

SPOTTED HYAENA SURVIVAL AND DENSITY IN A LION DEPLETED ECOSYSTEM:
THE EFFECTS OF COMPETITION BETWEEN LARGE CARNIVORES
IN AFRICAN SAVANNAHS

by

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DEDICATION

A special feeling of gratitude to my loving mother Mary Flora Nyatsanza M'soka

In memory of my late father Jassiel Lawrence Juma M'soka

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ABSTRACT

Competition is considered an important factor for large carnivore population dynamics, but the manner in which interspecific competition impacts these species are not well understood. This lack of knowledge is due to the ongoing declines of large carnivores, the loss of intact large carnivore guilds, the complexity of competitive relationships and how they can be impacted by ecological and anthropogenic factors. In light of rapid declines of carnivore populations across the globe, understanding how interspecific competition limits large carnivores is an important component for the management and conservation of these species. Using data from 233 individuals in five clans and capture–recapture robust design models we estimated the survival and density of spotted hyaena in 5 clans in the Liuwa Plain, where their main competitor, the African lion was reduced to a single individual. We tested for the effects of settlements, prey density, competition with lions and hyaena clan size on the mean hyaena survival. The average population size during the duration of study was $151.2 \pm 5.9(\text{SE})$ individuals. Population size fluctuated through time with the seasonal fluctuations of the main prey species, the blue wildebeest. Mean annual survival across all age classes was 0.93 (95%CI: 0.39 - 0.99). We found no detectable effects of variation in hyaena clan size, prey density, local variation in utilization by lions, or proximity to people on survival. We also estimated the densities of wildebeest, oribi and zebra, the main prey species for the carnivores in the system using distance sampling methods. We tested for the effects of variables in three classes: environmental (year, season, vegetation, grass height, burn, water presence), predation risk (hyaena density), and anthropogenic (distance to park boundary and settlements). Densities ranged from 6.2 - 60.8 individuals km^{-2} for wildebeest, 1.1-14.5 individuals km^{-2} for oribi, and 1.8-8.1 individuals km^{-2} for zebra. Results reveal resource partitioning among ungulate species and indicate that predation risk and proximity to humans affect ungulate distributions with implications for managing migrations in the Greater Liuwa Ecosystem. They suggest that the maintenance of native prey populations allows coexistence between humans and large carnivores in Liuwa Plain National Park.

CHAPTER ONE

INTRODUCTION TO THESIS

Thesis Overview

The Greater Liuwa Ecosystem (GLE) located in western Zambia is comprised of Liuwa Plain National Park (LPNP) and the Upper West Zambezi Game Management Area (UWZGMA). The LPNP which is the core of the GLE covers 3,660 km² of seasonally flooded grassland with isolated patches of open broad-leaved woodlands. Declared a National Park in 1972, LPNP has been a conservation area since the 1880s, when it was originally declared by the Lozi King, the Litunga. The GLE currently holds one of the largest remaining wildebeest migrations in Africa at approximately 46,000 animals, which move seasonally between the southern portion of LPNP in the rains and the UWZGMA during the dry season (APN, 2013).

During prolonged war in neighbouring Angola, the GLE experienced substantial human induced reductions of wildlife populations, including the near-complete extirpation of lions. The lion population consisted of a single lioness in 2003, with subsequent reintroductions of two males and two females in 2009 and 2011 respectively. As a consequence, hyaenas are the dominant large carnivore in the ecosystem, with a population in excess of 150 hyaenas. In interference competition between lions and hyaenas, lions are behaviourally dominant unless heavily outnumbered, and they frequently kill hyaenas and in a manner that can limit hyaena

numbers (Creel et al., 2001; Kruuk, 1972; Palomares and Caro, 1999; Watts and Holekamp, 2009). Although hyaenas are highly effective hunters (Holekamp et al., 1997; Kruuk, 1972; Mills, 1990), lions also provide them with scavenging opportunities, so that the net effect of lions on spotted hyaena demography includes both costs and benefits, and is in need of further investigation, particularly as conservation and management efforts attempt to address the continuing declines of large carnivores throughout Africa. Perhaps the most significant impediment to disentangling consequences of lion-hyaena competition is that the densities of both species are tightly linked to ungulate densities (Watts and Holekamp, 2008, Périquet et al., 2014), so that few ecosystems provide information on the performance of either species when the other is absent or rare. LPNP provides such an opportunity, and the focal point of this study was to investigate spotted hyaena demography and dynamics in a system in which the effects of lions are currently weak.

In Chapter 2 I look at the density and distribution of wildebeest, oribi and zebra the three most abundant ungulate and prey species in the LPNP and the factors that affect their density and distribution. Using distance sampling methods I examine the effects of 9 variables, distance to park boundary, distance to settlements, water availability, grass height, vegetation type, predation risk (hyaena density), burn, season and year on migratory wildebeest and zebra and resident oribi from 2010 to 2013.

Predators can have strong ‘top-down’ influences on the abundance and distribution of prey through direct predation and risk effects (Creel & Christianson 2008;

Estes et al. 2011). Direct predation can have clear demographic impacts on prey and has historically been the primary means of assessing the effect of predators. Predators also affect ungulates through changes in behaviour, habitat selection, nutrition and ultimately fitness; these effects of predation risk are easily misinterpreted as 'bottom-up' effects (Creel et al. 2005; Creel & Christianson 2008; Barnier et al. 2014).

Consequently, the distribution of ungulates and their behaviour is expected to be sensitive to the local density of predators and to attributes of the environment that affect the likelihood of predation (Brown et al. 1999; Creel et al. 2005; Creel & Christianson 2008; Kauffman et al. 2007; Liley & Creel 2008). Predator avoidance can be an important cause of ungulate migration (Fryxell et al. 1988), migratory and non-migratory species might be expected to show different responses to the distribution of predators (Hebblewhite & Merrill 2007).

Thus in chapter 3, tested the factors affecting the survival and density of spotted hyaena in LPNP, in the near absence of their main competitor; the African lion. We modelled the effects of prey availability, clan size, competition with lions and proximity to human settlements on hyaena survival. We provide estimates of survival across five age classes of hyaena and estimates of population size using robust design models in Mark. We further compute estimates of density and home range and compare these estimates to other African protected areas.

Conflict with people living on the boundaries of protected areas is a major cause of mortality for wildlife, even in protected areas (Balme et al., 2009; Brashares et al,

2001; Woodroffe, 1998), and is known to affect their demography and dynamics.

Human activities affect survival of large carnivores most obviously through direct killing (Becker et al., 2013; Rosenblatt et al., 2014; Watson et al., 2013), but also by reducing habitat quality and prey availability (Ripple et al., 2015; Watson et al., 2014), and by constraining space utilisation and activity patterns (Boydston et al., 2003; Kolowski and Holekamp, 2009; Kolowski et al., 2007; Schuette et al., 2013). Wildlife residing close to human settlements are expected to experience stronger anthropogenic effects than those inhabiting the interior of protected areas. Conversely, in some ecosystems where human settlements occur, ungulates have been known to use areas close to settlements to reduce the risk of predation (Hebblewhite & Merrill, 2007).

The LPNP is unique among African protected areas, in that it has people and settlements legally allowed inside the National park. This unique situation provided us an opportunity to study the effects of proximity to human settlements on survival of hyaenas and its effect on the density of ungulate prey in LPNP. It also allowed us to disentangle the effects of proximity to humans and distance to the park boundary on ungulate density and distribution. For migratory ungulate populations like wildebeest and zebra in LPNP, anthropogenic activities further affect their density and distribution through isolation and degradation of migratory corridors (Berger 2004; Thirgood et al. 2004; Bolger et al. 2008; Hobbs et al. 2008). Therefore, proximity to human settlements is a common theme in both chapters.

In chapter 4, I provide general conclusions from the two main chapters and discuss how my findings compare to other African systems and the way forward for research and management of carnivores and their prey in the GLE.

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CHAPTER TWO

ECOLOGICAL AND ANTHROPOGENIC EFFECTS ON THE DENSITY OF MIGRATORY AND
RESIDENT UNGULATES IN A HUMAN-INHABITED PROTECTED AREAContribution of Authors and Co-Authors

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Abstract

Understanding the influence of environmental conditions and people on ungulate density and distribution is of key importance for conservation. We evaluated the effects of ecological and anthropogenic factors on the density of migratory wildebeest and zebra and resident oribi in Zambia's Liuwa Plain National Park where human settlements were present. We conducted transect surveys from 2010-2013 using distance sampling methods, then developed a set of 38 candidate models to describe results and predict density. Models included the effects of variables in three classes: environmental (year, season, vegetation, grass height, burn, water presence), predation risk (hyaena density), and anthropogenic (distance to park boundary and settlements). Densities ranged from 6.2 - 60.8 individuals km⁻² for wildebeest, 1.1-14.5 individuals km⁻² for oribi, and 1.8-8.1 individuals km⁻² for zebra. The most complex models were strongly supported for all three species. The magnitude and sign of variable effects differed among species, indicating that local densities of wildebeest, oribi and zebra are affected by a complex set of anthropogenic and ecological factors. Results reveal resource partitioning among ungulate species and indicate that predation risk and proximity to humans affect ungulate distributions with implications for managing migrations in the Greater Liuwa Ecosystem.

Keywords: Human-influence, Liuwa Plain, Migration, Predation Risk, Zambia.

Introduction

Ungulates have strong ecological effects on grazing ecosystems (McNaughton, 1976; Frank & Groffman, 1998). Consequently, it is important to understand the mechanisms affecting the density and distribution of ungulates relative to interactions with plant communities (McNaughton, 1976), each other (Arsenault & Owen-Smith, 2011; Macandza, Owen-Smith & Cain, 2012) with predators (Pienaar, 1969; Kruuk, 1972; Schaller, 1972; Creel & Creel, 2002) and with people (Hewison et al., 2001; Bhola et al., 2012; Schuette, Creel & Christianson, 2013). Understanding these associations is particularly important for conservation and management of ungulate migrations, which are typically driven by combinations of resource availability and avoidance of predation (Fryxell, Greever & Sinclair, 1988) but are rapidly being modified or lost due to human activities (Bolger et al., 2008; Berger, 2004). Because seasonal movements of ungulates can generate strong spatio-temporal variation in grazing intensity and prey availability that dominate community structure and ecosystem function, the conservation of migratory populations is a high priority for the ecosystems they inhabit (Sinclair et al., 2007).

Environmental Effects

Several environmental factors can influence ungulate density and distribution, including vegetation type, phenology, rainfall, fire and water availability (McNaughton, 1985; Fryxell, Wilmschurst & Sinclair, 2004; Holdo, Holt & Fryxell, 2009). Herbivore

foraging strategies strongly influence their utilisation of and impact on the landscape, with dietary quality and spatial distribution of foraging patches being important considerations (Owen-Smith & Novellie, 1982). The nutrient content of grasses generally decreases as grass height or biomass increases, and energy uptake is optimized in areas of intermediate grass height or biomass (McNaughton, 1988; Fryxell et al., 2004). Beyond this basic trade-off between quantity and quality, the nutritional quality, type and phenology of vegetation is also affected by fire, rainfall and flooding in seasonal environments; thus these factors can also affect ungulate movements and habitat selection. Ungulate species also vary in their dependence on water, so water availability can be an important variable influencing distributions.

Predation Risk Effects

Predators can have strong 'top-down' influences on prey through direct predation and risk effects (Creel & Christianson, 2008; Estes et al., 2011). Direct predation can have clear demographic impacts on prey and has historically been the primary means of assessing the effect of predators. Predators also affect ungulates through changes in behaviour, habitat selection, nutrition and ultimately fitness; these effects of predation risk are easily misinterpreted as 'bottom-up' effects (Creel et al., 2005; Barnier et al., 2014). Consequently, the distribution of ungulates and their behaviour is expected to be sensitive to local predator density and environmental conditions that affect the likelihood of predation (Brown, Laundre & Gurung, 1999; Creel et al., 2005; Kauffman et al., 2007; Liley & Creel, 2008). Because predator

avoidance can be an important cause of ungulate migration (Fryxell et al., 1988), migratory and non-migratory species are expected to show different responses to the distribution of predators (Hebblewhite & Merrill, 2007).

Anthropogenic Effects

Ungulate populations can be negatively affected by anthropogenic factors such as human predation through poaching (Hilborn et al., 2006). Humans can also affect ungulate distributions through disturbance, habitat loss, isolation and degradation of migratory corridors (Berger, 2004; Thirgood et al., 2004; Bolger et al., 2008; Hobbs et al., 2008; Watson et al., 2014; Owen-Smith & Ogutu, 2012). Negative anthropogenic effects on abundance and distribution in ungulate-carnivore systems can be strong, particularly for migratory systems and at reserve peripheries (Kiffner et al., 2013). Conversely, in some ecosystems where human settlements occur, ungulates may use areas close to settlements to reduce the risk of predation (Hebblewhite & Merrill, 2007). Because settlements are typically prohibited within national parks, western Zambia's Liuwa Plain National Park (LPNP) is unique because settlements are permitted, allowing us to disentangle the effects of proximity to humans and distance to the park boundary.

We used distance sampling models that control for variation in detection to evaluate the effects of environmental, anthropogenic and top-down effects on the densities and distributions of the three most abundant ungulates in LPNP: migratory wildebeest *Connechaetes taurinus* Burchell and zebra *Equus quagga* Boddaert, and non-migratory oribi *Ourebia ourebi* Zimmermann. Inferences from these models identify the

conditions and locations expected to best support the conservation of this ungulate community.

Materials and Methods

Study Area

The Greater Liuwa Ecosystem (GLE) located in western Zambia is comprised of LPNP and the Upper West Zambezi Game Management Area (UWZGMA, Fig. 1), which is part of the proposed Liuwa-Mussuma Transfrontier Conservation Area with Angola. LPNP covers 3,660 km² of seasonally flooded grassland with isolated patches of open broad-leaved woodlands. Seasons include wet (Nov-Apr) and dry (May-Oct) with extensive rains and flooding during the wet.

Declared a National Park in 1972, LPNP has been a conservation area since the 1880s, when it was originally declared by the Lozi King (Litunga) and used as a royal hunting ground. Following park designation, settlements were still permitted and the human population numbered approximately 10,000 during the study (APN, 2009). The GLE currently holds one of the largest remaining wildebeest migrations in Africa at approximately 46,000 animals, which move seasonally between the southern portion of LPNP in the wet season and the UWZGMA and northern LPNP during the dry season (APN, 2013). It also contains an unknown but large number of oribi and approximately 9,000 migratory zebra whose movements are poorly understood (APN, 2013).

Due to poaching and conflict, the LPNP carnivore guild is unusual in its relative lack of lions (*Panthera leo* Linnaeus) and dominance of spotted hyaenas (*Crocuta crocuta* Erxleben), which are the most abundant apex predators in Liuwa. Approximately 233 individuals in five clans occurred in the study area during this study. In contrast, the lion population consisted of a single lioness in 2003, with subsequent reintroductions of two males and two females in 2009 and 2011 respectively. The park held three to five lions in one pride during this study. Small, recovering populations of wild dogs (*Lycaon pictus* Temminck, two packs of 15-22 dogs total) and cheetah (*Acinonyx jubatus* Schreber, 17 known individuals) were also present. Concurrent diet studies (517 kills) of all carnivore species indicated wildebeest were the primary prey for all carnivores, with oribi comprising an additional important prey species for cheetah and wild dog, but not lion or hyaena. Zebra were very rarely killed and only by lion and hyaena.

Survey Design

We counted ungulates on a 1,200 km² study area where we also monitored resident carnivores with radio-telemetry. The area included an array of habitats and human influences representative of the southern portion of LPNP (Figs. 1, S1). We systematically divided this area into eight 8x8 km quadrats, within which two east-west transect lines were set at 2 and 6 km on the north-south axis of each quadrat (Fig. 1). Fewster et al., (2009) recommended systematic, rather than random sampling when spatial trends in density are likely, which was expected of migratory wildebeest and

zebra. We oriented transects in an east-west direction, perpendicular to the migratory movements of wildebeest and zebra, to sample representatively during migratory movements. We reduced the likelihood of double-counting by surveying in the direction opposite to migratory movements during May-Jun (south-easterly) and Oct-Nov (north-westerly).

Transects were surveyed by vehicle at 15-20 km/h with a driver who served as navigator and two observers positioned to survey their respective transect side. A total of 128km were driven in each survey, for a total of 1,280km during ten complete surveys from 2010 to 2013. Transects were surveyed five times in 2010 for all three species, once in 2011 for oribi and zebra (wildebeest were excluded in 2011 as herds were out of the study area at that time), once in 2012 for all three species and three times in 2013 for all three species. We used distance sampling to record the size of each herd and its perpendicular distance from the transect line upon detection (Buckland et al., 2001). Data were analysed with the hierarchical model of Royle et al. (2004), using the *distsamp* function in the **unmarked** package of R (Chandler, 2015) of R. The *distsamp* function allows only transect-level estimation of covariate effects on density and detection probability (i.e., it does not allow estimation of effects at the level of single herds), so we partitioned transects into 41 segments based on vegetation type (open grassland or woodland). Segments varied in length from 400-4,000m, dependent on the spatial configuration of changes in vegetation type (Fig. 2).

Covariate Selection and Estimation

From the literature and our knowledge of the study area we identified nine covariates hypothesized to affect ungulate densities, which we categorized as anthropogenic, environmental, or predation. Some variables could perhaps span multiple categories, but this categorization was primarily organizational and did not alter the estimated effect of a given variable within a model.

Anthropogenic Covariates

Two variables quantified anthropogenic effects: distance to the nearest village (*vlg*) and distance to the park boundary (*bndry*). We used ArcGIS 10.2.2 (ESRI, Redlands, California, USA) to map locations of all villages and park boundaries.

Environmental Covariates

We recorded five variables to quantify environmental effects: 1) Vegetation type (*hab*), 2) Water availability (*wtr*), 3) Grass height (*ht*), 4) Presence of recent burning (*burn*) and 5) Season (*seas*). We classified vegetation types as grassland or woodland, estimated water by the presence of standing water within 1km of a transect line, categorized grass height by the predominance of short (<10cm), intermediate (10cm-1m), or tall (>1m) grasses, and visually recorded burned areas during transects. We categorized seasons as dry or wet.

Predation Covariates

We used hyaena density (*hy*) as a predictor of predation intensity because hyaenas greatly outnumbered all other large carnivores. We utilised call-in surveys (Mills, Juritz & Zucchini, 2001), conducted throughout the study area in 2010, 2011 and 2012 to estimate density. Because we expected some sampling variance in these estimates, we categorized density as low, medium or high based on the number of hyaenas that responded to call-in counts.

Modelling Density

We developed an *a priori* set of 38 models that spanned a range of complexity (Table S1). At the simplest, we tested univariate models of the effect of each predictor on density, and at the most complex, we tested the additive effects of all nine predictors. Models of intermediate complexity focused on testing effects we hypothesized might be particularly strong in this system (e.g., hyaena predation risk effects, effects of proximity to people). For each of the models, we considered two functional forms for the relationship between detection probability (p) and distance from the transect, using the halfnormal, $\hat{p}(x) = \frac{\sqrt{2}}{\sigma\sqrt{\pi}} e^{(-\frac{x^2}{2\sigma^2})}$, and hazard $\hat{p}(x) = 1 - e^{-(\frac{x}{\sigma})^{-\beta}}$ functions (Buckland et al., 2001). From preliminary analyses, we identified a maximum distance for observations of each species that depended on detectability and truncated the data at that threshold (300m for oribi, 500m for wildebeest and 1000m for zebra). Within these limits, detection was well-explained by distance alone as

expected in the open landscape of Liuwa (Fig. S2), so we did not include the effects of other covariates on p in the model set. For each species, we estimated goodness of fit for the best-supported model using the ‘brute-force’ method of Zuur et al. (2009) to estimate pseudo- R^2 as the reduction in deviance relative to the null model.

The *distsamp* function only estimates herd density, not individuals. Because herd size varied across the levels of our predictors, we used stratum-specific mean herd sizes to convert the density of herds to the density of individuals. For the continuous predictors (*vlg* and *bndry*), we converted to individual density using a single mean herd size for each species. For all predictors, we used parametric bootstrapping to propagate variance in herd size to variance in individual density with 1000 replicates, drawing from Poisson distributions of herd size with the appropriate mean. We report all mean values with standard error.

Results

Wildebeest densities ranging from 6.2-60.8 individuals km^{-2} across the range of conditions in the study area (Fig. 2). Densities of oribi and zebra were lower, ranging from 1.1-14.5 individuals/km and 1.8-8.1 individuals/km respectively (Figs. 3 & 4). Overall, wildebeest, oribi and zebra herds averaged 11.4 ± 0.98 , 2.3 ± 0.04 , and 13.9 ± 0.85 individuals respectively.

For all three species, local densities were strongly affected by combinations of ecological and anthropogenic variables; thus complex models of density were best-

supported by the data (Table 1). The full model was among the best-supported models for all three species (with ΔAIC of 0-1.79) and all of the models with $\Delta AIC \leq 2$ included all of the predictors or all but one. No simple models received strong support for any of the three species.

Environmental covariate effects differed across the three species (Figs. 2, 3 & 4, Table S2). Wildebeest and zebra densities increased during the wet season, while oribi density remained relatively constant. Wildebeest wet season density was 60.8 ± 2.34 individuals/km, and mean herd size 13.5 ± 1.38 individuals, compared to dry season density of 11.3 ± 0.67 individuals/km and mean herd size of 7.7 ± 1.17 individuals (Fig. 4). Oribi and zebra wet season densities were 2.4 ± 0.09 and 8.1 ± 0.59 individuals/km with mean herd sizes of 2.2 ± 0.07 and 14.4 ± 1.19 individuals respectively. The dry season densities for the two species were 2.2 ± 0.08 and 2.8 ± 0.31 individuals/km and herd sizes of 2.3 ± 0.05 and 13.3 ± 1.21 individuals respectively (Figs. 3 & 4). Wildebeest and oribi densities were higher in grassland versus woodland and highest in tall grass and short grass while zebra density was highest in woodland and short and tall grass. Wildebeest densities were not strongly related to water availability while oribi and zebra densities decreased with distance to water. Burning had no detectable influence on wildebeest and zebra densities, but positively influenced oribi density. Wildebeest densities decreased over time, zebra densities fluctuated, and oribi remained relatively constant.

Wildebeest and oribi densities were highest in areas of low and high hyaena density while zebra density declined with increasing hyaena density. The densities of all three herbivores varied in response to anthropogenic effects. Wildebeest density decreased with distance to the park boundary and distance to the nearest village (Fig. 2). In contrast, oribi and zebra densities increased with increasing distances to villages (Figs. 3 & 4), but park boundary distance had little effect on densities of either species.

Discussion

Our study provides the first test of factors affecting the distribution and abundance of the three dominant ungulate species in the GLE. Complex models incorporating environmental, predation and anthropogenic variables best explained densities of all three species, but the magnitude and sign of these effects varied among species. Broadly, these results suggest that focal points for conservation and management differ by species and must consider the entire suite of ecological and anthropogenic factors.

Environmental Influences

Similar to other ungulate communities in Africa, ungulate densities were influenced by an array of environmental variables reflecting life history strategies. Wildebeest and zebra densities fluctuated, sometimes considerably, across years and were higher during the wet season. Annual fluctuations for these species probably represented changes in migration timing relative to our sampling periods rather than

overall changes in population size because aerial surveys indicated growing populations of both species during the study (APN, 2011, 2013), and increased densities during the wet season reflected the migratory patterns of wildebeest and zebra grouping south of LPNP during the rains. The comparatively stable oribi density across seasons and years likely reflected the sedentary and territorial nature of the species. Zebra and oribi were strongly tied to the presence of water and are generally considered to require water. Wildebeest were not strongly tied to the presence of water on transects but are considered to be water dependent, perhaps indicating scale was an important influence on our analysis of water dependence. The differences in grass height selection between the large grazers suggests niche partitioning or grazing succession similar to that observed in Tarangire National Park (Voeten & Prins, 1999) and Serengeti National Park (Bell, 1971; Sinclair, 1985). All species, particularly wildebeest, selected new vegetation growth following fires; these fires typically occurred throughout the dry season when wildebeest and zebra had mostly migrated out of the study area, and their return in the wet season corresponded with a reduction in fires. In contrast, resident oribi remained on their territories year-round, selecting edges between grass height and recently burned areas for foraging (Brashares & Arcese, 2002). Such dynamics suggest that fire represents an important factor that influences the movements of all three species.

Predation Influences

Wildebeest and oribi density were highest in areas of low and high hyaena density, while zebra density was highest in areas of low hyaena density. While seasonal

migration into lower density hyaena areas during the dry season may reduce predation risk for wildebeest, the relatively high densities of wildebeest in areas heavily used by hyaenas indicated wildebeest may experience a trade-off between meeting nutritional demands and avoiding predation. Similarly, the relatively high densities of zebra in woodland habitats may reflect avoidance of hyaena predation risk (Sinclair & Norton-Griffiths, 1982) given hyaena are coursing predators hunting primarily in open grasslands in LPNP. In contrast ambush predators such as lions prefer areas of higher cover (Grant et al., 2005), so these effects may change with lion recovery. Oribi did not avoid areas of high hyaena density, probably because they were not commonly preyed upon by hyaena; however their selection of heterogeneous grass heights perhaps also reflected their need to better detect cheetah and wild dog (Mduma & Sinclair, 1994; Klop, Goethem & de Long, 2007).

Anthropogenic Influences

Considering the growing literature on the negative impacts of humans on protected areas, insights from the GLE are unique, given that local herbivores utilise an area settled by humans for more than a century. Understanding factors that affect density of these ungulate species in this human-inhabited system is thus important in developing conservation strategies. Water often confounds evaluations of the impact of villages on herbivores because human settlements are typically situated near water (Ogutu et al., 2010), but in Liuwa the broad distribution of seasonal pans allowed us to account for this. While oribi and zebra appeared to avoid settlements, wildebeest

densities were higher than expected close to villages and decreased with park boundary distance. These contrasting results suggest differences in sensitivity to risk and disturbance, as well as differential patterns of migration for wildebeest and zebra, with wildebeest migrating across park boundaries in the northwest and zebra migrating in a more north-easterly direction in the park. Given that migrations traverse protected area boundaries for many herbivores, Owen-Smith & Ogotu (2012) recommended increasing protected area boundaries to buffer the effects of climate change and protect migratory routes and ranges. Such actions are critical for the GLE, given the influence of seasonal flooding and rainfall, which can be severely impacted by climate change.

Broadly, our results show that densities of wildebeest, oribi and zebra, are affected by a complex set of ecological factors, including effects of humans and predators. The influences of environmental variables were all consistent with results from studies in other ecosystems and reveal a degree of resource partitioning among species. The influence of hyaena density suggests that predation risk can affect space use, and for some species high predation risk areas cannot be avoided while meeting nutritional needs. Anthropogenic effects have potentially broad impacts on species and their migrations, and protection of migratory routes and ranges outside LPNP should be considered highest priority.

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Table 2. 1 Model selection results for wildebeest, oribi and zebra density in Liuwa Plain National Park, Zambia. Each model included a detection function used to estimate detection probability and predictor variables to explain density. Predictors included yr (2010 – 2013), hab (open grassland, woodland), ht (grass height short, intermediate, high), burn (recently burned or not), wtr (standing water present or absent), seas (wet or dry season), hy (hyaena density low, medium or high), vlg (distance to nearest village), bndry (distance to park boundary). Models were evaluated using AICc scores, and those with little empirical support ($w_i < 0.01$) are not shown.

	Wildebeest				Oribi				Zebra			
Model (detection function ¹ , density predictors)	Rank	K	Δ AICc	w_i	Rank	K	Δ AICc	w_i	Rank	K	Δ AICc	w_i
H _z ~yr+hab+ht+burn+wtr+seas+hy+vlg+bndry	1	15	0.0	1.000	2	16	1.8	0.230	2	16	2.9	0.19
H _n ~yr+hab+ht+burn+wtr+seas+hy+vlg+bndry	2	14	11.7	0.003	6	15	15.1	<0.001	1	15	0.0	0.79
H _z ~yr+hab+ht+seas+hy+vlg	3	12	47.8	<0.001					9	13	14.7	0.00
H _n ~yr+hab+ht+seas+hy+vlg	4	11	59.6	<0.001					4	12	11.8	0.00
H _z ~yr+hab+seas+hy+vlg	5	10	85.4	<0.001					5	11	11.9	0.00
H _z ~yr+ht+seas+hy+vlg	6	11	95.0	<0.001								
H _n ~yr+hab+seas+hy+vlg	7	9	97.1	<0.001					3	10	9.1	0.01
H _n ~yr+ht+seas+hy+vlg	8	10	106.8	<0.001					8	11	14.0	0.00
H _z ~yr+seas+hy+vlg	9	9	123.0	<0.001					10	10	14.9	0.00
H _z ~yr+hab+ht+seas+hy+bndry	10	12	126.9	<0.001								
H _z ~yr+hab+ht+burn+wtr+hy+vlg+bndry					1	15	0.0	0.570				
H _z ~yr+hab+ht+burn+wtr+hy+vlg					3	14	3.1	0.120				
H _z ~yr+hab+burn+wtr+hy+vlg					4	12	4.1	0.070				
H _n ~yr+hab+ht+burn+wtr+hy+vlg+bndry					5	14	13.3	0.001				
H _n ~yr+hab+ht+burn+wtr+hy+vlg					7	13	16.4	<0.001				
H _n ~yr+hab+burn+wtr+hy+vlg					8	11	17.4	<0.001				
H _z ~yr+hab+wtr+hy+vlg					9	11	23.9	<0.001				
H _z ~yr+hab+burn+wtr+hy+bndry					10	12	25.6	<0.001				
H _n ~yr+seas+hy+vlg									6	9	12.0	0.00
H _n ~yr+hab+seas+hy+bndry									7	10	12.3	0.00

¹: H_z = Hazard function, $\hat{p}(x) = 1 - e^{-(\frac{x}{\sigma})^{-\beta}}$ H_n = halfnormal function, $\hat{p}(x) = \frac{\sqrt{2}}{\sigma\sqrt{\pi}} e^{(-\frac{x^2}{2\sigma^2})}$

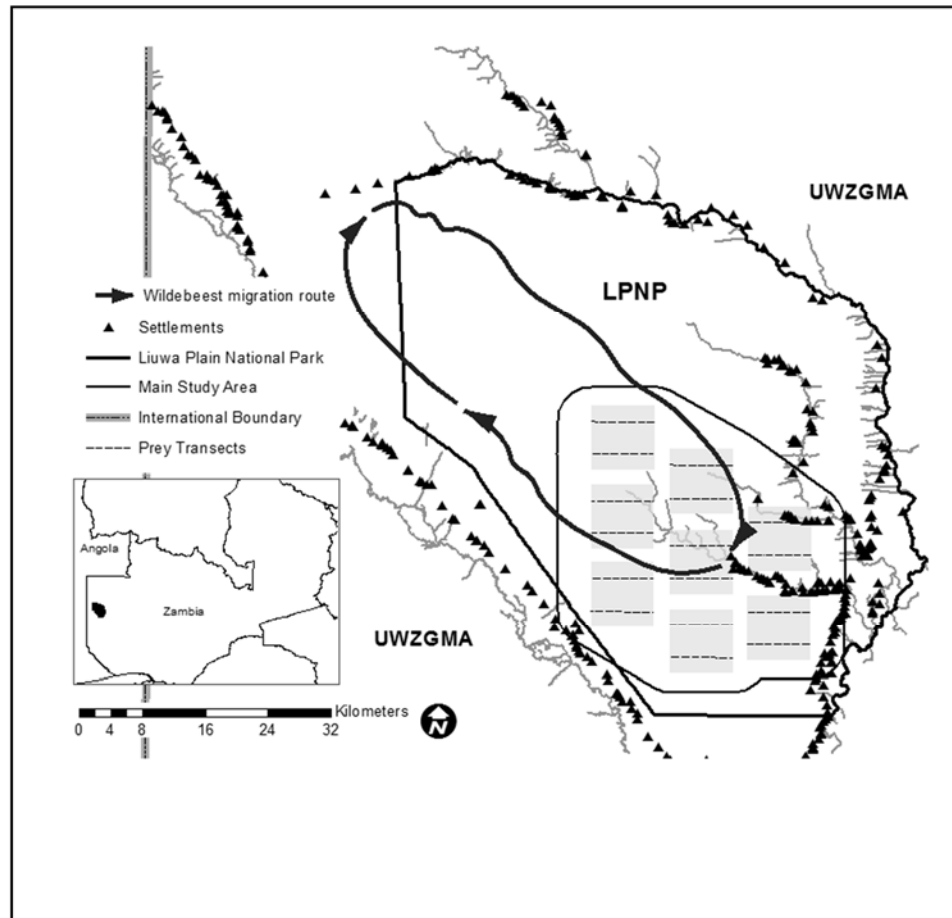


Figure 2. 1 Greater Liuwa Ecosystem, Zambia showing the study area, transect surveys, human settlements, and the general wildebeest migration route.

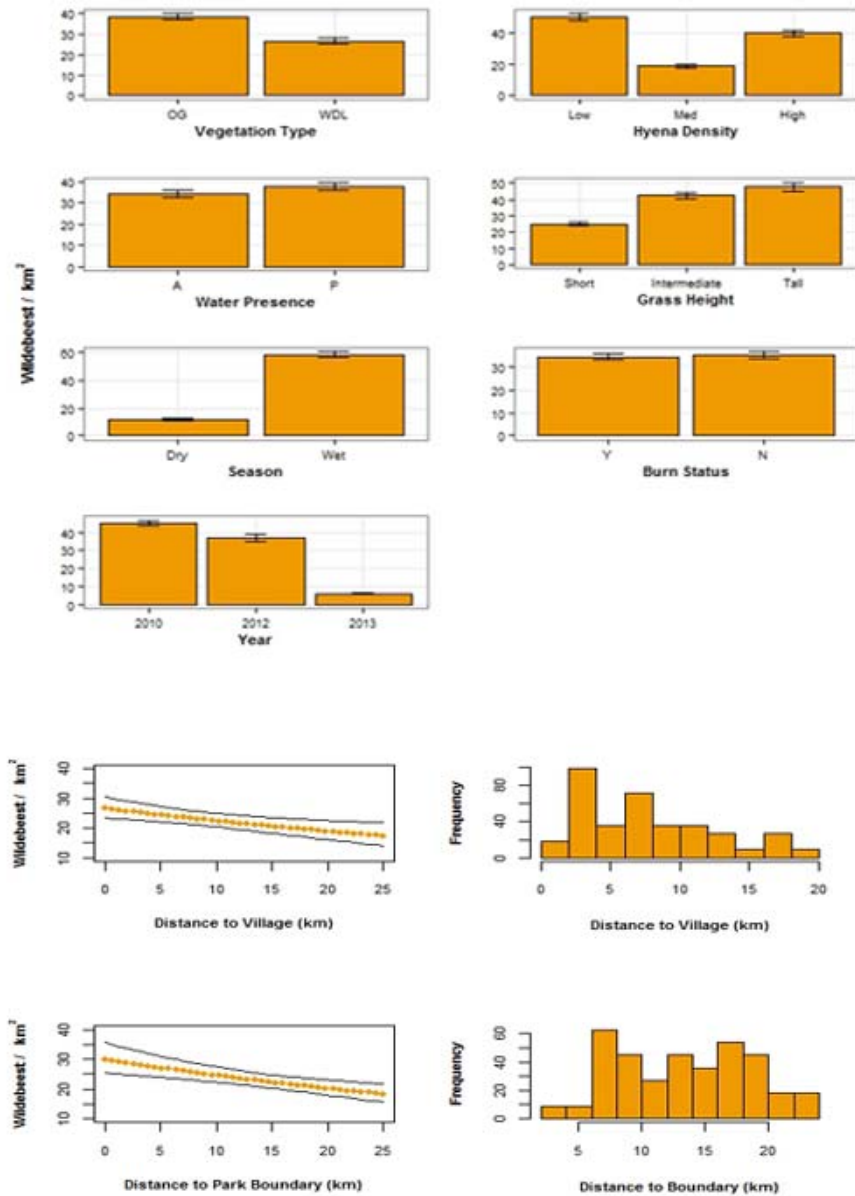


Figure 2. 2 Ecological and anthropogenic effects on wildebeest density in LPNP. Effects predicted from a best supported model of count data from transect surveys. For categorical predictors, bars show least-squares means (holding all other effects at their mean) with standard errors. For the continuous predictors 'distance to nearest village' and 'distance to the park boundary' lines show predicted relationships (holding all other effects at their mean) and 95% confidence limits, with the frequency distribution of observed distances to the right.

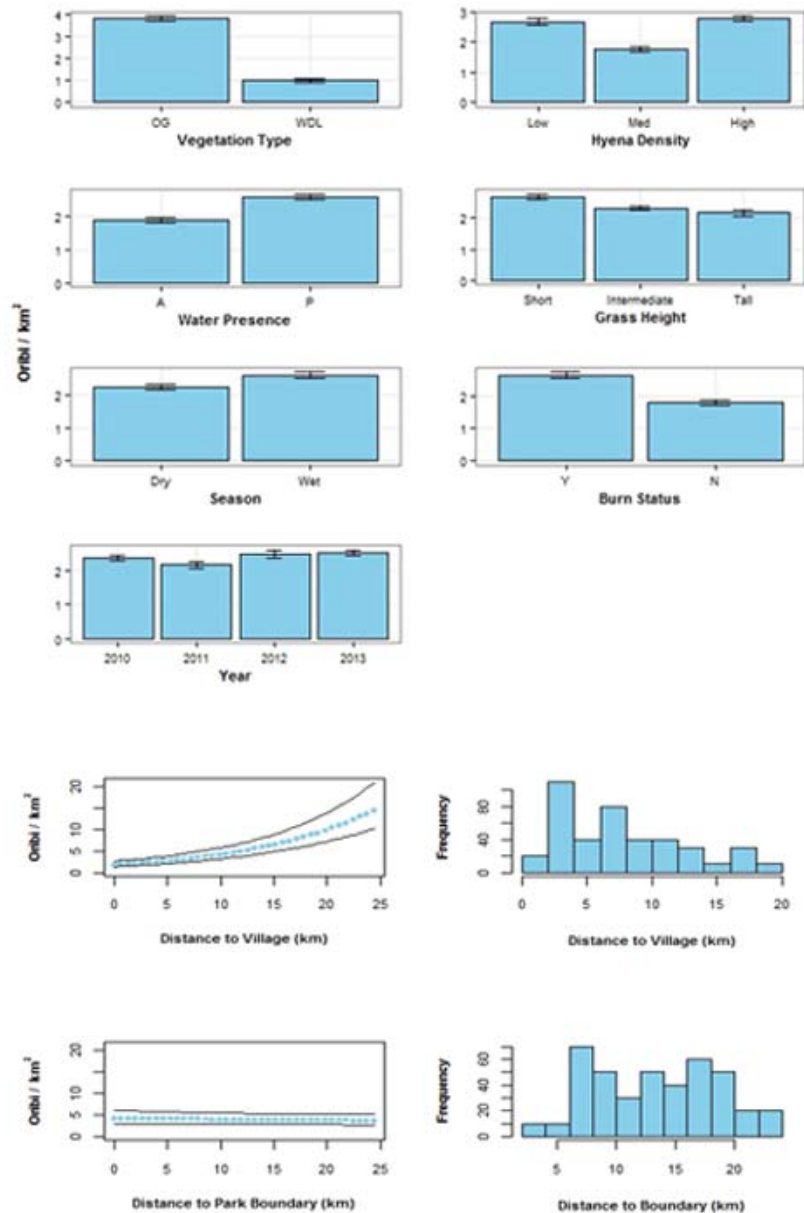


Figure 2. 3 Ecological and anthropogenic effects on oribi in LPNP. Effects predicted from the full model of count data from transect surveys, which was within 2 AIC scores of the best supported model. For categorical predictors, bars show least-squares means (holding all other effects at their mean) with standard errors. For the continuous predictors 'distance to nearest village' and 'distance to the park boundary' lines show predicted relationships (holding all other effects at their mean) and 95% confidence limits, with the frequency distribution of observed distances to the right.

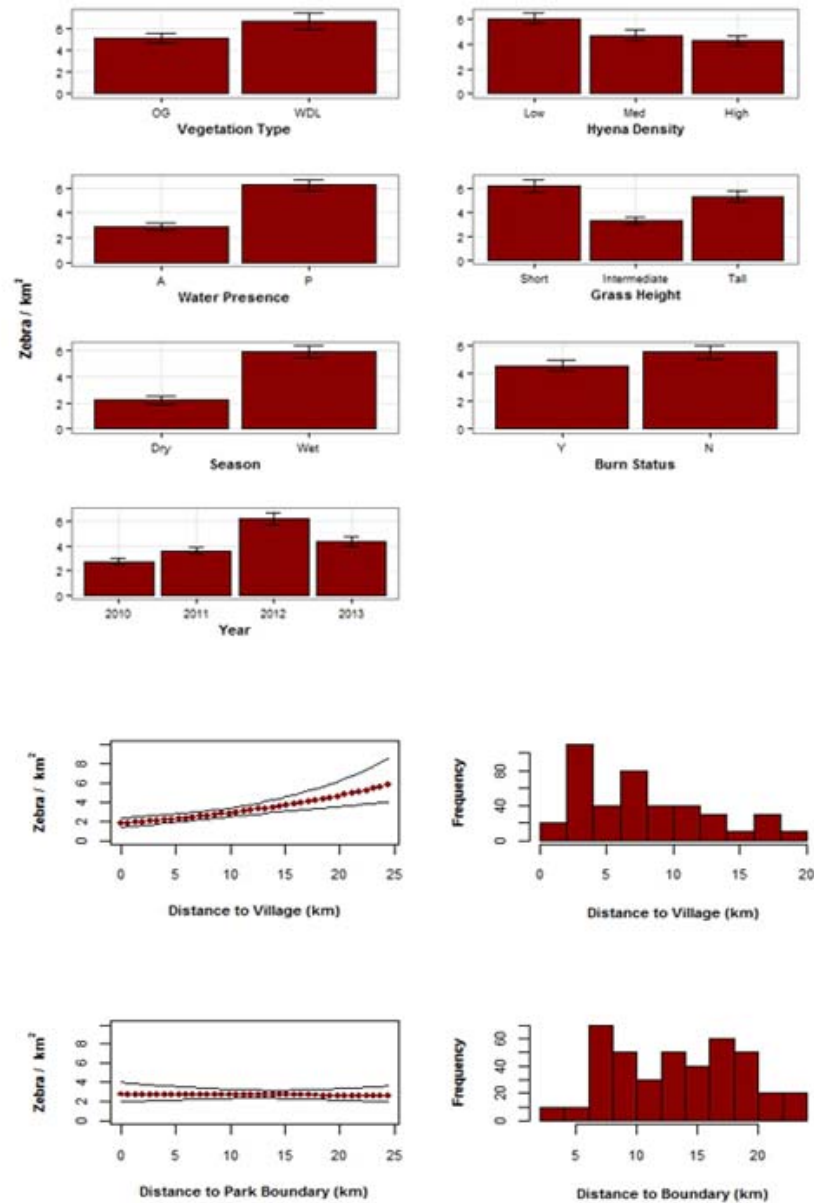


Figure 2. 4 Ecological and anthropogenic effects on zebra density in LPNP. Effects predicted from a best-supported model of count data from transect surveys. For categorical predictors, bars show least-squares means (holding all other effects at their mean) with standard errors. For the continuous predictors 'distance to nearest village' and 'distance to the park boundary' lines show predicted relationships (holding all other effects at their mean) and 95% confidence limits, with the frequency distribution of observed distances to the right.

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CHAPTER THREE

SPOTTED HYAENA SURVIVAL AND DENSITY IN A LION DEPLETED ECOSYSTEM: THE EFFECTS OF COMPETITION BETWEEN LARGE CARNIVORES IN AFRICAN SAVANNAHS

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Abstract

Interspecific competition between large carnivores is not well understood due to the complexity of predator guild dynamics and the array of biological, environmental and human factors that affect each competing species. Therefore, much can be learned when a dominant species has been lost from an ecosystem's large carnivore guild. In this study we estimate the survival of spotted hyaena from Zambia's Liuwa Plain National Park, where the spotted hyaena's main competitor, the African lion, was reduced to a single individual. Using data from 233 individuals in five clans and capture-recapture robust design models we estimate population size, density and trend for the Liuwa Plain spotted hyaena population from 2010 to 2013, estimate age- and sex-specific annual survival rates and test for the effect of settlements, prey density, competition with lions and hyaena clan size on the mean hyaena survival. The average population size during the duration of study was $151.2 \pm 5.9(\text{SE})$ individuals. Population size fluctuated through time with the seasonal fluctuations of the main prey species, the blue wildebeest, in our study area. Mean annual survival across all age classes was 0.93 (95%CI: 0.39 - 0.99), with male individuals surviving at a slightly higher rate than female individuals. We found no detectable effects of variation in hyaena clan size, prey density, local variation in utilisation by lions, or proximity to people (and their livestock) on survival. These results suggest that the maintenance of native prey populations allows coexistence between humans and large carnivores in Africa.

Keywords: African lion; Anthropogenic effects; Intraguild competition; Survival; Robust design; Spotted hyaena.

Introduction

Large carnivores are extinction prone because they typically live at low density, require large areas with sufficient ecological integrity to provide adequate prey and are susceptible to conflict with encroaching human populations. Despite their low densities, top carnivores often have strong direct and indirect influences on ecosystem structure and function and provide economic and social benefits for the systems in which they reside (Estes et al., 2011; Terborgh, 2010). Competition has long been considered an important factor for large carnivore population dynamics, but the manner in which interspecific competition impacts these species are not well understood. This lack of knowledge is due to the ongoing declines of large carnivores, the loss of intact large carnivore guilds, the complexity of competitive relationships and how they can be impacted by biological, environmental and anthropogenic factors (Finke and Denno, 2005; Polis and Holt, 1992). In light of rapid declines of carnivore populations across the globe, understanding how interspecific competition limits large carnivores is an important component for the management and conservation of these species (Palomares and Caro, 1999).

The spotted hyaena (*Crocuta crocuta*; hereafter hyaena) is widely regarded as one of Africa's most successful large carnivore, inhabiting diverse habitats, persisting in areas facing anthropogenic pressures and attaining high densities in areas with high

prey availability (Kruuk, 1972; Mills, 1990; Cardillo et al., 2004, Périquet et al., 2014; Bohm and Honer, 2015). The hyaena's importance to conservation efforts cannot be understated as it is often the last member of the African large carnivore guild to remain in an ecosystem after other species have been eliminated. Within the diverse large predator guilds that typify savannah ecosystems in sub-Saharan Africa, the dominant carnivore species, primarily the hyaena and African lion (*Panthera leo*), compete with each other and have strong limiting effects on the populations of subordinate competitors (e.g., African wild dogs, *Lycaon pictus*, and cheetahs, *Acinonyx jubatus*) (Creel and Creel 1996, 2002; Durant, 1998; Swanson et al., 2014).

An array of factors are likely to affect the strength of competition between lions and hyaenas, including the density and composition of the prey base, the size of lion prides and hyaena clans, and anthropogenic factors that can affect the distribution, dynamics and behaviour of both species (Kruuk, 1972; Palomares and Caro, 1999; Kolowski and Holekamp, 2009; Schuette et al., 2013). However, disentangling the effects of interspecific competition between lion and hyaena has been difficult in ecosystems where both species occur (Watts and Holekamp, 2008). The densities of both species correlate positively with the availability of ungulate prey (Laurenson, 1995; Périquet et al., 2014) and they compete intensely due to overlap in diet and habitat selection (Creel and Creel, 1996; Périquet et al., 2014; Purchase, 2004). Lions are behaviourally dominant unless heavily outnumbered, and they frequently kill hyaenas and in a manner that can limit hyaena numbers (Creel et al., 2001; Kruuk, 1972; Palomares and Caro,

1999; Watts and Holekamp, 2009). Although hyaenas are highly effective hunters (Holekamp et al., 1997; Kruuk, 1972; Mills, 1990), lions also provide them with scavenging opportunities, so the net effect of lions on spotted hyaena demography includes both costs and benefits.

It is generally expected that intensity of exploitative and interference competition should decrease as prey availability increases, but this expectation can be altered for large carnivores, where kleptoparasitism can greatly reduce the costs of obtaining carcasses even when prey are abundant (Creel and Creel, 1996). Although hyaenas have impressive adaptations to low prey availability (for example, hyaenas in the Ngorongoro Crater can move hundreds of kilometres to follow migratory prey: Höner et al., 2005), the local density and distribution of prey is expected to affect the survival of young, which cannot make long distance movements (Benoit-Bird et al., 2013). Prey size also affects competitive interactions between hyaenas and lions: ecosystems rich in large prey (> 200kg) favour lions, whereas ecosystems with medium sized prey (100 – 200kg) favour hyaenas (Hayward, 2006; Owen-Smith and Mills, 2008).

In hyaenas and other large carnivores, group size has a strong effect on the outcome of interference competition (Creel and Creel, 1996, 2002; Fanshawe and FitzGibbon, 1993; Palomares and Caro, 1999), and thus on survival (Holekamp et al., 2012; Watts & Holekamp, 2009). Large hyaena clans are more effective in food acquisition than smaller clans (Kruuk, 1972; Schaller, 1972), and clan size has a positive effect on cub survival (Watts and Holekamp, 2009). Nonetheless, kills made by bigger

clans are attended by more individuals, which reduces the provisioning of food by lower ranking females to their cubs (Frank, 1986; Kolowski et al., 2007), so the benefits of large clan size are not apportioned equally to all individuals, as is true for other social carnivores (e.g., African wild dogs: Creel and Creel, 2015).

Conflict with people living on the boundaries of protected areas is a major cause of mortality of large carnivores, even in protected areas (Balme et al., 2009; Woodroffe, 1998), and is known to affect their demography and dynamics. Human activities affect survival of large carnivores most obviously through direct killing (Becker et al., 2013; Rosenblatt et al., 2014; Watson et al., 2013), but also by reducing habitat quality and prey availability (Ripple et al., 2015; Watson et al., 2014), and by constraining space utilisation and activity patterns (Boydston et al., 2003; Kolowski and Holekamp, 2009; Kolowski et al., 2007; Schuette et al., 2013). Carnivores residing close to human settlements are expected to experience stronger anthropogenic effects than those inhabiting the interior of protected areas. For example, hyaenas close to human activity in the Maasai Mara National Reserve spent far less time attending to cubs at the den, when compared to hyaena clans further from human activity in the same ecosystem (Kolowski et al., 2007).

As densities for both species are tightly linked to ungulate densities, few ecosystems provide information on the performance of either species when the other is absent or rare. During prolonged war in neighbouring Angola, western Zambia's Greater Liuwa Ecosystem (GLE), centred on Liuwa Plain National Park (LPNP) experienced

substantial human induced reductions of wildlife populations, including the near-complete extirpation of lions. As a consequence, hyaenas are the dominant large carnivore in the ecosystem, which now holds 5 lions and >150 hyaenas (see Results). Here, we used intensive photographic monitoring and robust design capture-recapture models to assess the population density and survival of spotted hyaenas in Liuwa Plains National Park, where their main competitor the lion is found at very low densities. Juxtaposed with prior studies in ecosystems with typical lion densities, our results help to understand interactions between the two dominant predators in African savannah ecosystems. More broadly, this analysis provides the first methodologically and statistically rigorous estimates of hyaena density in this ecosystem, and to evaluate the effects of a broad range of ecological and anthropogenic effects on survival.

Materials and Methods

Study Area

The Greater Liuwa Ecosystem (GLE) is located in western Zambia and is comprised of Liuwa Plains National Park (LPNP) and the Upper West Zambezi Game Management Area (UWZGMA). The LPNP covers 3660 km² of seasonally flooded grassland with isolated patches of open broad-leafed woodlands. The GLE experiences extensive rains and flooding during the wet season (Nov–Apr) and isolated seasonal and permanent water sources remain during the dry season (May – Oct).

Declared a National Park in 1972, LPNP has been a conservation area since the 1880s, when it was originally declared by the Lozi King, the Litunga, and used as a royal hunting ground. Following park designation, settlements were still permitted and the human population within LPNP numbered approximately 10 000 people during this study (APN, 2009a). The GLE currently holds one of the largest remaining wildebeest (*Connochaetes taurinus taurinus*) populations in Africa at an estimated 46 000 animals, which move seasonally between the southern portion of LPNP in the rains and the UWZGMA and northern LPNP during the dry season (APN, 2013). It also contains an unknown but large number of oribi (*Ourebia ourebi*) and approximately 9000 migratory zebra (*Equus burchelli*) whose movement pathways are poorly understood, as well as smaller numbers of red lechwe (*Kobus leche leche*), tsessebe (*Damaliscus lunatus lunatus*), reedbuck (*Redunca arundium*), common duiker (*Sylvicapra grimmia*), and eland (*Tragelaphus oryx*) as potential prey species (APN, 2009b, 2011, 2013).

Due to depletion by poaching and conflict, the GLE carnivore guild is unusual because of its relative lack of lions and dominance of spotted hyaena. By 2003 the lion population was reduced to a single lioness, with subsequent reintroductions of two males and two females in 2009 and 2011, respectively, so that the park held 3-5 adult lions in one pride during this study. Small, recovering populations of wild dogs (1-2 packs of 15-22 dogs total during this study) and cheetahs (17 known individuals) were also present. Concurrent studies of prey selection by all large carnivores in LPNP ($N = 517$ kills) indicated that wildebeest are the primary prey for all carnivores in LPNP,

although oribi are also an important prey species for cheetahs and wild dogs, but not lions or hyaenas. Zebras were very rarely killed and only by lions and hyaenas. While hyaenas were present throughout the GLE, we confined our investigations to an approximately 1200 km² intensive study area in the southern portion of LPNP, which held the majority of the park's hyaena population and fully contained the territories of five clans (Fig. 3.1).

Study Design

Our basic study design used restricted stratified random sampling to collect observations of individually-recognized hyaenas on a 1200 km² study area. These observations yielded a record of monthly detection/non-detection for 233 individuals over a period of 38 months from October 2010 to November 2013. We used these detection histories to fit robust design capture-recapture models, providing estimates of population size and annual survival and testing how survival was affected by a set of demographic, ecological and anthropogenic factors.

Anesthesia and Radio-collaring

Because hyaena clans are highly social (Kruuk, 1972) and radio-collars strongly facilitate intensive capture-recapture studies for social carnivores (Rosenblatt et al., 2014), we equipped 20 female and 3 male adult hyaenas from 5 clans with VHF (15) and GPS (8) radio collars (Telonics, Telemetry Solutions and Advanced Telemetry Solutions). Because hyaena societies are strongly matriarchal, we focused our collaring effort on

females, who provide better monitoring of uncollared clan-mates. We typically maintained collars on at least three adult female in each clan throughout the study. Anaesthetics were remotely administered via a Dan-Inject JM rifle and consisted of a mixture of Tiletamine/Zolazepam (Zoletil, Virbac, South Africa) and Medetomidine (Domitor, Kyron Laboratories/Pfizer Animal Health, South Africa), reversed with Atipamezole (Antisedan, Novartis Animal Health, South Africa) (Kock et al., 2006). During immobilization, the animals' eyes were protected with a cloth, vital signs were monitored, and dart injection sites were treated with topical antibiotics. All immobilization procedures were conducted with permission, following animal welfare standards and protocols required by the Zambia Department of Veterinary and Livestock Services and the Zambia Wildlife Authority.

Observations of Recognized Individuals

We employed restricted stratified random sampling to ensure an unbiased distribution of observation effort amongst the respective clans. We randomly selected the order in which clans were observed, and within each clan we randomized the order of search for collared individuals. We typically observed one clan per day, and all clans were sampled before beginning a new randomized sample. This procedure also allowed for unbiased estimates of home range sizes. When searching for collars or observing a collared animal, we recorded the identity of all hyaenas that we encountered, including the location (using GPS), group size, sex, habitat type and activity. We regularly visited communal dens in the clan to assess reproduction and to record the identities of all

individuals present. We attempted to photograph both sides of all individuals at all sightings to increase the reliability of individual identification from spot patterns and markings. During the 4 years of study we used > 25 000 such photos to develop a photographic identification file that included 233 recognized individual hyaenas in 5 clans (Fig. 3.2). Clan membership was determined through association and behaviour and was typically unambiguous (Kruuk, 1972). Sex determination was accomplished through differences in body outline (Frank, 1986), reproductive status, and from the third month onwards using the shape of the phallic glans (Frank et al., 1990).

Estimating Hyaena Home Range

From the observations described above, we obtained 4405 locations from hyaenas in the five focal clans. The size of each clan's home range and core area were determined using the 90% isopleth and 70% isopleth from a kernel utilisation distribution, respectively, created using the fixed Gaussian Kernel Density Estimate (KDE) function in Geospatial Modelling Environment (GME; Beyer, 2012). Kernel bandwidth was determined by least squares cross-validation (LSCV) (Gitzen et al., 2006). We used these home ranges to determine the total area occupied by the five focal clans, and used this total area in conjunction with estimated population size to produce an upper bound on population density.

Evaluating Ecological and Anthropogenic Factors Affecting Hyaena Survival

From studies of hyaenas in other ecosystems and our knowledge of this system we hypothesized that survival may be affected by hyaena age class and sex, competition with lions, prey density, and proximity to human settlements.

Competition with Lions

We hypothesized that hyaena survival would be lower in areas of higher lion use. We intensively monitored the single GLE pride using VHF and GPS radio-collars. These lions occupied our focal study area when migratory wildebeest and zebra were present at high densities (From mid-October to mid-July) and moved north-east outside the main study area following migratory prey from mid-July to mid-October, making occasional forays back into the main study area.

Using 5697 GPS and VHF lion locations we created a kernel utilisation distribution in the same manner as for hyaenas, and rasterized this distribution (cell size: 100 x 100 m) so the value of each pixel of the raster map represented the likelihood of encountering a lion within that cell. We used the 90th percentile of the distribution of lion daily movement distances as the bandwidth for this utilisation distribution so that it had relatively strong smoothing, and thus our inferences about differences between locations in lion use were conservative. We used the “lsectpolyst” tool in GME (Beyer, 2012) to intersect the lion raster with the 70% isopleth ‘core’ area

for each of the hyaena clans, providing a quantitative measure of variation among hyaena clan territories in the intensity of use by lions (Fig. 3.1).

Prey Density

Prey density was determined from distance sampling models fit to data from systematic line transects located in eight survey quadrats distributed evenly across the study area (Fig. 3.1). Detailed methods and results for these data are presented elsewhere (M'soka et al., in review), but briefly, each quadrat was 8 km x 8 km with two transect lines running east-west at 2 km and 6 km along the north-south axis, for a total of 128 km of transects that we surveyed 10 times from 2010 to 2013. Of these transects, 83 km fell within the territories of the 5 hyaena clans (Fig. 3.1). Because wildebeest comprised 92% (CI: 85% - 96%) of 100 observed hyaena kills, and were by far the most common ungulates in the study area (with estimated densities ~4X higher than oribi, the next most common species: M'soka et al., in review), we restricted our analysis of prey availability to wildebeest. We estimated wildebeest density (corrected for detection probability) for each clan's home range using the distance-sampling model that was best-supported by AIC scores. This model included effects of vegetation type, grass height, the presence of water and burned areas, season, local hyaena density, distance to the park boundary and distance to the nearest village (M'soka et al., in review).

Proximity to Human Settlements

We quantified the effect of human settlements on hyaena survival by calculating the distance from the geometric centre (or ‘centroid’) of each clan’s home range to the nearest village, hypothesizing that hyaenas closer to settlements are likely to have higher mortality due to conflict with humans and livestock. Centroid locations were calculated in ArcGIS 10.2.2 (ESRI, Redlands, California, USA) using the locations of all females in a clan, each weighted by the number of hyaenas observed at that location. We used data only for females because occasional extra-territorial forays by males include locations that are rarely (if ever) used by most individuals in the same clan. We then used ArcGIS 10.2.2 (ESRI, Redlands, California, USA) to determine the distance from each centroid to the nearest village, which were mapped systematically from the air. These distances ranged from 4.2 km to 13.8 km.

Estimating Hyaena Survival

With the methods described above, we used the monthly detection histories of 233 individually identified hyaenas in a robust design capture-recapture analysis. We used the robust design model to estimate population size and annual survival rates while accounting for imperfect detection, and to test the demographic, ecological and anthropogenic factors affecting survival. The robust design estimates population size within ‘primary’ periods for which the population is assumed to be demographically closed (by analysis of secondary periods nested within primary periods), and survival rates by comparisons across the intervals between primary periods. We compiled

monthly detections for each hyaena over the study period from October 2010 to November 2013. We partitioned this study period of 38 months into a set of seven primary periods for which demographic closure was reasonably approximated and field effort was high, separated by periods considered demographically open (during which field effort was lower) to allow estimation of survival rates. Closed primary periods were Oct - Dec 2010, Apr - Jul 2011, Oct 2011 - Jan 2012, May - Jul 2012, Oct 2012 - Jan 2013, Apr - Jul 2013, and Oct - Nov 2013. The intervening six open periods were Jan - Mar 2011, Aug - Sep 2011, Feb - Apr 2012, Aug - Sep 2012, Feb - Mar 2013, and Aug - Sep 2013. Small differences between years in the timing of open and closed periods reflected variation in the timing of intensive efforts to locate hyaenas in the radio-collared clans.

We fit robust design models (Kendall et al., 1995; Kendall and Nichols, 1995; Kendall et al., 1997) to these data using the **RMark** package (Laake, 2013) in R (R Core Team, 2014). Our original intent was to use Akaike's Information Criterion corrected for small sample size and extrabinomial variation (QAICc) to compare a set of *a priori* models, but this approach could not be implemented because some parameters could not be estimated in some of the *a priori* models. Consequently, we used a sequential model-fitting process to obtain QAICc scores for a set of models that yielded precise estimates of population size and annual survival, and allowed tests of the factors affecting survival. We adjusted for extrabinomial variation by estimating median $\hat{c}$ using a Cormack-Jolly-Seber model in Program Mark (White and Burnham, 1999) with our

dataset collapsed to primary occasions, as recommended by Laake (2015). This analysis showed that over dispersion was minor in these data (median $\hat{c} = 1.4$). In our first step, we determined the best-supported parameterization of temporary emigration, defined as γ' (the probability of remaining unavailable) and γ'' (the probability of becoming unavailable). Because hyaenas in some ecosystems are known to leave their typical home ranges for extended periods when following migratory prey (Kruuk, 1972; Hofer and East, 1995) we assumed that the likelihood that an individual would be present and available for detection each primary period was affected by a Markovian process of temporary emigration. QAICc model selection between robust design models varying only by Markovian and no-movement temporary emigration indicated higher support for Markovian models. In our second step, we determined that models allowing detection probability (p) to vary within and between primary periods consistently received more support than otherwise-identical models that held p constant or only considered differences between primary periods. Finally, we combined these models of detection probability and Markovian temporary emigration with nine candidate models of ecological and anthropogenic effects on survival, shown in Table 3.1. We annualized the survival estimates from these models using the `time.intervals()` function in **RMark**, and used model-averaging to estimate anthropogenic and ecological effects on survival, using the `model.avg()` and `model.sel()` functions of the **MuMIn** package.

Not all of the above models could be fit to data partitioned by sex and age-classes, so we fit a final model to estimate mean annual survival for each sex in each of

five age classes (young cubs, old cubs, sub adults, adults and old adults). For this model, $\hat{p}$, $\hat{\gamma}'$ and $\hat{\gamma}''$ were modelled as described above.

Estimating Population Size and Density

Estimates of population size were obtained from the top ecological model, which had the effects of distance to human settlements. For comparison to other estimates of hyaena population density, we converted population size to population density in two ways. For comparison to estimates that include unused locations within a broad area (e.g. from call-up surveys or spoor counts), we divided the population estimate by the area of our focal study site (1200 km²). For comparison to more localized estimates (e.g. from intensive study of radio-collared clans), we divided the average population estimate by the area known to have been used by these hyaenas (291.1 km²).

Results and Discussion

Our robust design (ecological) models yielded precise estimates of population size and survival rates, largely because the intensity of sampling was high enough that few individuals went undetected (mean $f_0 = 0.44$, upper 95% CL = 1.52) and monthly detection probabilities were estimated to be high ($\hat{p}$) = 0.51, range = 0.33 to 0.71). Model-averaged estimates of Markovian temporary emigration were $\hat{\gamma}'' = 0.13$ (95% CI: 0.09 – 0.19) and $\hat{\gamma}' = 0.75$ (95% CI: 0.71 – 0.78). While the parameters just described were not of direct interest, they allowed statistically and methodologically rigorous estimates of population size and survival. These results also indicate that the excellent

visibility of this population and intensive monitoring combined to allow detection of most individuals over the study period.

Hyaena Population Size and Density

Averaged across the seven primary periods, we observed 136.4 individuals in each primary session and estimated an average population size of 151.2 ± 5.9 (SE) individuals. We estimated a minimum density of 0.13 hyaenas/km² and maximum density of 0.52 hyaenas/km². For comparison, Périquet et al. (2014) comprehensively reviewed estimates of hyaena density and reported values ranging from 0.005 to 1.8 individuals/km² (mean = 0.39 ± 0.10 individuals/km²). While the density of hyaenas in LPNP is not comparable to the >1 individual/km² that has been reported for some prey-rich systems (e.g. Serengeti NP: Kruuk, 1972), our density estimates indicates a healthy and stable population.

Our estimates indicate that the Liuwa hyaena population is stable or slightly increasing over the duration of the study period (Fig. 3.3). After the first primary period there is an apparent seasonal pattern in hyaena abundance (see below for discussion of short term patterns). There is an increase in the Liuwa hyaena population after the first primary period (Oct-Dec 2010), but this increase is largely due to the number of known individuals increasing after the first primary period. For example, in one clan (Mutata) only 8 individuals were detected in the first primary period and increased to between 29 and 40 individuals detected in subsequent periods. Because we did not estimate detection independently for each clan in each period, we believe that detection for this

clan was overestimated in the first primary period, so that the size of this clan (and thus total population size) was underestimated. Although population size did not trend systematically upward or downward over the long-term, the population estimates over the 6 primary periods (excluding the first primary period, for reasons just explained) fluctuated systematically with the estimates of the Oct – Jan periods generally higher than the estimates of the May – Jul periods (Fig. 3.3). This pattern, is probably due to the migratory nature of the prey species in this ecosystem, with wildebeest being locally more abundant in the wet season (Nov-Apr) than the dry season (May-Oct) (M'soka et al. in review). Migratory prey movements drive temporary immigration in other hyaena populations (Hofer and East, 1993a, 1993b), and provide a logical explanation for this observed pattern in the size of the Liuwa hyaena population. This is further supported by the proportional change in population size between primary periods loosely matching our estimates of $\hat{\gamma}'$ and $\hat{\gamma}''$, further suggesting that temporary immigration driven by prey availability plays a role in the dynamics of this hyaena population, as elsewhere (Hofer and East, 1993b; Höner et al., 2005).

Prey Density and Hyaena Density in LPNP

Prior research has established that hyaena density is positively correlated with prey density (Hayward, 2006; Höner et al., 2005). Périquet et al. (2014) used data from 20 studies to describe this relationship quantitatively as

$$\log(\text{hyaena density}) = -4.11 + 0.97 \times \log(\text{prey biomass})$$

Wildebeest were by far the most common ungulates in the study area, with a density that ranged from 60.8 ± 2.34 (SE) individuals/km² to 11.3 ± 0.67 individuals/km² in the wet and dry season respectively (M'soka et al., in review). With this prey base, LPNP hyaena predation ($N = 100$ observed kills) focused primarily on wildebeest (92% of observed kills), and particularly on adult wildebeest (89%). For the ungulate prey community of LPNP (with estimated mean prey mass = 180 kg) the relationship described by Périquet et al. (2014) predicts a hyaena density of 0.17 individuals/km² based on dry season prey densities, and 0.88 individuals/km² based on wet season prey densities. Our estimates of hyaena density in LPNP are comparable to mean of these two seasonal estimates, suggesting that the prey base of LPNP supports the hyaena population that would be expected on the basis of data from other protected areas.

Clan Size and Home Range Size

Mean clan size in LPNP during the study period was 48.6 hyaenas. Though somewhat smaller than the clan sizes supported by the ungulate migration across the Serengeti, Ngorongoro and Mara populations, LPNP clans tend to be larger than comparably-sized parks in Southern Africa, and larger than the mean clan size of 30.84 ± 7.39 reported by Périquet et al. (2014). Hyaena home range sizes ranged from 52.2 km² to 102.4 km², tending to be smaller than the mean of 178 ± 79.19 km² from 15 other studies (Périquet et al., 2014), but well within the reported range of 24.5 - 1095 km².

Survival: Variation among Age-Sex Classes

On the basis of relatively high prey density and low levels of competition with lions, we hypothesized that hyaena survival would be high. Supporting this hypothesis, estimated annual survival rates were high, and varied little across age-sex classes (Fig. 3.4). Frank et al (1995), reported little variation in survival between sexes up to 24 months old in the Mara in Kenya, however the small variation in estimated differences between the sexes in the adult age classes in our data is somewhat unusual (Clutton-Brock and Isvaran, 2007), but hyaenas are relatively monomorphic, have very low reproductive rates, and reproductive effort by females is offset by female dominance, all of which predict that survival should show less age-sex variation in hyaenas than in most large carnivores. This could also be a reflection of our ability to track adult males beyond their natal clans after dispersal. Male dispersal hinders the estimation of survival rates in most ecosystems as fates of dispersed males are rarely known (Holekamp and Smale, 1995).

Ecological Effects on Survival

Comparison of QAICc scores shows distributed support for models that include effects of clan size, prey density within the home range, proximity to people, and local competition with lions (Table 3.1). However, as Fig. 3.5 shows, the confidence intervals for all of these effects overlap substantially with zero, suggesting that none of these variables had appreciable effects on the survival of hyaenas in LPNP.

The high survival rates we found for all age-sex classes suggest that, if reproduction is typical, this hyaena population is probably stable or growing, supported by our estimates of population size. We could not detect any significant effects of proximity to people on hyaena survival, even though people are allowed to reside within the park with their livestock. It is our reasoning that the negative effects of anthropogenic activities are ameliorated by the high density of prey and low levels of competition from lions in the study area. Studies in other African ecosystems have shown that hyaena survival and abundance are closely related to prey abundance (Hofer and East, 1993a; Kruuk, 1972; Watts and Holekamp, 2009). Thus, the patterns observed in LPNP suggest that hyaenas can compensate for any negative effects of anthropogenic activities if prey density remains high and competition from lions is low. More generally, this result confirms that finding ways to promote coexistence of people and livestock with ungulate prey is a strong determinant of the persistence of large carnivores in human dominated ecosystems (Schuette et al., 2013).

We were not able to detect any effect of the Liuwa lion pride on hyaena survival (Fig. 3.5), most likely due to seasonal movements of lion or the small lion population in LPNP. During the course of our study, lions consistently occupied the study area when migratory wildebeest were present at high densities (From mid-October to mid-July) and moved north-east outside the main study area following migratory prey from mid-July to mid-October, making occasional forays back into the main study area. It is possible that lions shift their range during this period not only to follow prey, but also to reduce

interference competition with spotted hyaenas during this time of reduced prey availability. However, this behaviour of lions has been reported in other ecosystems with migratory prey species (Schaller, 1972, Hanby et al, 1995). Temporal variation in prey availability may ameliorate the competitive interactions between hyaena and lion in this ecosystem, though this possibility must be evaluated with the recognition that a single lion pride occupied the study area, at a density lower than many other populations, so the effect of lions is expected to be weak.

Conclusions

Overall, our results show that the migratory wildebeest population that has recovered in LPNP over the last decade supports a healthy and stable hyaena population at the density that would be expected from studies elsewhere in Africa. Survival is an important demographic component of population growth and for modelling ecological and anthropogenic risk to the viability of species. Annual survival is uniformly high for all age-sex classes, with no detectable effects of variation in prey density, local variation in utilisation by lions, or proximity to people (and their livestock). If recovery of the lion population continues (the resident pride has recently produced and raised cubs after males were translocated into the system), competitive effects on hyaenas and other carnivores may increase, and this possibility should be a focus for ongoing monitoring. With the relatively high availability of wildebeest as prey, hyaena survival was high and was not affected by proximity to villages, even though settlement are allowed within the

National Park itself. This is an encouraging pattern which suggests that, as elsewhere (Schuette et al., 2013), maintenance of native prey populations allows coexistence between humans and large carnivores in Africa. Despite being well studied and abundant on the African continent there are few reliable estimates of survival in this species.

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Table 3. 1 QAICc scores for a set of model of ecological effects on annual survival rates of LPNP hyaenas.

model	npar	QAICc	DeltaQAICc	weight	QDeviance	chat
S(~village)	21	405.8073	0	0.19567837	363.2726	1.4
S(~lion)	21	406.1798	0.3724429	0.16243061	363.645	1.4
S(~size)	21	406.2448	0.4374429	0.15723648	363.71	1.4
S(~prey)	21	406.271	0.4636429	0.15519012	363.7362	1.4
S(~size + village)	22	407.3718	1.5644508	0.08950075	362.7858	1.4
S(~lion + village)	22	407.7816	1.9742508	0.07291884	363.1956	1.4
S(~prey + village)	22	407.8447	2.0373365	0.07065466	363.2587	1.4
S(~prey + size)	22	408.2314	2.4241079	0.05823103	363.6454	1.4
S(~lion + size + village)	23	409.0767	3.2694141	0.03815914	362.4371	1.4

Village = distance to the nearest settlement, lion = probability of lion presence, size = clan size, prey = prey density

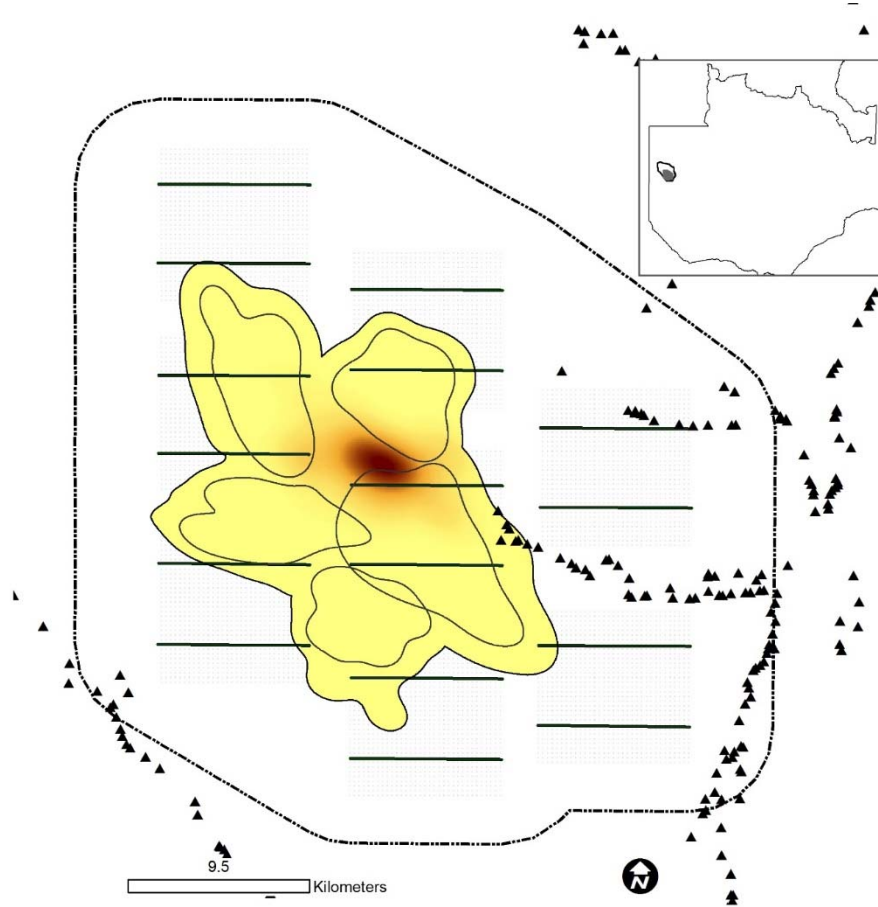


Figure 3. 1 Map showing the study area. The location of LPNP within Zambia is shown in the inset, with the location of the intensive study area within LPNP in solid black. Within the main map, the 1200 km² focal study area is shown by the outer dot-dashed line, and contour lines represent the 70% and 90% isopleths of the 5 resident hyaena clans. Lion use of the area during the period July 2010 – November 2013 is shown by colour: the darker an area, the higher the probability of lion presence. Straight lines represent transects along which wildebeest density was monitored. Black triangles show the location of villages.

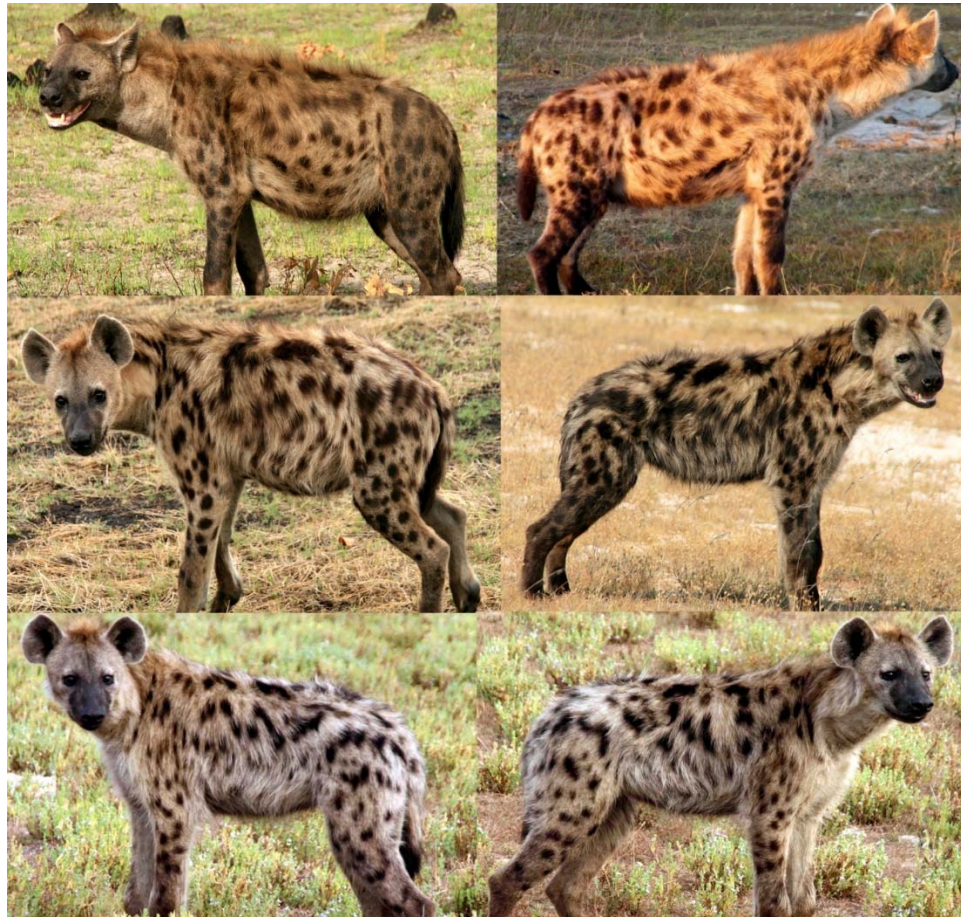


Figure 3. 2 Photographic identification showing the unique spots of the pelage of spotted hyaenas: three of the study hyaenas with right and left side photos used for identifying individual hyaenas in the field. Hyaenas in this system typically allow vehicles to approach within a few meters without moving away, facilitating accurate identification.

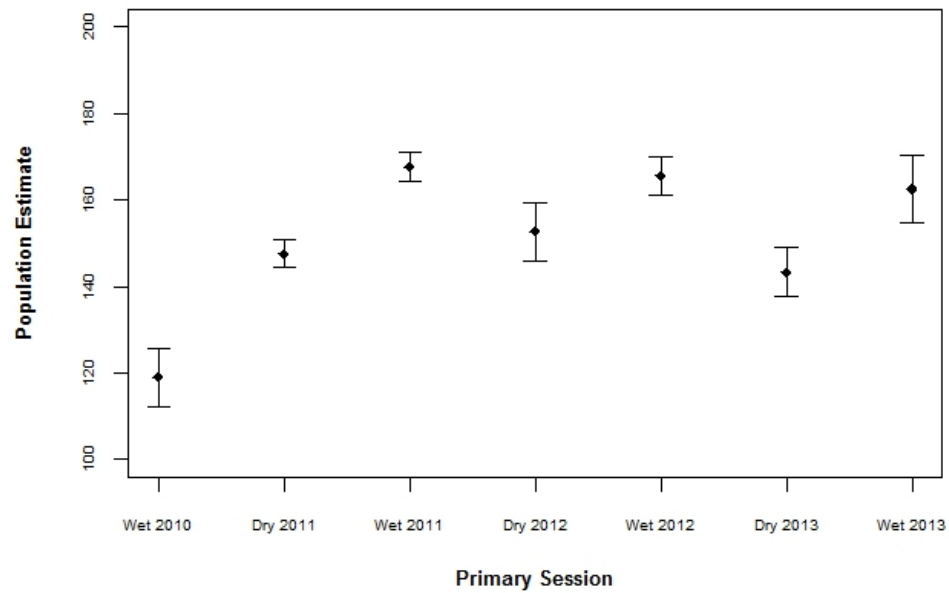


Figure 3. 3 Liuwa hyaena population estimates from the robust design model with the probability of detection allowed to vary across primary and secondary sampling sessions from 2010 to 2013.

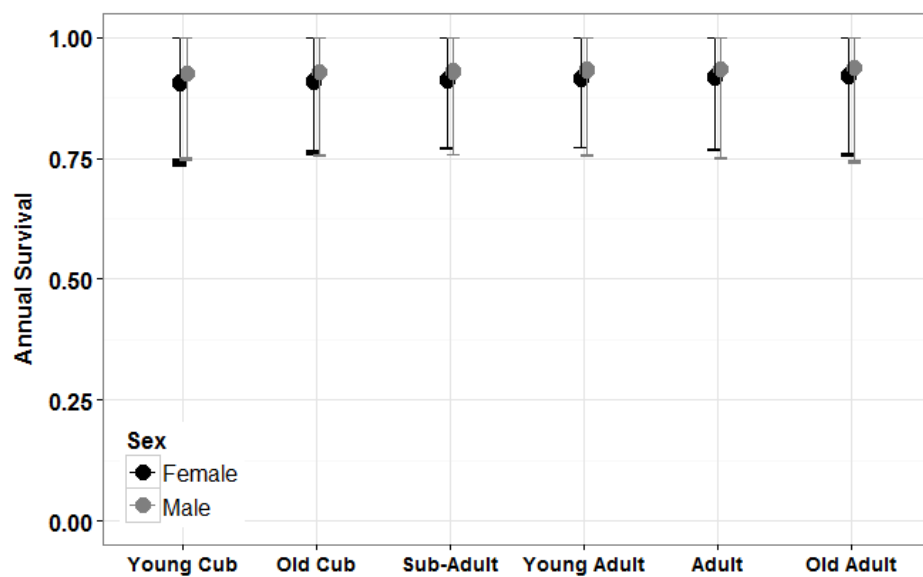


Figure 3. 4 Estimated annual survival was above 0.90 for all age-sex classes, with a very small and non-significant tendency for males to survive better than females, and adults to survive better than younger age classes.

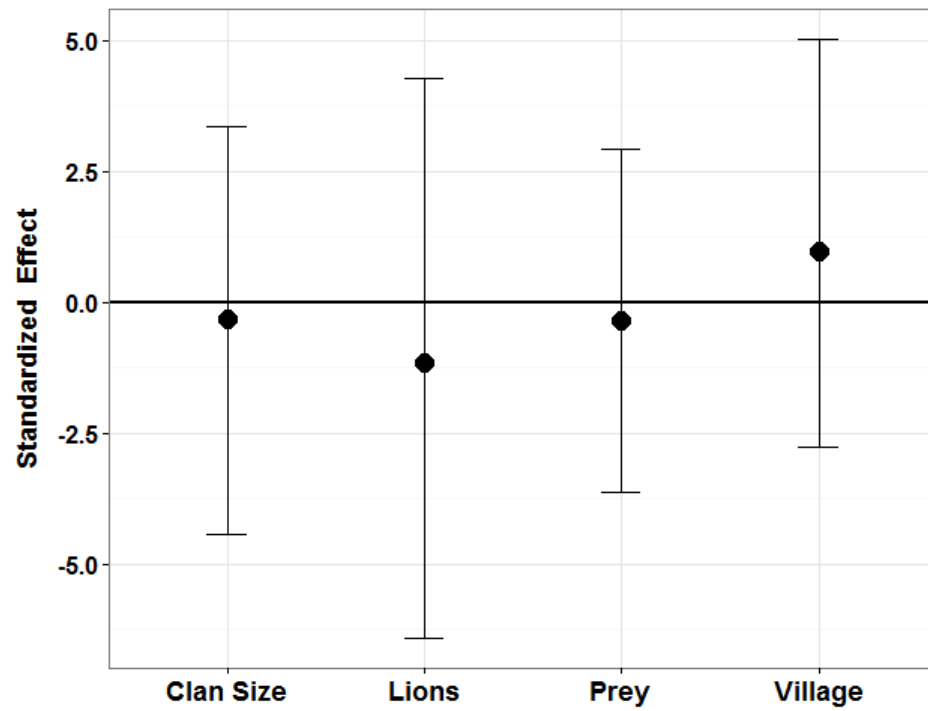


Figure 3. 5 Model-average effects of ecological variables on annual survival rates of LPNP hyaenas. Variables were standardized as z-scores so that effect sizes could be compared directly. Point estimates and 95% confidence intervals are shown.

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CHAPTER FOUR

CONCLUSION TO DISSERTATION

Overall Conclusions

Considering the growing literature on the negative impacts of humans on protected areas, insights from the GLE are unique, given that the local carnivore and ungulate population utilise an area settled by humans for more than a century. Understanding factors that affect the survival and density of these wildlife species in this human-inhabited system is thus important in developing conservation strategies. This study provides the first test of factors affecting the density and abundance of the three dominant ungulates species in this ecosystem. It further provide the first test of the factors affecting the survival of this spotted hyaena population in the absence of its main competitor the African lion. We provide rigorous estimates of density of the main carnivore and ungulates species in this system, using sampling designs and analytic methods that reduce bias and increase precision relative to many studies of large carnivores and their prey.

In chapter 2 we looked at the ecological and anthropogenic effects on the density of migratory wildebeest and zebra, and resident oribi, the three most abundant ungulates in the GLE. While oribi and zebra appeared to avoid settlements, wildebeest densities were higher than expected close to villages and decreased with park boundary distance. These contrasting results suggest differences in sensitivity to risk and

disturbance. Given that migrations traverse protected area boundaries for many herbivores, Owen-Smith & Ogutu (2012) recommended increasing protected area boundaries to buffer the effects of climate change and protect migratory routes and ranges. Such actions are critical for the GLE, given the influence of seasonal flooding and rainfall, which can be severely impacted by climate change.

Broadly, our results show that densities of wildebeest, oribi and zebra, are affected by a complex set of ecological factors, including effects of humans and predators. The influences of environmental variables were all consistent with results from studies in other ecosystems and reveal a degree of resource partitioning among species. The influence of hyaena density suggests that predation risk can affect space use, and for some species high predation risk areas cannot be avoided while meeting nutritional needs. Anthropogenic effects have potentially broad impacts on species and their migrations, and protection of migratory routes and ranges outside LPNP should be considered highest priority. These results suggest that focal points for conservation and management differ by species and must consider the entire suite of ecological and anthropogenic factors.

In chapter 3, we show that the migratory wildebeest population that has recovered in LPNP supports a healthy and stable hyaena population at the density that would be expected from studies elsewhere in Africa. Annual survival is uniformly high for all age-sex classes, with no detectable effects of variation in prey density, local

variation in utilisation by lions, or proximity to people (and their livestock). On the basis of relatively high prey density and low levels of competition with lions, we hypothesized that hyaena survival would be high. Supporting this hypothesis, estimated annual survival rates were high, and varied little across age-sex classes. Frank et al (1995), reported little variation in survival between sexes up to 24 months old in the Mara in Kenya, however the small variation in estimated differences between the sexes in the adult age classes in our data is somewhat unusual (Clutton-Brock and Isvaran, 2007), but hyaenas are relatively monomorphic, have very low reproductive rates, and reproductive effort by females is offset by female dominance, all of which predict that survival should show less age-sex variation in hyaenas than in most large carnivores. This result could also be a reflection of our ability to track adult males beyond their natal clans after dispersal. Male dispersal hinders the estimation of survival rates in most ecosystems as fates of dispersed males are rarely known (Holekamp and Smale, 1995).

The hyaena population estimates fluctuated systematically between the early dry and late dry season. This pattern, is probably due to the migratory nature of the prey species in this ecosystem, with wildebeest being more locally abundant in the late dry, than in the early dry season and was shown in chapter 2. Migratory prey movements drive temporary immigration in other hyaena populations (Hofer and East, 1993a, 1993b; Höner et al., 2005), and provide a logical explanation for this observed pattern in the size of the Liuwa hyaena population.

Overall, we show that with increased prey density and low levels of competition with lions, hyaenas in LPNP can compensate for the negative effects of anthropogenic activities. Broadly, our results suggest that conditions that maintain adequate populations of native prey are key in promoting coexistence of people and livestock with large carnivores in human dominated ecosystems (Schuette et al., 2013).

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APPENDIX A

SUPPLEMENTARY INFORMATION FOR CHAPTER TWO

Table S2.1. The set of models considered for effects on the density of wildebeest, oribi and zebra in Liuwa Plain National Park, Zambia. All models were fit with detection probability as a function of distance, considering both hazard and half-normal detection functions.

Univariate Models

~year, ~hab, ~ht, ~burn, ~water, ~season, ~hy, ~vlg, ~boundary

Two-Predictor Models

~hab+water, ~hab+season, ~hab+hy, ~ht+hy, ~burn+water, ~burn+vlg, ~hy+vlg

Four-Predictor Models

~year+hab+water+hy, ~year+burn+hy+vlg, ~year+water+hy+vlg, ~year+season+hy+vlg,

~year+season+hy+boundary

More Complex Models

~year+hab+burn+water+hy, ~year+hab+season+hy+vlg, ~year+burn+water+hy+vlg,

~year+ht+burn+water, ~year+ht+season+hy+vlg, ~year+hab+burn+water+hy+vlg,

~year+hab+burn+water+hy+boundary, ~year+hab+water+hy+vlg,

~year+hab+season+hy+boundary ~year+ht+season+hy+boundary,

year+hab+ht+season+hy+vlg

~year+hab+ht+season+hy+boundary, ~year+ht+burn+water+hy+vlg

~year+hab+ht+burn+water+hy+vlg, ~year+hab+ht+burn+water+hy+boundary

~year+hab+ht+burn+water+hy+vlg+boundary

Full Model

~year+hab+ht+burn+water+season+hy+vlg+boundary

Table S2.2. Parameter estimates describing the effects of predictor variables on wildebeest, oribi, and zebra density (animals km⁻²) in Liuwa Plain National Park, Zambia. Values are from the best-supported models for each species: wildebeest ($\Delta\text{AICc} = 0$, $w_i = 1.00$, pseudo- $R^2 = 0.78$), oribi ($\Delta\text{AICc} = 0.89$, $w_i = 0.30$, pseudo- $R^2 = 0.91$) and zebra ($\Delta\text{AICc} = 0.00$ and $w_i = 0.79$, pseudo- $R^2 = 0.92$). Detection probability was modelled as either a hazard function¹² or half-normal function³ of perpendicular distance from the transect line.

Effect	Wildebeest				Oribi				Zebra			
	Estimate	SE	z	P(> z)	Estimate	SE	z	P(> z)	Estimate	SE	z	P(> z)
(Intercept)	1.192	0.13	9.49	<0.001	0.190	0.22	0.86	0.388	-2.460	0.26	-9.42	<0.001
^a Yr: 2011	x	x	x	x	-0.230	0.17	-1.30	0.193	0.730	0.25	2.90	0.004
Yr: 2012	-0.194	0.13	-1.50	0.133	-0.110	0.15	-0.72	0.469	0.620	0.26	2.36	0.018
Yr: 2013	-1.260	0.10	-12.61	<0.001	-0.060	0.11	-0.53	0.599	0.090	0.18	0.51	0.608
^b Hab: Woodland	-0.532	0.10	-5.49	<0.001	-1.410	0.24	-5.76	<0.001	-0.320	0.23	-1.38	0.169
^c Ht: Short	0.223	0.07	3.16	0.002	-0.010	0.10	-0.11	0.913	-0.190	0.15	-1.24	0.214
Ht: Tall	-0.273	0.10	-2.68	0.007	-0.270	0.15	-1.83	0.067	0.020	0.21	0.09	0.927
^d Burn: Yes	-0.001	0.07	-0.01	0.988	0.500	0.10	5.09	<0.001	0.040	0.15	0.24	0.807
^e Wtr: Present	0.492	0.07	6.91	<0.001	0.290	0.10	2.92	0.003	0.610	0.15	4.06	<0.001
^f Seas: Wet	1.236	0.07	18.60	<0.001	X	x	x	x	1.070	0.15	7.01	<0.001
^g Hy: Low	-0.597	0.08	-7.11	<0.001	-0.400	0.12	-3.22	0.001	-0.350	0.17	-2.03	0.042
Hy: Medium	0.066	0.07	0.94	0.346	0.100	0.10	1.06	0.291	-0.230	0.15	-1.51	0.130
vlg	-0.061	0.01	-8.13	<0.001	0.050	0.01	5.33	<0.001	0.040	0.01	2.45	0.014
bndry	-0.026	0.01	-4.25	<0.001	-0.020	0.01	-2.24	0.025	-0.010	0.01	-0.83	0.407

Reference levels for categorical effects: **a**: Yr (year) = 2010, **b**: hab (vegetation type) = grassland, **c**: ht (grass height) = intermediate, **d**: burn=no, **e**: water = absent, **f**: season = dry, **g**: hy (hyaena density) = intermediate.

¹Parameter estimates for wildebeest detection function. Shape parameter = -1.71 ± 0.08 SE, scale parameter = 0.58 ± 0.09 SE.

²Parameter estimates for oribi detection function. Shape parameter = -2.52 ± 0.37 SE, scale parameter = 0.27 ± 0.26 SE.

³Parameter estimate for zebra detection function: = -0.85 ± 0.06 SE.



Figure S2.1. Typical grassland (Top, photo credit: Jassiel M'soka) and woodland vegetation (Bottom, photo credit: Noeline Tredoux) in the study area in Liwua Plain National Park, Zambia.

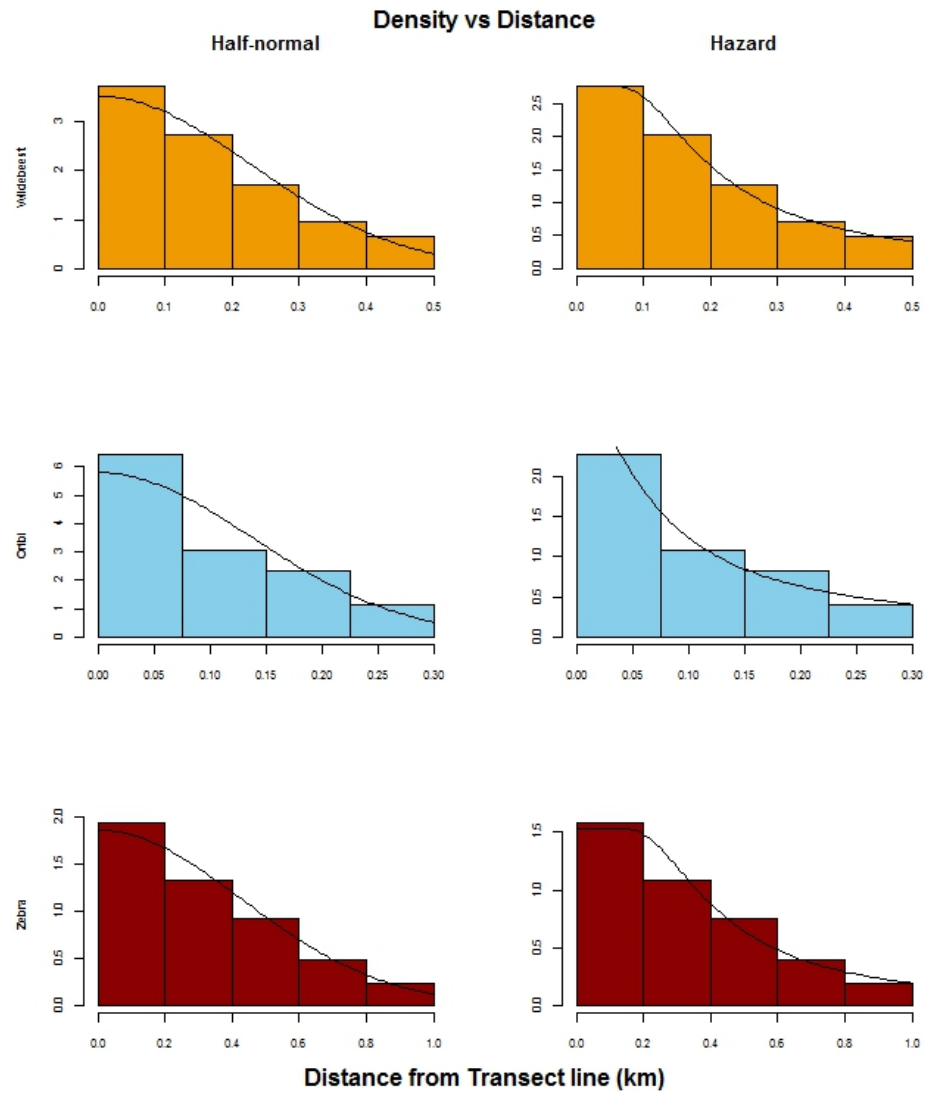


Figure S2.2. Frequency distributions for observations of ungulate herds relative to perpendicular distance from line transects for wildebeest, oribi, zebra. Scales differ between plots on both axes.