Wildlife Management*, **73**, 586–597.

Lindsey, P.A., Roulet, P.A. & Romañach, S.S. (2007) Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation*, **134**, 455–469.

Lovari, S., Boesi, R., Minder, I., Mucci, N., Randi, E., Dematteis, A. & Ale, S. (2009) Restoring a keystone predator may endanger a prey species in a human-altered ecosystem: the return of the snow leopard to Sagarmatha National Park. *Animal Conservation*, **12**, 559–570.

Manly, B.F.J., Mcdonald, L.L., Thomas, D.L., McDonald, T.L. & Wallace, W.P. (2002) *Resource selection by animals: statistical design and analysis for field studies*, 2nd edn. Kluwer Academic Publishers, Dordrecht, Netherlands.

McLellan, B.N., Serrouya, R., Wittmer, H.U. & Boutin, S. (2010) Predator-mediated Allee effects in multi-prey systems. *Ecology*, **91**, 286–292.

McLoughlin, C. & Owen-Smith, N. (2003) Viability of a diminishing roan antelope population: predation is the threat. *Animal Conservation*, **6**, 231–236.

Morris, L.M., Proffitt, K.M. & Blackburn, J.K. (2016) Mapping resource selection functions in wildlife studies: Concerns and recommendations. *Applied Geography*, **76**, 173–183.

Muchiru, A.N., Western, D.J. & Reid, R.S. (2008) The role of abandoned pastoral settlements in the dynamics of African large herbivore communities. *Journal of Arid Environments*, **72**, 940–952.

Nadal-Romero, E., Lasanta, T. & Cerdà, A. (2016) Integrating extensive livestock and soil conservation policies in Mediterranean mountain areas for recovery of abandoned lands in the central Spanish Pyrenees. A long-term research assessment. *Land Degradation & Development*. DOI:10.1002/ldr.2542.

Ng'weno, C.C., Maiyo, N.J., Ali, A.H., Kibungei, A.K. &. Goheen, J.R. (2017) Lions influence the decline and habitat shift of hartebeest in a semiarid savanna. *Journal of Mammalogy*, **98** (4), 1078–1087.

Odadi, W.O., Karachi, M.K., Abdulrazak, S.A. & Young, T.P. (2011) African wild ungulates compete with or facilitate cattle depending on season. *Science*, **333**, 1753–1755.

Orrock, J.L., Witter, M.S. & Reichman, O.J. (2008) Apparent competition with an exotic plant reduces native plant establishment. *Ecology*, **89**, 1168–1174.

Owen-Smith, N. & Mason, D. (2005) Comparative changes in adult vs. juvenile survival affecting population trends of African ungulates. *Journal of Animal Ecology*, **74**, 762–773.

Palmer, S.C.F., Hester, A.J., Elston, D.A., Gordon, I.J. & Hartley, S.E. (2003) The perils of having tasty neighbors: grazing impacts of large herbivores at vegetation boundaries. *Ecology*, **84**, 2877–2890.

Porensky, L.M. (2011) When edges meet: interacting edge effects in an African savanna. *Journal of Ecology*, **99**, 923–934.

Porensky, L.M. & Veblen. K.E. (2015) Generation of ecosystem hotspots using short-term cattle corrals in an African savanna. *Rangeland Ecology and Management*, **68**, 131–141.

Powell, R.A. (2000). Animal home ranges and territories and home range estimators. *Research techniques in animal ecology: controversies and consequences* (eds L., Boitani & T.K., Fuller), pp. 65–110. Columbia University Press, New York.

Roemer, G., Donlan, C. & Courchamp, F. (2002) Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey. *Proceedings of the National Academy of Sciences*, **99**, 791–796.

Prins, H.H.T. & Grootenhuis, J.G. (2000) Introduction: the value of priceless wildlife. *Wildlife conservation by sustainable use* (eds H.H.T., Prins, J.G., Grootenhuis & T.T Dolan), pp. 1–12. Kluwer Academic press, Boston.

R Development Core Team. (2017) R: *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL https://www.R-project.org/.

Ripple, W., Estes, J., Beschta, R., Wilmers, C., Ritchie, E., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M., Schmitz, O., Smith, D., Wallach, A. & Wirsing, A. (2014) Status and Ecological Effects of the World's Largest Carnivores. Science, **343**, 1241484–1241484.

Rondeau, V., Commenges, D. & Joly, P. (2003) Maximum Penalized likelihood estimation in a gamma-frailty model. *Lifetime Data Analysis*, **9**(2), 139–153.

Rondeau, V., Mazroui, Y., & Gonzalez, J. (2012) Frailtypack: R package for the analysis of correlated survival data with frailty models using penalized likelihood estimation or parametric estimation. *Journal of Statistical Software*, **47**, 1–28.

Schmidt, K.A. (2004). Incidental predation, enemy-free space and the coexistence of incidental prey. *Oikos*, **106**, 335–343.

Seaman, D.E., & Powell, R.A. (1996) Accuracy of kernel estimators for animal home range analysis. *Ecology*, **77**, 2075–2085.

Sinclair A.R.E. (1985) Does interspecific competition or predation shape the African ungulate community? *Journal of Animal Ecology*, **54**, 899–918.

Sinclair, A.R.E., Mduma, S. & Brashares, J.S. (2003) Patterns of predation in a diverse predator-prey system. *Nature*, **425**, 288–290.

Sinclair, A., Pech, R., Dickman, C., Hik, D., Mahon, P. & Newsome, A. (1998) Predicting Effects of Predation on Conservation of Endangered Prey. *Conservation Biology*, **12**, 564–575.

Stein, A.B., Fuller, T.K., Damery, D., Siever, P.R. & Marker, L.L. (2010) Farm management practices and financial analysis of farmer tolerance of leopards in the Waterberg region, North-central Namibia. *Animal Conservation*, **13**, 419–27.

Stephens, P.A., Sutherland, W.J. & Freckleton, R.P. (1999) What is the Allee effect? *Oikos*, **87**, 185–190.

Sundararaj, V., McLaren, B.E., Morris, D.W. & Goyal, S.P. (2012) Can rare positive interactions become common when large carnivores consume livestock? *Ecology*, **93**, 272–280.

Terborgh, J., Estes, J.A., Paquet, P., Ralls, K., Boyd-Heigher, D., Miller, B.J. & Noss, R.F. (1999) The role of top carnivores in regulating terrestrial ecosystems. *Continental conservation: scientific foundations of regional reserve networks* (eds M., Soulé. & J., Terborgh), pp 39–64. Island Press, Washington, DC.

Therneau, T. (2017) survival: R Package for Survival Analysis version 2.41-3. http://www.CRAN.R-project.org/package=survival.

Veblen, K.E. & Young, T.P. (2010) Contrasting effects of cattle and wildlife on the vegetation development of a savanna landscape mosaic. *Journal of Ecology*, **98**, 993–1001

Wahungu, G.M., Mureu, L.K., Kimuyu, D.M., Birkett, A., Macharia, P.G. & Burton, J. (2011) Survival, recruitment and dynamics of *Acacia drepanolobium Sjostedt* seedlings at Ol Pejeta Conservancy, Kenya, between 1999 and 2009. *African Journal of Ecology*, **49**, 227–233.

Wittmer, H., Serrouya, R., Elbroch, M. & Marshall, A. (2013) Conservation strategies for species affected by Apparent competition. *Conservation Biology*, **27**, 254–260.

Young, T.P., Patridge, N. & Macrae, A. (1995) Long-term glades in acacia bushland and their edge effects in Laikipia, Kenya. *Ecological Applications*, **5**, 97–108.

Zar, J.H. (2010). *Biostatistical analysis*. 5th edn, Prentice-Hall, New Jersey.

Figures

Figure 1: Annual instantaneous rates of increase (r) for hartebeest as a function of hartebeest population size; a) with type 2 predation (control, r = 0.365ln(N) - 1.786; $R^2 = 0.33$), and b) without predation (exclusion, r = -0.241ln(N) + 1.058; $R^2 = 0.09$). Error bars are 95% confidence intervals.

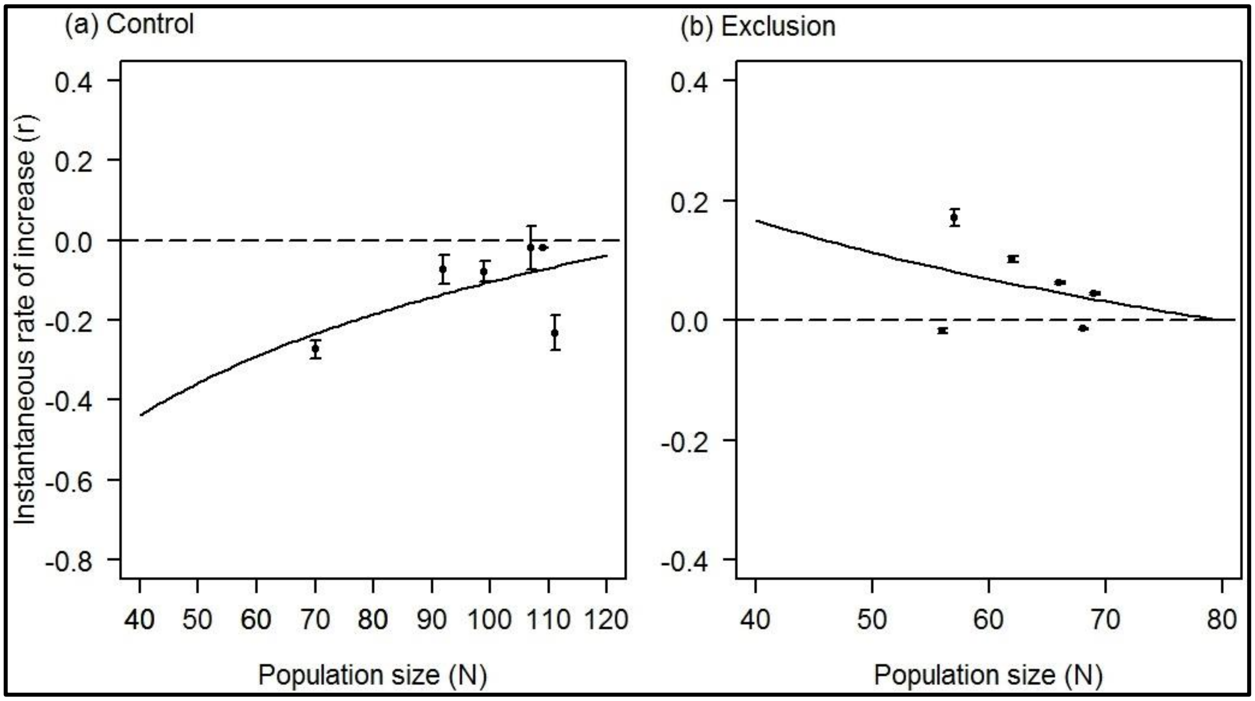


Figure 2: Selectivity index (Jacob's index of selection) of prey by five lion prides during wet and dry season. Error bars are standard error (SEM).

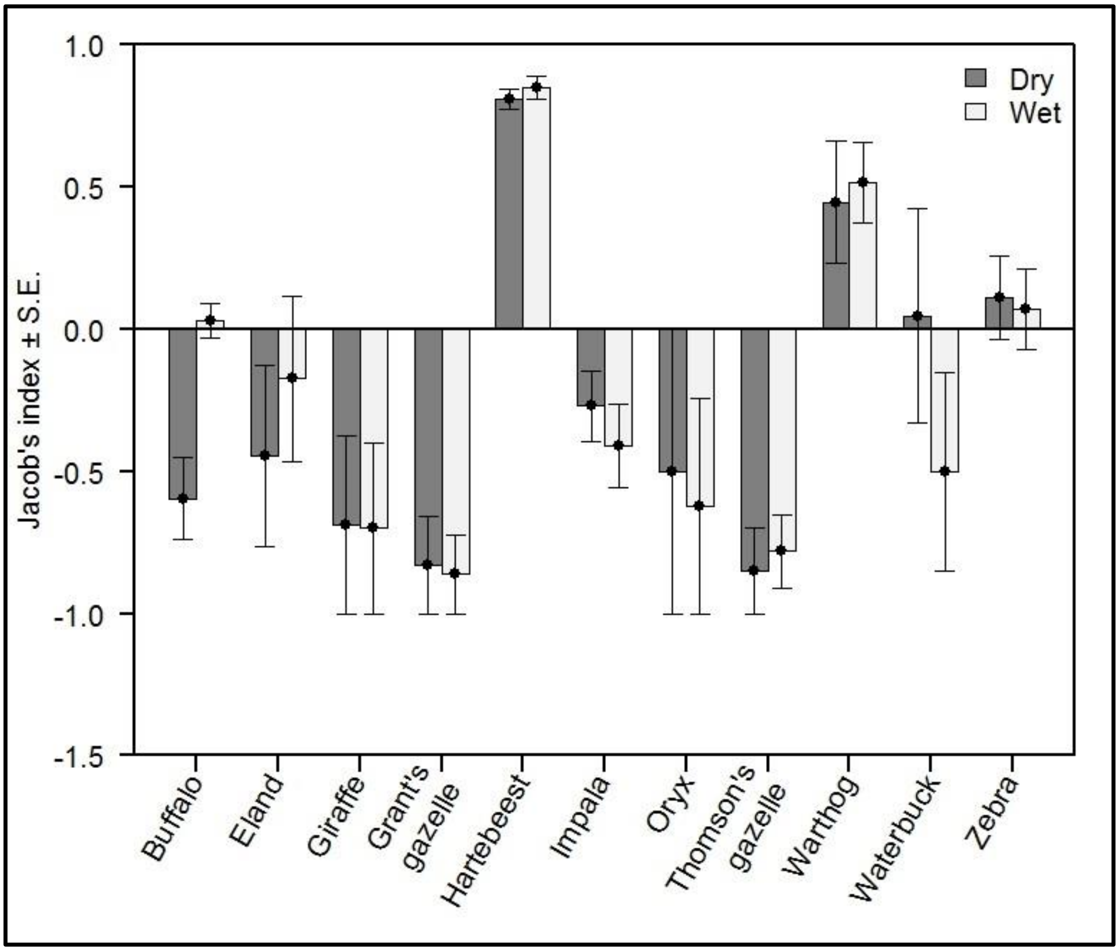


Figure 3: Map showing glades (≥3 years of age, n=37) and hartebeest kill sites (n = 27) superimposed on zebra spatially-explicit density surface. Estimates of zebra density (individuals/km^2) transitions from high (red) to low (green).

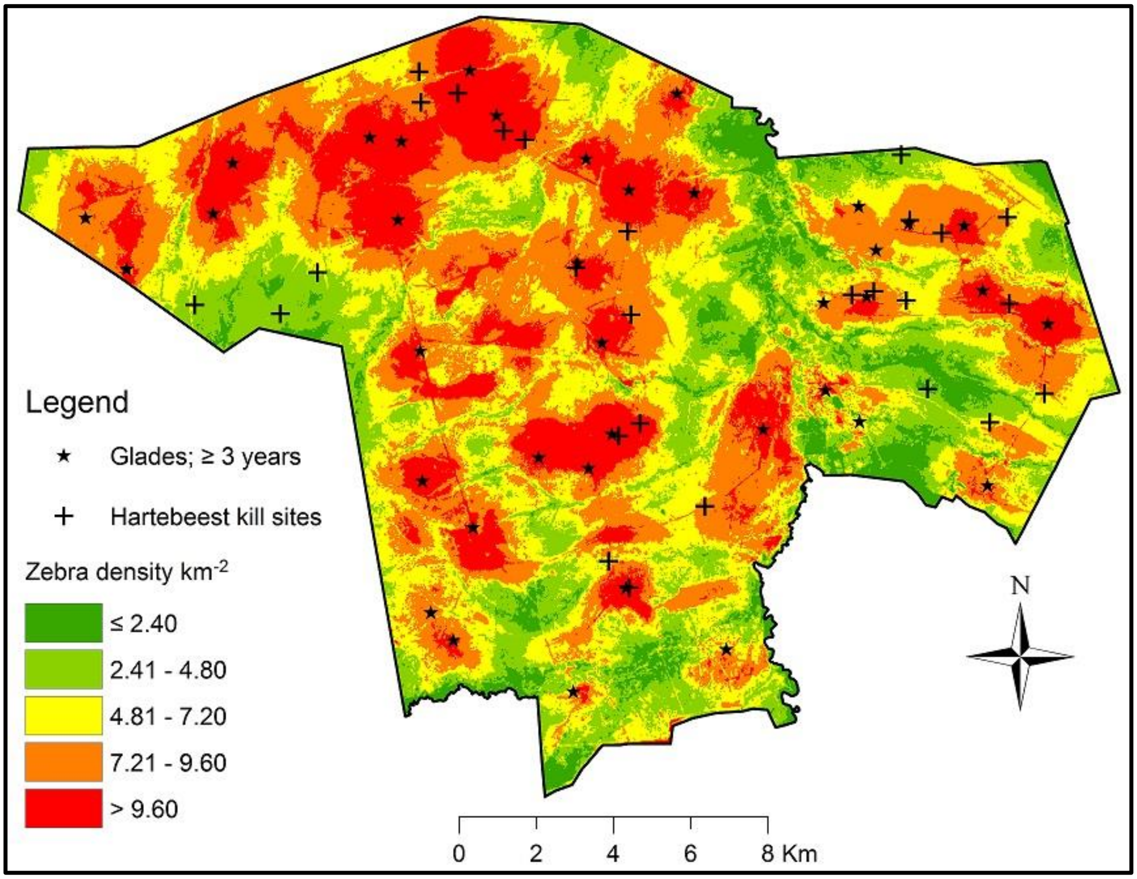
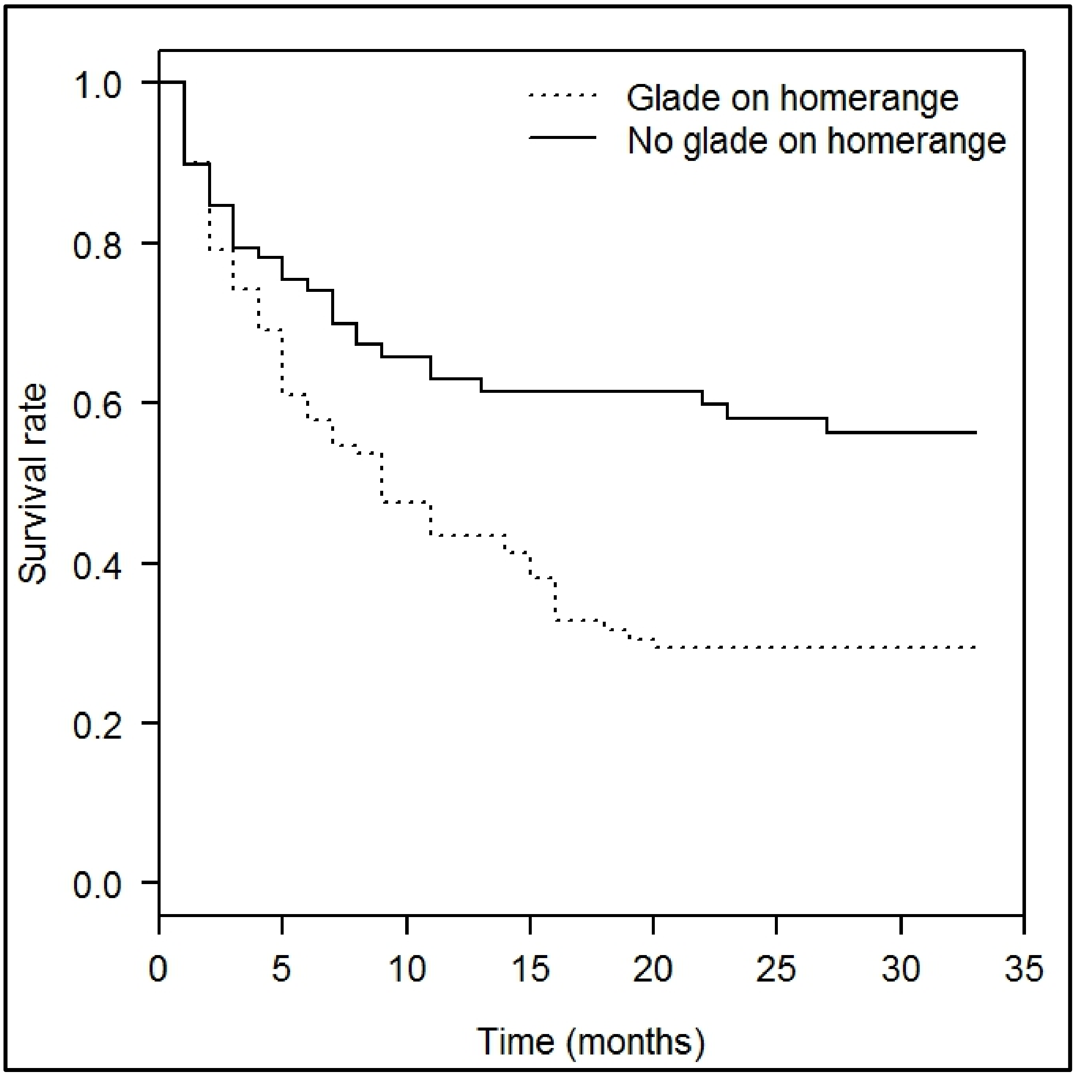


Figure 4: Cox proportional hazards survival rates for hartebeest with home ranges containing vs. not containing glades. Showing that survival of individual hartebeest whose home ranges contain glades (n = 101) decline faster than those whose home ranges had no glade (n = 78).



Supplementary Materials

Chapter 1 (Tables)

Table S1: Densities of large carnivores within control and lion-exclusion zones at Ol Pejeta Conservancy based on camera-trap surveys from 2012 to 2015. Additionally, estimates of lion densities based on ground surveys are reported.

	Individuals/Km^2					
Species	2012	2013	2014	2015	Average	S. E
Control						
Black-backed jackal (*Canis mesomelas*)	0.564	0.575	0.581	0.549	0.567	0.006
Spotted Hyena (*Crocuta crocuta*)	0.520	0.509	0.511	0.512	0.513	0.002
Lion (*Panthera leo*)	0.206	0.215	0.212	0.209	0.210	0.002
Lion estimates from ground survey	0.187	0.190	0.228	0.235	0.210	0.020
Exclusion						
Black-backed jackal (*Canis mesomelas*)	0.559	0.587	0.560	0.576	0.571	0.006
Spotted Hyena (*Crocuta crocuta*)	0.362	0.367	0.356	0.349	0.358	0.003
Lion (*Panthera leo*)	0.000	0.000	0.000	0.000	0.000	0.000

Table S2: Hartebeest at Ol Pejeta Conservancy, Kenya showing unique marks used to identify individuals and herds (deformed right horn [A]; notch in the upper left ear [B]; missing left horn [C]).

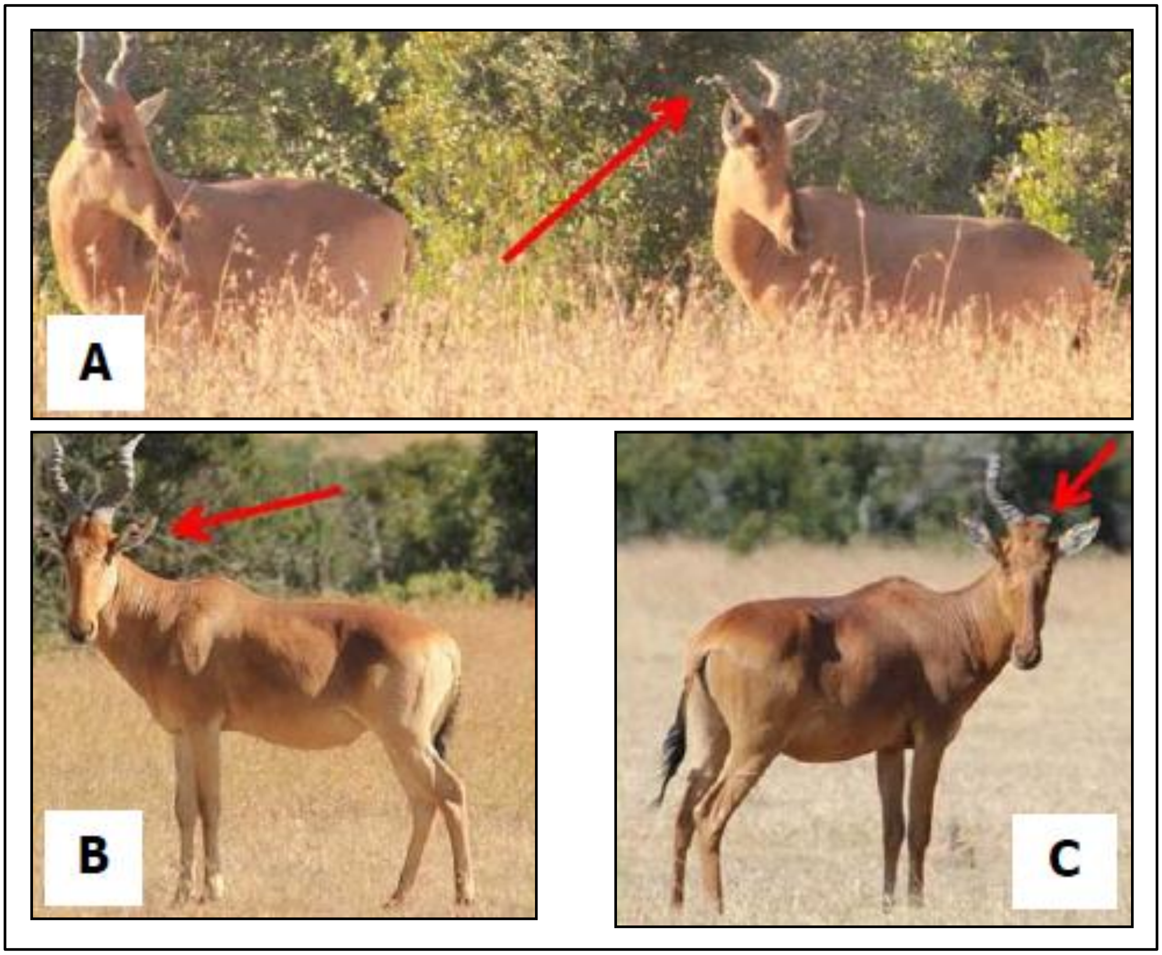


Table S3: Hartebeest age categories, based on horn development (modified from Andanje 2002).

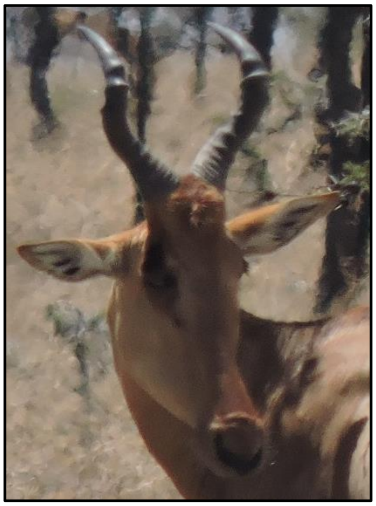
		
Calf: 0 - 12 months Without horns or emerging straight horns, up to or just exceeding ear-length	Subadult:13 - 24 months Horn tip curved inwards, widening toward the center	Adult: ≥ 2 years of age Mature curved horns that curve inward then outwards

Table S4: Life cycle graph of hartebeest that depicts transitions from calf (0-12 months), to subadult (13-23 months), to adult (≥ 2 years of age). In the life cycle graph, arcs that points the same node indicate the probability of surviving and remaining in the same stage, while the other arc represent the probability of surviving and fecundity. Age-specific survival (calf survival [Sc], subadult survival [Ssa], adult survival [Sad], and fecundity [Fa], following Caswell (2001

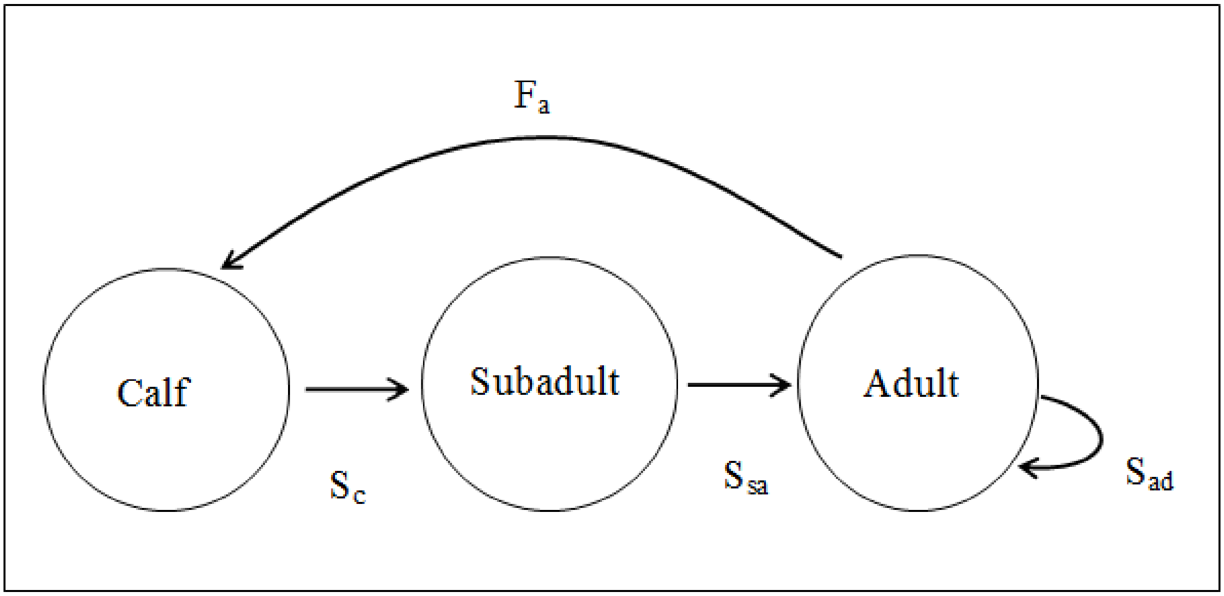


Table S5: Number of pregnancies and detections noted among hartebeest within each treatment every biological year and births (% of individuals giving birth, given pregnancy).

	Control		Exclusion	
Biological Year	Pregnancies (% of adult females)	Births (% of pregnancies detected)	Pregnancies (% of adult females)	Births (% of pregnancies detected)
2012-2013	31 (51.7%)	29 (93.5%)	29 (80.6%)	28 (96.6%)
2013-2014	28 (51.9%)	27 (96.4%)	29 (80.6%)	27 (93.1%)
2014-2015	11 (23.9%)	10 (90.9%)	24 (66.7%)	24 (100%)
Average	23 (43.8%)	22 (94.3%)	27 (75.9%)	26 (96.3%)

Table S6: Change in mean vital rates, sensitivity, elasticity and LTRE contribution in exclusion vs. control paired setting for period 2012-2015.

Vital rates	Exclusion	Control	Change in rate	Sensitivity Exclusion	Sensitivity Control	Mean Sensitivity	Elasticity Exclusion	Elasticity Control	Mean Elasticity	LTRE % contribution
2012/2013										
Calf survival	0.961	0.689	0.272	0.146	0.228	0.190	0.119	0.132	0.126	25
Subadult survival	0.971	0.804	0.167	0.145	0.195	0.170	0.119	0.132	0.126	14
Adult survival	0.994	0.978	0.016	0.761	0.736	0.750	0.642	0.604	0.334	6
Fecundity	0.559	0.277	0.282	0.511	0.287	0.400	0.119	0.132	0.126	55
Lambda (λ)	1.179	1.191				$\lambda_{Exclusion} - \lambda_{Control}$		0.079		
2013/2014										
Calf survival	0.847	0.498	0.349	0.117	0.137	0.130	0.089	0.068	0.079	18
Subadult survival	0.830	0.372	0.458	0.119	0.183	0.150	0.089	0.068	0.079	28
Adult survival	0.985	0.917	0.068	0.821	0.863	0.840	0.732	0.795	0.764	23
Fecundity	0.461	0.212	0.249	0.473	0.161	0.320	0.089	0.068	0.079	32
Lambda (λ)	1.105	0.996				$\lambda_{Exclusion} - \lambda_{Control}$		0.108		

2014/2015										
Calf survival	0.628	0.166	0.462	0.057	0.038	0.050	0.038	0.008	0.023	15
Subadult survival	0.424	0.124	0.300	0.084	0.051	0.070	0.038	0.008	0.023	14
Adult survival	0.908	0.821	0.087	0.925	0.985	0.960	0.887	0.977	0.932	58
Fecundity	0.260	0.143	0.117	0.275	0.030	0.150	0.038	0.008	0.023	12
Lambda (λ)	0.947	0.827				$\lambda_{Exclusion} - \lambda_{Control}$		0.212		
AVERAGE										
Calf survival	0.812	0.451	0.361	0.107	0.134	0.12	0.083	0.069	0.076	22
Subadult survival	0.742	0.433	0.308	0.116	0.143	0.13	0.083	0.069	0.076	21
Adult survival	0.962	0.905	0.057	0.836	0.861	0.85	0.75	0.794	0.772	25
Fecundity	0.427	0.211	0.216	0.42	0.159	0.29	0.083	0.069	0.076	32
Lambda (λ)	1.069	0.983				$\lambda_{Exclusion} - \lambda_{Control}$		0.086		

Chapter 2 (Tables)

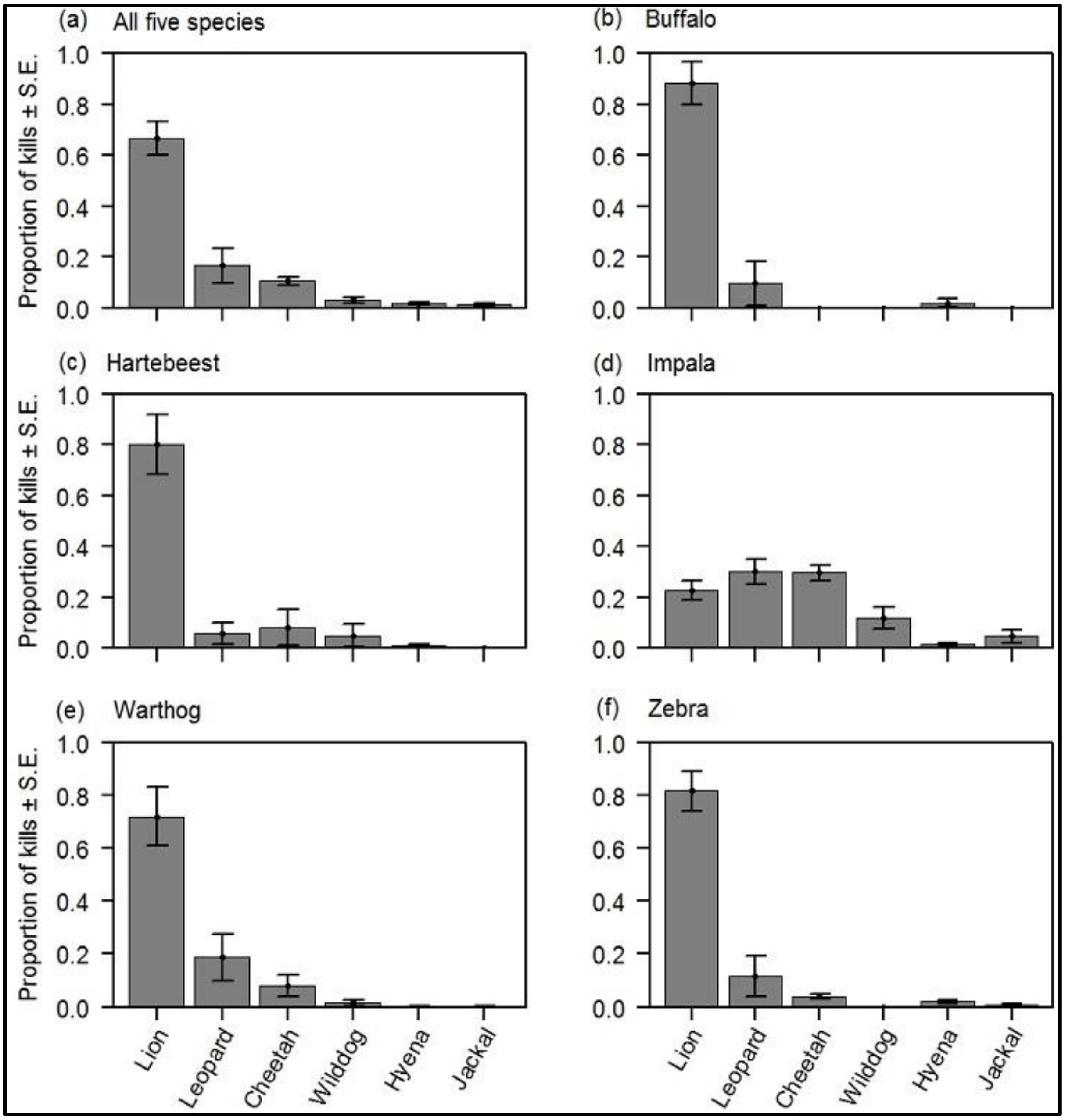
Table S1: Estimates of density and mean effective strip widths from distance sampling of five species of lion prey for six quarterly surveys. Error bars are standard error (SEM). The number of kill sites also are reported for each focal species of lion prey, which account for 93.8% of kills.

	Density (km^2)				
Survey period	buffalo (450kg)	hartebeest (135kg)	impala (50kg)	warthog (60kg)	zebra (250kg)
Survey 1	2.69	0.47	12.16	3.75	12.91
Survey 2	10.26	1.05	9.99	5.23	10.96
Survey 3	4.06	1.08	11.59	7.91	7.25
Survey 4	1.42	2.78	10.13	2.72	9.59
Survey 5	0.38	0.66	11.59	5.01	12.62
Survey 6	9.47	0.43	10.49	2.59	15.89
Mean ± SEM	4.65 ± 1.68	1.08 ± 0.36	10.99 ± 0.37	4.53 ± 0.81	11.55 ± 1.22
Mean ESW (m)	329 ± 34	429 ± 67	257 ± 31	246 ± 30	373 ± 14
Number of kills	35	27	34	37	98
Proportion of kills (%)	14.2	11	13.8	15	39.8

Note: ESW = the effective strip width, i.e. the distance for which as many animals were detected beyond that distance as were detected within that distance (Durant *et al.* 2011).

Chapter 2 (Figures)

Figure S1: Annual proportion of kills of common ungulates attributed to carnivores at Ol Pejeta Conservancy: (a) all ungulates, n = 812 kills; (b) buffalo, n = 76 kills; (c) hartebeest, n = 52 kills; (d) impala, n = 199 kills; (e). warthog, n = 44 kills; and (f) zebra, n = 441 kills. The data are based on kills identified opportunistically by rhino patrol units between 2010 and 2015.



Chapter 3 (Figures)

Figure S1: Effect plot of lion and hartebeest numbers (fitted ± 95% CI); Negative correlation (r= -0.88), showing hartebeest population declining with increasing lion numbers.