FACTORS AFFECTING THE SIZE AND DISTRIBUTION OF LARGE HERBIVORES IN KAFUE NATIONAL PARK, ZAMBIA

by

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ABSTRACT

The distribution and abundance of African ungulates are limited by abiotic factors (soil nutrients and water), bottom-up processes (forage availability and density-dependent competition for food), top-down processes (direct predation and the costs of avoiding predation) and anthropogenic effects. The relative importance of biotic factors such as food limitation and predation have been well-studied for some species (e.g. wildebeest, *Connochaetes taurinus*), particularly in flagship ecosystems such as Serengeti and Kruger National Parks. Research on complete ungulate communities is needed to describe differences between ungulate species in the relative importance of these limiting factors, and how their importance varies across ecosystems. Moreover, ungulate populations are in decline across much of Africa, and research is needed to examine the importance of anthropogenic effects and the manner in which anthropogenic effects alter the strength of other limiting factors. Here, we used line transect data collected over three years to estimate population densities and determine what factors limit the distribution of large herbivores in Kafue National Park – North (KNP – N) of Zambia, in Southern Africa. With temporal replication within and among years, we sampled a set of systematically distributed transects, and used distance sampling models to correct for non-detection and test the effects on ungulate distributions of vegetation type, grass height and color, recent burning, distance to rivers and lagoons, soil type, pH and nutrients, lion use, and the distance to roads, tourist camps, and park boundaries. Our results show that the most abundant large herbivores in KNP are impala (*Aepyceros melampus*), puku (*Kobus vardonii*) and warthog (*Phacochoerus africanus*). Using AIC scores to test a set of distance sampling models, we found substantial variation among species in the relative importance of abiotic, bottom-up, top-down and anthropogenic effects. These results suggest that a range of species-specific strategies may be needed to conserve African large herbivores and ameliorate recent declines.

CHAPTER ONE

FACTORS AFFECTING THE SIZE AND DISTRIBUTION OF LARGE HERBIVORE HERDS IN KAFUE NATIONAL PARK, ZAMBIA: ORGANIZATION OF THE RESEARCH AND THESIS.

Ecologists, biologists and wildlife estate managers aim to understand whether animal numbers are increasing or declining, and the possible causes of observed trends. Their overarching goals include answering questions of population dynamics and determination of whether populations are being sustainably conserved for posterity. Africa as a continent has experienced unprecedented population declines of its fauna despite concerned governments' intervention. Loss of iconic species, such as the black rhino, have occurred across much of their historic range and the Northern white rhino is on the verge of extinction despite extensive conservation investment (Chansa et al 2011; Hillman 1980, 1981, 1983 cited by Western et al 1985;). The reasons why Africa's rich wildlife resources have declined to levels at or near extinction in some species requires further research attention. Is it a question of failure to identify factors affecting such animals? Or have species been given a 'one size fits all' approach type of management that has been effective for some and not others?

Factors affecting herbivore herd size and distribution are often difficult to determine, given that they may be mediated by a wide range of evolutionary adaptations and environmental covariates. Disentangling the evolutionary causes of differences among herbivore species is beyond the scope of this study; however, it suffices to state that the ecological niches of animals differ in a manner that allow them to respond to environmental patterns and to coexist with similar species (Begon et al 2007). In this research, my focus was on identifying the environmental covariates that are associated with the distribution and abundance of large herbivores, using data from a three year study in Kafue National Park. I examined the importance of bottom-up limitation by factors such as access to water and the quantity or quality of food, top-down limitation by the risk of predation by lions, and anthropogenic effects that may be responsible for enhancing or deteriorating the status of flora and fauna in general. If species are affected by the same set of factors, then managers could apply similar management strategies for all species. This is unlikely given the breadth of body sizes, foraging strategies, and social structures in African ungulates. Rather, we expect differences in the patterns of response to anthropogenic, environmental, and ecological conditions among species, which if supported, could increase the effectiveness and efficiency of conservation efforts that target individual species. Determination of factors affecting each species may also help managers predict with greater accuracy how global climate change and alteration to the environment may affect their long-term viability.

My research identifies similarities and differences in environmental and anthropogenic effects on large herbivores in Kafue. Kafue National Park is the fifth largest national park in Africa, with diverse, intact guilds of large herbivores and carnivores. Animal censuses have been conducted periodically since inception of the park and various articles and books written about the park, but to our knowledge, no one has systematically evaluated the factors affecting large herbivore distribution and herd size. We carried out vehicle-based animal counts of large herbivores on 18 transects using distance sampling methods (Buckland 2001). We measured environmental covariates on each transect with a goal of testing for abiotic factors, bottom-up and top-down biotic factors and anthropogenic factors affecting herbivore distribution. The primary response variables we considered were herd density (Chapter 2), which we examined using distance a spatially-explicit distance sampling model. With the same data and covariates, we examined for effects on herd size (Chapter 3) using zero-truncated Poisson generalized linear models (GLMs). Sets of environmental covariates tested include effects of water (presence, absence and distance to river), soil pH / nutrients, grass color / height, burn status, vegetation type, habitat structure (habitat edge density, proportions of grassland, open forest and closed forest), distance to roads, camps and the park boundary, and predation risk from lions.

My basic *a priori* working hypotheses were that ungulate densities and herd size numbers would be high in areas with high food quality, low with increasing distance to water (Hopcraft et al 2014; Mduma et al 1999; Bailey et al 1996), low in areas with high lion usage as estimated for by lion utilization densities, alternatively, lions seek out areas of high prey density (Owen-Smith & Mills 2008; Sinclair et al. 2003; Christianson & Creel 2014; Creel & Christianson 2008; Creel et al. 2007; Creel et al 2005) and low in proximity to human activities (Hofer et al, 2000 cited by Hopcraft et al 2014; Cincotta et al 2000; Brashares et al 2001). More detailed hypotheses are presented in Chapters 2 and 3, together with discussion of the ways in which associations might differ among species.

Our analyses revealed that the most abundant large herbivores in KNP are impala (*Aepyceros melampus*), puku (*Kobus vardonii*) and warthog (*Phacochoerus africanus*).

Using AIC scores to compare a set of distance sampling models, we found substantial variation among species in the relative importance of abiotic, bottom-up, top-down and anthropogenic effects on the local density of herds (Chapter 2). Of equal interest was the finding that more factors affected herd size than local herd density, these differed among species and were not necessarily the same as drivers of local herd density (Chapter 3). Broadly, these results suggest that a range of species-specific strategies may be needed to conserve African large herbivores and ameliorate recent declines.

CHAPTER TWO

FACTORS AFFECTING LARGE HERBIVORE DISTRIBUTION AND DENSITY IN KAFUE NATIONAL PARK, ZAMBIA

2.1. Introduction

The African continent, once known as a haven of teeming multitudes of both large and small mammals, is threatened with loss of biodiversity due to a range of factors emanating from both the environment and anthropogenic effects. Whereas the “scramble for Africa” in the early to mid-1800s ushered the birth of conservation treaties in the interest of posterity, the unforeseen “scramble for game” in post-colonial era has left many wilderness areas depleted of their wildlife resources (Bonner 2013; Adams & McShane 1982). The results are evident through a continued decline in mammal densities and geographic ranges despite stringent management policies in government protected areas. Kafue National Park (KNP) of central Zambia is a prime example of a protected area with its resident wildlife vulnerable to anthropogenic pressures and environmental change. Kafue National Park is the fifth-largest national park in Africa (22,840 km^2) with an ungulate community of more than 20 species and intact guilds of large and small predators. Furthermore, KNP and its surrounding Game Management Areas are a central component of the multinational Kavango -Zambezi Transfrontier Conservation Area encompassing five Southern African countries (Angola, Botswana, Namibia, Zambia and Zimbabwe). Protection of the area for the purpose of conservation is a high priority at the national and continental levels. Despite its regional importance, relatively little research exists to describe wildlife densities and the factors that limit them within KNP. The park formerly held a population of black rhino that was extirpated by widespread poaching from 1970s to 1980s (Chansa et al 2011; Mike 1983). It is thought that poaching might currently limit large herbivore densities, thus limiting the density of carnivores such as the African lion (*Panthera leo*; Midlane 2013). Other threats posed to animal populations in KNP include human encroachment on park boundaries (potentially leading to contraction of animal ranges, escalated poaching and increased burning), climate change, and the regional expansion of mining activities. Baseline data on the distribution and abundance of KNP's large herbivore community are needed for effective conservation and management in the face of these threats.

In addition to these anthropogenic effects, large herbivore distribution and density are impacted by food limitation, predation and abiotic factors. Migratory ungulates, for example, move across gradients of food quality and abundance, and by doing so, reduce the limiting effects of predation (Hopcraft et al 2014; Mduma et al 1999). These migratory species can therefore maintain high reproductive rates and low mortality rates. However, when there is shortage of food, populations experience a density dependent decrease in reproduction and increase in juvenile mortality, as predicted by the 'food hypothesis' (Gaillard et al 1998; Gaillard et al 2000; Sinclair et al 1985). In a broader sense, availability of food is impacted by water and soil nutrients (Bell 1982), because of their limiting effects on plant growth (Augustine et al 2003; Frank et al 1998; McNaughton 1985). Therefore, forage quality, water and nutrient availability are likely to impact ungulate distributions as well.

Food distribution and availability is also affected by wildfire. Wildfire reduces or eliminates plant biomass temporarily and then stimulates production of new growth (Holdo et al. 2007), a process that varies temporally by season and spatially by vegetation type. Ungulates may also be limited by top-down pressures from a combination of direct predation (Owen-Smith & Mills 2008; Owen-Smith & Mills 2008; Sinclair et al. 2003) and the costs of avoiding predation (Christianson & Creel 2014; Creel & Christianson 2008; Creel et al. 2007; Creel et al 2005).

Based on these patterns, we hypothesized that ungulate densities and distributions in KNP would be affected in two broad classes as follows:

A. Abiotic

Bottom-up effects

Burn status

- Ungulate densities will be low in areas that have recently burned and remain brown, but will be high in areas that have recently burned and have proceeded to a green flush of new growth. This effect will be strong for selective feeders and weak or absent for bulk feeders.

Water

- Ungulate density will decrease with increasing distance to water, and this effect will be stronger for the species with low tolerance to water deprivation.

Soil pH & Nutrients

- Ungulate densities will be greater in locations with high soil nutrient availability.

B. Biotic

Bottom-up effects

Vegetation & edge structure

- Ungulate density will be high in nutritious and productive short (S) green (Gr) grass, followed by intermediate height(I) brown-green (BrGr) grass, and tall (T) brown (Br) grass, respectively. These effects will be stronger for pure grazers and selective grazers, and weaker for mixed feeders and bulk foragers.

Top-down effects

Predation and predation risk

- The relationship of local ungulate densities to predation risk (represented by lion utilization distributions) is difficult to predict *a priori* if predators seek out prey concentrations and prey try to avoid predators. If constraints on habitat selection due to 'bottom-up' factors force prey to use areas of higher than average risk (even though using low risk sites would be favored by selection if not nullified by foraging constraints), then there will be a positive relationship between risk and prey density, and the intensity of predation risk will follow the sequence described in B(iv) above: highest in short green grass (S-Gr), intermediate in brown-green grass of intermediate height (I-BrGr), and lowest in tall brown grass (T – Br), respectively. This result would imply that ungulates cannot maximize diet quality and minimize risk simultaneously (Barnier et al. 2014; Christianson & Creel 2010). In contrast, a negative relationship between ungulate density and predation risk would imply that ungulates successfully reduce the limiting effect of predation through their broad patterns of distribution.

- With logic parallel to A (ii), permanent water will be associated with high predation risk (high lion utilization density), so that a positive association of ungulate density with proximity to water entails increased exposure to predation risk (Crosmary et al. 2012).

C. Anthropogenic Effects

- Ungulate densities will be low in proximity to indicators of human access or use (e.g. the park edge, tourist camps and roads). Alternatively, proximity to tourist camps might confer protection from poaching and thus might affect density positively.

2.2. Materials and Methods

2.2.1. Study Area

Our study took place in Northern Kafue National Park of Zambia (14˚ S, 25˚ E; 17 ˚ S, 27 ˚ E - Figure 1). Historically the Kaonde people of North-West Zambia inhabited the northern park until the late 1940s before repatriation to pave way for the protected area in 1950 (Mwima 2001). The park covers an area of 22,840 km^2, with nine Game Management Areas (GMAs) spanning another 44,100 km^2 around the park

(Namukonde et al 2015). The park is characterized by a dry season with no rainfall (May-November) and a wet season with rainfall ranging between 600 mm to 1,200 mm (December- April). Mean maximum temperatures range from 22-35^0 C across these seasons (Mwima, 2001). The Kafue River drains from the north of the park to the south with the Lufupa River as a major tributary draining from the Busanga plains in the north-west of the park into the Kafue (Figure 3.2). Other small rivers and seasonal streams are found across the park contributing to these waterbodies. The vegetation in and around the park are mainly closed and open miombo woodlands dominated by *Brachystegia and Julbernardia* species and mixed with thorny *Acacia* species in munga and termitaria woodlands (Midlane et al 2014). There are two major areas of grass plains, the Busanga plains in the North and Nanzhila plains in the South. Open, low bushland is common in areas of vertisols with high composition of clay.

The park is divided by the main highway from the capital city of Lusaka to Mongu in western Zambia (Figure 3.2). Our study area covered approximately 480 km^2 of the north-west region of KNP (Figure 2.2). This area was defined by the Kafue and Lufupa rivers to the east, the western park boundary to the west, the Lusaka -Mongu highway to the south, and the papyrus area within the Busanga Plains to the north.

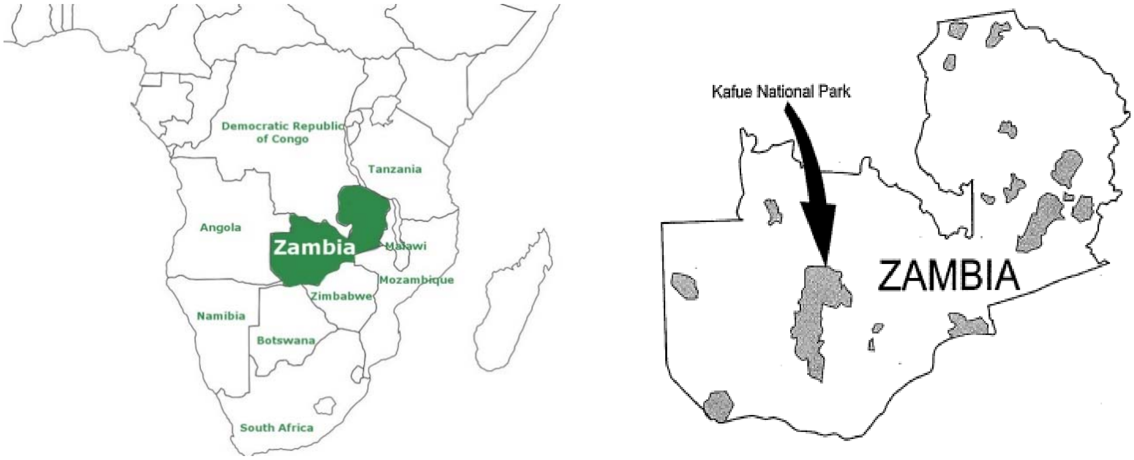

Figure 2.1. Map of East, Central and Southern Africa (left) showing the location of Zambia (source: Victoria falls – guide.net), and (right) the location of Kafue National Park within Zambia (Source: Mwima 2001).

2.2.2. Study Design

2.2.2.1. Sampling Design. In order to systematically and representatively sample the study area for distance sampling analysis (see Section 2.3), we defined eighteen (18) approximately linear transects ranging in length from 2 to 16 km (Figure 2.2). These transects ran in an east-west direction, with even spacing at 4 km intervals from north to south. This spacing was selected to ensure a low likelihood of introducing bias by double-counting herds, allowed an even distribution of effort over the sampled area with approximately 5 days' effort on each occasion, and provided sample sizes with reasonable power to test the hypotheses described above. The total length of the 18 transects summed to 119.1 kilometers surveyed per sampling occasion.

Our distance sampling analysis (Section 2.3) required covariate measurement on the transect scale (as opposed to covariate measurement for each observed herbivore group). Therefore, we split these 18 transects into smaller segments to produce a more detailed sampling unit across covariate values. We segmented each transect based on changes in the dominant vegetation type, or at 2 km intervals if the vegetation type remained constant (range= 0.3km – 2km), resulting in a total of 77 segments. We defined four classes of vegetation type, namely open grassland (OG – 23.4 %), open bushland (OB – 3.96 %), open woodland (OW – 50.19 %), and closed woodland (CW – 22.45 %). Soil and vegetation covariates were measured from sample points at the midpoint of every segment (see below). Segment midpoints were determined in ArcGIS 10 (ESRI) and marked with an environmentally-friendly marker to allow exact relocation on each sampling occasion.

We sampled transects on seven occasions across 3 years, which resulted in data recorded for 530 segment-sampling occasion combinations surveying 833.6 km (a few segments were inaccessible on a few occasions due to muddy clay soils that still retained high moisture content).

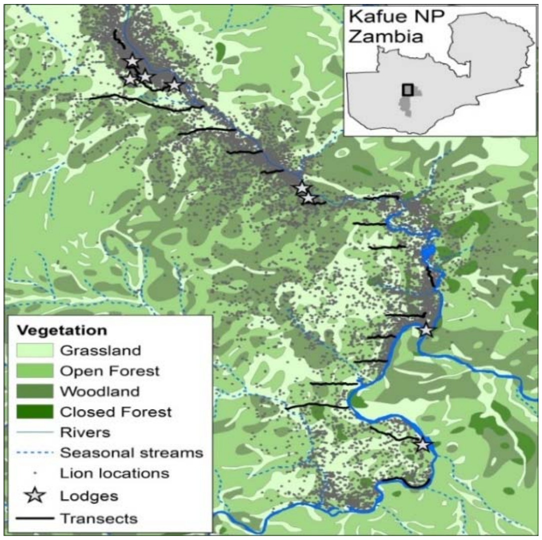

Figure 2.2. Location of transects within the KNP – North study site. Note the fixes from GPS collars showing use of the study area by lions (Midlane et al 2013), illustrating contiguous home ranges for collared prides within our study area.

2.2.3 Covariate Measurement

Our repeated, systematic survey design allowed us to measure covariates of density that varied temporally and spatially. Spatially, these covariates were either measured by continuous observation within each segment (e.g. presence of water) or at the segment midpoint designated as described above (e.g. soil nutrient availability). We created a 500 m buffer on each side of each transect segment (e.g. a transect segment of 2 km length had a buffer 2km long x 1 km wide) using ArcGIS 10 (ESRI), and determined the percent cover of each of the four dominant vegetation types. This area encompasses the maximum distance on either side that we typically observed ungulate herds. We truncated animal detections at 300-500 m based on body size (see Results), so this buffer is appropriate for describing the vegetation characteristics of ungulate locations.

2.2.3.1 Abiotic Factors. The section that follows describes abiotic, top-down factors.

2.2.3.1. a. Soil Chemistry and Texture. With the exception of the single survey in 2012, we collected soil samples at each transect midpoint on each survey occasion, using a protocol from the US Environment Protection Agency (EPA) described by Mason (1992). We collected samples using a soil augur, to a depth of 30 cm from four randomly selected sub-sites within a 5 m radius of each segment midpoint. The four samples were mixed thoroughly and a representative subsample of the mixture collected in a sealed plastic bag, labelled and stored away from direct sunlight.

We measured factors that might affect plant productivity or nutritional value (Bell 1982) including soil acidity (pH), organic matter, nitrogen (N), phosphorous (P), potassium (K), calcium (Ca), magnesium (Mg), and soil type (UNZA Practical manual 2013 / 2014). To determine soil pH, the pH-H_2O method was used where a 10 gram air dried sample was placed in a 50 cm^3 beaker and 25 ml distilled water added while stirring intermittently with glass rod. The pH was measured with a pH meter (model GTM-24- Geotechnical engineering Bureau) after 18 hours that allowed for equilibration (MCClean 1973 cited by UNZA Practical manual 2013 / 2014). For determination of total soil nitrogen percentage, we used the Macro Kjeldahl method as described by Bremner (1960). Soil organic matter percentage was determined by the Walkley & Black method (Walkley A et al 1934, 1946; Allibon 1965 - cited in University of Zambia [UNZA], School of Agricultural Sciences Practical manual 2013/ 2014). Phosphorous (mg / Kg soil) was determined by the Bray test method (Bray et al 1945 – cited in UNZA Practical manual 2013 / 2014). Potassium, calcium and magnesium concentrations were determined by Atomic Absorption Spectrophotometer (AAS) after extraction as described by Doll et al 1975 (cited in UNZA Practical manual 2013 / 2014). Soil textural size was determined using the hydrometer method (Bouyoucos 1962; Gee et al 1979).

2.2.3.1.b. Water Availability. We determined the minimum distance to permanent rivers for each segment using ArcGIS 10 (ESRI). In order to assess the effect of available water other than permanent rivers on herbivore distributions, we recorded presence of standing water within each segment (A – Absence, 78.87 %; P – Presence 21.13%). We also recorded the presence of grassy lagoons within each segment (A - Absence, 76.98 %; P – Presence, 23.02 %) as these act as natural water catchments that can retain green grass late into the dry season.

2.2.3.2 Bottom-Up Processes. The section that follows describes abiotic, bottom-down factors.

2.2.3.2.a. Vegetation Communities and Edge Density. We used the intersect tool in ArcGIS 10 and a vegetation layer based on satellite imagery for Kafue (Midlane et al. 2013) that classified the area into 'grassland', 'open forest', 'closed forest/woodland' to extract the proportion of each of these vegetation types in each segment buffer. The proportions of each vegetation type ranged from 0 to 0.995 for open grassland, 0 to 1 for open forest (open woodland) and 0 to 1 closed forest (closed woodland). In addition, we used the perimeter tool in ArcGIS 10 to determine the density of edges between vegetation types (from the satellite imagery) within each segment buffer, as a measure of habitat variability. Vegetation edge density ranged from 0 km/km^2 (uniform vegetation with no habitat type edges) to 4.34 km/km^2.

2.2.3.2.b. Vegetation Characteristics. In each segment we noted the average grass height (S – Short < 10cm, 22.45 %; I – Intermediate 10cm to 50cm, 66.04 %; T – Tall > 50 cm, 11.51 %), grass color (Gr - Green, 27.36 %; BrGr-Brown - Green, 16.23 %; Br - Brown 56.42 %), and whether or not the segment had been burned (C - Complete burn, 46.23 %; P - Partial burn, 35.09 %; N - No burn 18.68 %).

2.2.3.2.c. Anthropogenic Effects. Anthropogenic influences on ungulate distributions were assessed by measuring the distance to camps or lodges within the park and the distance to graded roads and park boundary. These distances were measured using GPS units in the field and using ArcGIS 10 (ESRI).

We also tested whether herbivore distributions were related to the type of transect surveyed. Transects were located either off-road (O - 47.55 %), following minor seasonal tracks (S – 19.06 %) or along permanent, graded dirt tracks (T – 33.4 %).

2.2.3.3. Top-down Processes: Predation Risk. To determine whether herbivore distributions were affected by spatial variation in the risk of predation, we fit a single kernel utilization distribution (Van Winkle 1975; Keating et al 2009; Worton 1989) to 24,944 lion locations collected over a period of three years (2010 to 2013) from GPS radio collars deployed in six resident lion prides and one male coalition (Midlane et al. 2013). Based on the contiguous distribution of these ranges (Figure 2.2), we believe that most or all prides were sampled so that this utilization distribution provides a realistic measure of the local probability of encountering lions. We used the ‘sp’, ‘rgdal’ and ‘plyr’ packages in R to calculate the distribution of daily distance moved, which ranged from 85 m to 24,226 m and used the mean daily distance moved as the smoothing parameter for the utilization distribution (UD), with an output grid of 300m X 300m. We fit the UD using the adehabitatHR package in R. The shape of the UD was not strongly affected by the specific kernel function used (as is typical: Silverman 1986, Calenge 2015) and the results reported here use the default (bivariate normal) kernel function for adehabitatHR.

This UD revealed substantial spatial variation in the risk of encountering lions, with the 50% isopleth (546 km^2) only covering approximately one-eighth of the 99% isopleth (4,468 km^2), and approximately one fourth of the 90% isopleth (2,336 km^2). To relate the risk of lion predation to transect data, we converted the UD from adehabitatHR to a raster using the ‘sp’ and ‘raster’ packages in R, and overlaid the raster with the buffered transects (as described above) to determine the mean lion utilization value for each transect segment.

2.2.4. Animal Counts

Animal counts were conducted during the dry season (June-November) during seven survey periods from 2012 – 2014 (2012=1 survey, 2013=3 surveys, 2014=3 surveys). Each survey period spanned several days due to the size of the study area, difficulty traveling off-road, and simultaneous soil/vegetation sampling at segment midpoints. On three occasions surveys were completed over longer periods due to logistical constraints (e.g. rainfall, vehicle maintenance).

We conducted transects with two observers on the roof rack of a vehicle, while the driver drove at a speed of 10~15 kph following the path of each segment with the aid of a dash-mounted GPS – Garmin62C model. Upon detection of a group, the driver immediately stopped the vehicle and recorded a GPS location. Roof-top observers would then measure the distance (in meters) and bearing to the herd location using a laser range finder and compass (Model: Bushnell). The vehicle bearing was also recorded, and the sighting angle was calculated from the difference between the two bearings. With the sighting angle and distance, we calculated the perpendicular distance from the transect line to the herd location. We recorded the composition of the detected herd with the aid of binoculars, including the species detected, whether it was a single or mixed species herd, the size of the herd, the number of individuals in each age class (calves, sub-adults and adults), and sex distributions of the herd members. Animals whose sex could not be determined (as was common) were assigned to an age class if possible.

2.3. Distance Sampling Analysis

We used distance sampling methods to estimate ungulate herd density, in which the true local herd abundance of a species is treated as a 'latent' or unobservable variable that is estimated using the observed counts and the estimated probability of detection. We implemented this model using the *distsamp()* function in the *unmarked* package for R (Chandler et al 2011, Sillett et al 2012) which estimates herd abundance and detection probability, as well as the effects of covariates on both (Thomas et al 2010; Fiske & Chandler 2011 cited by Royle et al 2004).

2.3.1. Model Set and Model Selection

An extremely large number of models of herbivore densities could have been tested, given the many variables we measured that could be tested for effects on density, detection or both. We adopted a multi-step process of model selection that limited the number of models fit while maintaining our ability to assess the relative importance of variables representing abiotic, bottom-up, top-down and anthropogenic limits on herbivore populations. The process described here was repeated for each species with a sufficient number of detections ($N > 40$) to allow convergence of maximum likelihood estimates of model parameters. For each species analyzed, we first used AIC scores to determine the best model of detection, considering uniform, half-normal and hazard functions of distance from the transect line, with and without vegetation type as a covariate, and (at this stage) modelling only mean density. This process identified the best model of detection probability from six candidate models for each species, and always identified a very well-fit detection model, as assessed by comparing the fitted detection function to raw detections binned by distance from the transect. Hazard and half-normal functions both performed well, with variation between species in which function yielded a better AIC score. The uniform function was not well-supported for any species. AIC scores supported the inclusion of vegetation type effects on detection for all species.

With the selected model of detection, our second step was to identify the best-supported model of effects on density within seven sets of predictors. In this step we began with sets of environmental covariates describing ecologically similar limiting effects, and used AIC scores to identify which combinations of variables were included in the best-supported model within each set. Within each set, we tested all single-predictor models and all combinations of predictors, but did not test for interactions between predictors within sets. The seven sets of models we examined at this stage were as follows:

- Water models consisting of lagoon presence, distance to permanent rivers, and distance to any water source.
- Soil type, pH and nutrients (nitrogen, organic matter, phosphorous, potassium, calcium, magnesium)
- Grass models represented by grass height, color and burn status.

- Vegetation type (closed woodland, open woodland, open grassland and open bushland). This is the only covariate that was also included in effects on detection, in addition to distance from the transect to the observed animals.
- Anthropogenic effects including the type of transect (off track, seasonal track, year-round graded track) and the distance to roads and tourist camps
- Habitat structure models including habitat-edge density, proportion of grassland, proportion of open forest and proportion of closed forest.
- Predation risk as estimated by the lion utilization distribution.

Within each of these sets, models with different combinations of covariates represent multiple working hypotheses, and information –theoretical approaches allowed evaluation of support from the data for each of the hypotheses outlined in the introduction (Burnham et al, 2011). In the final stage of model selection, we identified (for each species) all models within 2.5 AIC units of the best fitting model in each set, and used AIC scores to compare all combinations of these models across sets. The models identified in this final stage were considered the best general models of herbivore distribution and abundance in KNP. At this stage we used model-averaging with AIC weights to estimate coefficients and their variances, averaging across all models within 2.5 AIC units of the top model. We used a relatively conservative threshold ΔAIC value of 2.5 units because higher thresholds tended to support complex models that included effects with confidence intervals overlapping zero.

2.3.2. Analysis of the Complete Model Set for Two Years' Data and a Partial Model Set for Three Years' Data

Soil samples were not collected in the first field season, so the complete set of models just described could not be compared using data from all three field seasons. Thus, we conducted the complete analysis on data restricted to two years, and conducted a restricted analysis that did not consider the set of soil predictors for data from all three years. Results for the two-year and three-year analyses were generally similar, although there were substantial differences for warthogs. We report the results for both analyses but focus our inferences on results from the three-year analysis because (a) they are based on more extensive sampling, and (b) herbivore densities typically showed little relationship to soil nutrients in the two-year analysis.

2.4. Results

2.4.1. Sample Size

The species that had sufficient number of observations for distance sampling were impala, puku and warthog, table 1, species (a) to (c) refers. A set of bulk grazers consisting of hartebeest, roan, wildebeest and zebra had too few sightings to allow for distance sampling analysis (Table 1, species (d), (e), (f) and (g)). Therefore, we pooled the group of bulk grazers to a total of 71 observations and attempted a single analysis for the aggregated data for these four bulk grazers, but problems with model fitting and implausible results caused us to drop this approach.

Table 2.1. Number of observations and range of group sizes for herbivore species analyzed using distance sampling.

Species	Number of groups	Group size range
a) Impala	177	1 - 75
b) Puku	286	1 - 83
c) Warthog	91	1 - 10
d) Hartebeest	18	1 - 21
e) Roan	15	1 - 22
f) Wildebeest	21	1- 42
g) Zebra	17	2 - 15

The most abundant large herbivores in KNP were puku with mean density of 1.74 herds/km^2 (95 % CI: 1.58 – 1.89), followed by impala at a density of 0.92 herds/km^2 (95 % CI: 0.88 – 0.96), and warthog at 0.47 herds/km^2 (95 % CI: 0.43 – 0.51). The composite group of obligate grazers (wildebeest, hartebeest, roan and zebra) occurred at a mean density of 0.20 herds / km^2 (95 % CI: 0.15 – 0.25). The factors limiting these herbivores varied among species, with some effects that were important for most or all species, and some effects that were species-specific, a result that has important ramifications for conservation and management.

Akaike information criteria (ΔAIC), model weights (ω) and factors limiting the distribution and density of each herbivore species (Table 2a & 2b refers)

Table 2.2 (a) and (b). Distance sampling models with results from model selection using Akaike's information criteria (ΔAIC) and model (ω). The detection probability parameter was modeled best by habitat type, while the density parameter was modeled best by edge density, grass color and height, anthropogenic, water and lion utilization density [LUDS] (proxy of predation risk) as environmental covariates.

a) Three (3) years data

Species	**Log mean density models**	**Detection Covariate**	**Detection function**	**K**	**AIC**	**ΔAIC**	**ω**
Impala	~Habitat ~ DPB	Habitat	Hazard	7	1,169.15	0.00	0.62
	~Habitat ~ DPB + LUDs	Habitat	Hazard	8	1,171.14	2.00	0.23
Puku	~Habitat ~Lgn + DtR + LUDs	Habitat	Hazard	9	1,393.86	0.00	1.00
Warthog	~Habitat ~DCL + TT	Habitat	Half – normal	8	627.81	0.00	0.33
	~Habitat ~DCL + TT+LUDs	Habitat	Half – normal	9	628.53	0.72	0.23
	~Habitat ~DR + DCL + TT	Habitat	Half –normal	9	629.01	1.21	0.18
	~Habitat ~DR + DCL + TT + LUDs	Habitat	Half –normal	10	629.61	1.80	0.13
	~Habitat ~GH + GC	Habitat	Half –normal	9	629.69	1.88	0.13

DCL - Distance to camp lodges; DPB - distance to park boundary; DR - distance to roads; DtR - distance to river; GC – Grass color; GH - Grass height; Lgn - Lagoon; LUDS - lion utilization densities; TT - transect type

Table 2.2 (b)

b) Two (2) years data

Species	Log mean density models	Detection Covariate	Detection function	K	AIC	ΔAIC	ω
Impala	~Habitat ~ DPB	Habitat	Half-normal	6	943.98	0.00	0.69
	~Habitat ~ DPB + LUDs	Habitat	Half-normal	7	945.98	2.00	0.25
Puku	~Habitat ~Lgn + DtR	Habitat	Hazard	8	1095.04	0.00	0.69
	~Habitat ~Lgn + DtR + LUDs	Habitat	Hazard	9	1096.68	1.64	0.31
Warthog	~Habitat ~ DCL + TT	Habitat	Hazard	9	518.39	0.00	0.51
	~Habitat ~DR + DCL + TT	Habitat	Hazard	10	519.94	1.55	0.24
	~Habitat ~ DCL + TT + LUDs	Habitat	Hazard	10	520.02	1.63	0.23

DCL - Distance to camp lodges; DPB - distance to park boundary; DR - distance to roads; DtR - distance to river; GC - Grass color; GH - Grass height; Lgn - Lagoon; LUDS - lion utilization densities; TT - transect type

Table 2.3 (a) and (b). Coefficient estimates of impala, puku and warthog herd density from highest ranking models.

a) Three years data	**Impala**			**Puku**			**Warthog**		
	Coefficient	LCL	UCL	Coefficient	LCL	UCL	Coefficient	LCL	UCL
Anthropogenic									
• Distance to roads	-	-	-	-	-	-	0.86	0.61	1.20
• Distance to camp lodges	-	-	-	-	-	-	0.88	0.82	0.94
• Seasonal (s) tracks transects	-	-	-	-	-	-	0.72	0.39	1.34
• Permanent (T) track transects	-	-	-	-	-	-	0.38	0.22	0.67
Edge effect	-	-	-	-	-	-	-	-	-
Distance to park boundary	1.08	1.05	1.11	-	-	-	-	-	-
Soil pH & Nutrients	NA	NA	NA	NA	NA	NA	NA	NA	NA
Vegetation (grass & structure models)									
• Short (S) grass height	-	-	-	-	-	-	1.71	1.05	2.77
• Tall (T) grass height	-	-	-	-	-	-	0.26	0.06	1.08
• Brown-Green (BrGr) grass color	-	-	-	-	-	-	2.45	1.32	4.54
• Green (Gr) grass color	-	-	-	-	-	-	2.78	1.62	4.78
Water effects									
• Lagoon presence	-	-	-	1.96	1.42	2.72	-	-	-
• Distance to river	-	-	-	0.50	0.43	0.58	-	-	-
Predation effect									
• Lion UDs	0.9998	0.9964	1.0032	1.0018	0.9999	1.0037	0.9961	0.9904	1.0018

LCL - Lower confidence limit; UCL - Upper confidence limit. Effects not detected in the top model are denoted with dashes. The two year dataset allowed models of soil effect to be tested. Coefficients were back transformed to the original scale of measurement, and thus represent multiplicative effects.

Table 2.3 (b)

b) Two years data

	Impala			**Puku**			**Warthog**		
	Coefficient	LCL	UCL	Coefficient	LCL	UCL	Coefficient	LCL	UCL
Anthropogenic									
• Distance to park boundary	1.08	1.05	1.11	-	-	-	-	-	-
• Distance to roads	-	-	-	-	-	-	0.88	0.60	1.29
• Distance to camp lodges	-	-	-	-	-	-	0.89	0.83	0.96
• Seasonal (S) track transects	-	-	-	-	-	-	0.39	0.17	0.86
• Permanent track (T) transects	-	-	-	-	-	-	0.47	0.26	0.84
Edge effect	-	-	-	-	-	-	-	-	-
Soil pH & Nutrients	-	-	-	-	-	-	-	-	-
Vegetation (grass & structure models)	-	-	-	-	-	-	-	-	-
Water effects									
• Lagoon presence	-	-	-	2.51	1.72	3.65	-	-	-
• Distance to river	-	-	-	0.46	0.39	0.55	-	-	-
• Predation effect									
• Lion UDs	0.9999	0.9963	1.0035	1.006	0.9985	1.0027	0.9977	0.9915	1.0040

LCL - Lower confidence limit; UCL - Upper confidence limit. Effects not detected in the top model are denoted with dashes. The two year dataset allowed models of soil effect to be tested. Coefficients were back transformed to the original scale of measurement, and thus represent multiplicative effects.

2.4.2. Impala

The log mean density models were the same for the three and two years analysis with difference observed at detection function that is half-normal in the two years data verses hazard detection function in the three years data. The number of parameters for each model varied slightly. In the two years data the top two models received 94 % of the model weight and 85 % variation in the three years. Distance to park boundary (DPB) was the sole covariate from the top model identified to be limiting impala density and distribution. Addition of the predation risk covariate to the top model received a model weight of 23 % for the three year data and 25% for the two years data (See table 2.2 (a) and 2.2 (b)). Thus, anthropogenic effects dominated other effects on the distribution of impala.

Impala density showed a strong positive relationship to distance to park boundary, with a 1.08 fold herd increase / km^2 (95% CI: 1.05 – 1.11) for every km^2 away from the park boundary (Figure 2.3). The relationship between impala density and predation risk was not strong, with a confidence interval overlapping one (95% CI: 0.996 - 1.003, see Figure 2.3 and table 2.3 (a)). The result however, suggests that impala may be constrained by other factors to concentrate in areas with heavy use by lions. Similar estimates were obtained from models fit to the two-year and three-year datasets.

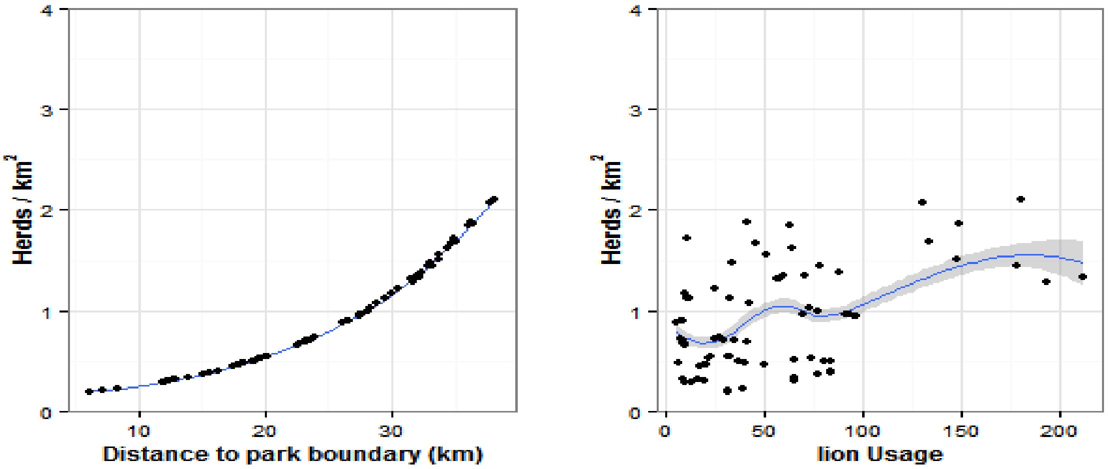

Figure 2.3. Effects on impala density (herds/km^2) from the top model: (left) anthropogenic effect of distance to the park boundary, (right) effect of predation risk, as measured by the intensity of use by lions.

2.4.3. Puku

A single model of puku herd density received all of the AIC weight for the three-year analysis, including effects of distance to river, grassy lagoon presence and lion utilization. For the two years we had two models as top ranking, again including effects of distance to river and grassy lagoons, the first without LUDs and the second with LUDs. The two models account for 69 % and 31 % of the AIC weight. In both analyses the hazard detection function was used to model density. For puku, lagoon presence, distance to river (hypothesis A (ii) – bottom-up abiotic effect) and predation risk (hypotheses B (v) and B (vi) – top-down biotic effect) are the limiting factors of greatest importance

As expected from prior studies of their ecology (Goldspink et al. 1998), the density of puku was strongly associated with proximity to rivers and lagoons (Figure 4). Puku herds were almost twice as common (1.96-fold increase, 95% CI: 1.42 – 2.72) in transect segments that held seasonal lagoons, and puku herds declined by 0.5 fold / km^2 (95% CI: 0.43 – 0.58) for every km moved away from the river (Figure 2.4).

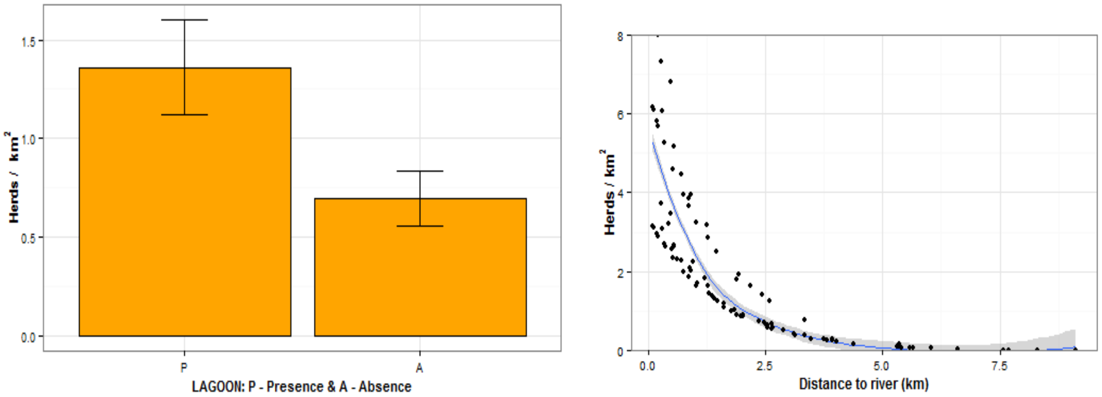

Figure 2.4. Effects on puku density (herds/km2) from the top model: presence of lagoons (left), distance to rivers (right).

In KNP-north, the presence of lagoons was associated with the presence of surface water well into the dry season, with continued availability of green grass when the surrounding grass had become dry and brown. Puku were commonly observed in these patches of fresh green grass (Figure 2.5).

Figure 2.5. Puku observed grazing in lagoons that still retained fresh green grass in the dry season.

2.4.4. Warthog

In the three years analysis half-normal detection function was used versus the hazard in the two year analysis. The top ranking model in the three years analysis accounted for 33 % of the AIC weight, and included two anthropogenic effects: transect type and distance to tourist camps or lodges. The two years top model contained the same covariates as the three year model, accounting for 51 % of AIC weight. Inclusion of lion utilization with these predictors yielded a model with 23% of AIC weight, for both the three year and two year analysis. The notable difference between the two analyses is that grass color and height featured in the three years data accounting for 13 % of the model weight. In essence we had five (5) selected models in the three years analysis. The top ranking model in the three years data still retained the top rank in the two year data analysis but with higher model weight (51%). Anthropogenic, vegetation and predation risk are the three broad ranges of limiting factors identified by the models. Specifically the covariates with the strongest effects on warthog are distance to tourist camp lodges and transect type, (hypothesis C (vii) – bottom-up biotic effect), lion UDs (hypothesis B (v) and B (vi) – top-down biotic effect), grass height and color (hypothesis A (i) – bottom-up biotic effect, hypothesis B (iv) – bottom-up biotic effect). Contrary to the simplest formulation of hypothesis B (vii), but compatible with the hypothesis that tourist camps can provide a refuge from poaching, warthog density was higher in proximity to tourist camp lodge and distance to roads (see Figure 2.6).

The herd density of warthogs decreased with increasing distance to tourist camps (0.88 fold / km^2 from the lodge, 95% CI: 0.82 – 0.94) and decreased very similarly with increasing distance to the nearest road (0.86 fold / km^2, 95% CI: 0.61 – 1.20). These effects suggest that proximity to tourist activity might convey some protection for warthogs, but this inference is complicated by the finding that warthog density was significantly higher in off-track segments than near seasonal tracks (0.72 fold decrease km^2, 95 % CI: 0.39 to 1.34), and lowest near permanent tracks (0.38 fold decrease km^2, 95 % CI: 0.22 to 0.67) – see Figure 2.6 and table 2.3 (a). Warthogs were very sensitive to grazing conditions, with densities approximately three times higher in short grass areas (1.71 fold increase / km^2, 95 % CI: 1.05 to 2.77) than in tall grass areas (0.26 fold decrease / km^2, 95 % CI: 0.06 to 1.08), and approximately three times higher in areas with green grass (2.78 fold increase / km^2, CI: 1.62 to 4.78) than in areas with dormant brown vegetation (Fig. 2.6). The intermediate brown-green grass also supported a considerably high numbers with 2.45 fold increase / km^2 (95 % CI: 1.32 to 4.54). Finally, the effect of predation was weak, with a 95% CI of 0.991 – 1.002.

Coefficient estimates for the two year and three year data sets, produced appreciably different results for warthog, unlike the other species. It is here seen that vegetation (or grass) models did not feature among the top predictors in the two years data. They only do so after inclusion in the analysis of the three year data. It is noted that seasonal (S) tracks transect had herd density decrease of 0.72 fold / km^2 in the three year data compared to 0.39 fold for the two year data, so the direction of this effect was consistent, but not the magnitude. The permanent track (T) transects had density of 0.38 fold decrease in three years compared to 0.47 fold in two year data set. Lion UDs coefficient for the three year data was 0.997 compared to 0.998 for the two year (Table 2.3 (a) and 2.3 (b) refers – for all the species under consideration).

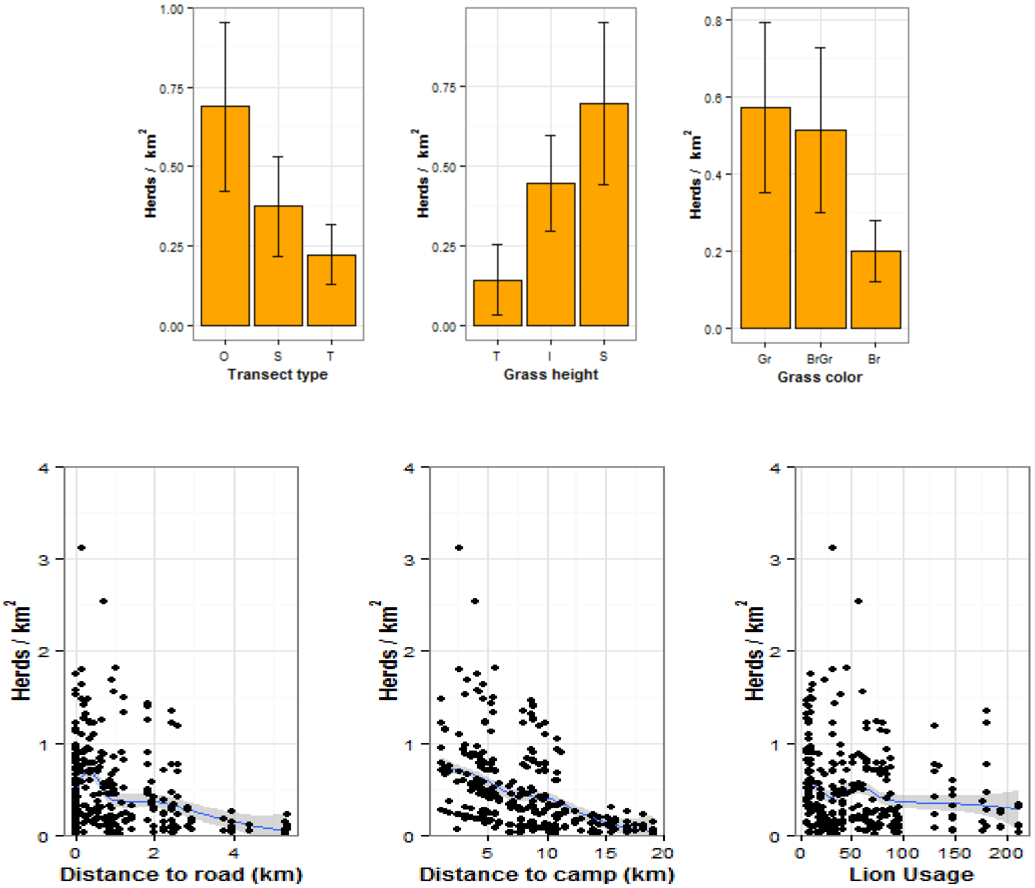

Figure 2.6. Effects on warthog density (herds/km2) from the top model: (top left) transect type, (top middle) grass height, (top right) grass color, (bottom left) distance to the nearest road, (bottom middle) distance to the nearest tourist camp, (bottom right) effect of predation risk as measured by the intensity of use by lions.

2.5. Discussion

Many herbivore surveys in sub-Saharan Africa are concerned only with animal numbers particularly reporting on whether there is increase or decrease in the species under consideration. These surveys are often conducted from the air using methods that do not correct for variation in the probability of detection, and often focus on temporal trends in density without directly testing what factors affect density. In this study we reported both the herd density and factors affecting the spatial distribution of the herbivores. Selection from multiple competing candidate models that made biological sense from Akaike's information criteria (AIC) attest that factors affecting large herbivore distribution and density in KNP - North are (i) distance to park boundary and predation risk (impala), (ii) lagoon presence, distance to river and predation risk (puku), (iii) distances to graded roads, tourist camp lodges, transect type, grass height and color and predation risk (warthog). We also noted a degree of consistency in the coefficients realized over a segmented time frame of two and three years data analyzed separately with major difference in warthog that showed effects of grass color and height in three years and not at two years of data collection.

2.5.1. Impala

Impala density is influenced by distance to park boundary (i.e. anthropogenic effect - hypothesis C(vii) and a weak relationship with lion UDs, which represent a very coarse scale of predation risk (top-down effect - hypothesis B (v) and B (vi). It is not surprising that grass height and color did not have any effect as impala is a mixed feeder that can browse and graze (Wronsky 2002), so their location is not necessarily driven by presence of green grass but other factors such as available browse. Distance to water did not arise as an important factor for the impala either, though they are regular drinkers especially in the dry season when their foraging is strategically located in areas with access to water. Impala seem to be more tolerant to water deprivation than puku, perhaps due to compensatory moisture obtained from succulent browse during feeding. Their diet is however dictated by local seasonal conditions and often preferring palatable grasses when available and shifting to browsing in the dry season (Monro 1980; Rodgers 1976; Stewart 1971).

It is however revealing that distance to park boundary had such a profound and negative effect on impala density. Causation for the reported effect from the observational data cannot be attributed to park boundary in isolation. Three years sampling seasons from dry to just the beginning of the wet season has yielded the general observation that the home range for impala contracts inwards and away from the park boundary. Low density near park boundaries suggests avoidance, but could also be due to direct mortality from poaching near the park boundary. This scenario will tend to gravitate to both inter and intra-species competition for shared food resource.

Further investigation may be required to pinpoint the direct causes driving the relationship between density and distance to the park boundary. Other studies assessing disturbance of animals in general due to anthropogenic effect scale the distance and density of people to established protected areas and typically measure density of animals adjacent to such human settlements. The high probability of illegal off-take in such adjacent areas providing access routes to the park usually reveal low animal density in comparison to areas without and / or far away from human settlements and some cases linked to prediction of extinction (Hofer et al, 2000 cited by Hopcraft et al 2014; Cincotta et al 2000; Brashares et al 2001). In other monitoring programs of anthropogenic disturbance indicators, heightened levels of wire snaring in protected areas adjacent to human settlement have been detected (Becker et al, 2013; Lindsey et al 2013; Watson et al 2013). Increase in bush meat trade is linked to increased illegal off-take of wildlife resources with observation that human settlement near parks act as a conduit of illegal hunting activities. They often target areas with high numbers of wildlife especially in the dry season when most wildlife is concentrated near water sources. Landscapes outside protected areas have had wildlife resources extirpated thus leaving illegal hunters with little choice but to target protected areas for bush meat used to generate money and to provide household food security (Lindsey et al 2013). This provides a credible explanation as to why impala density declines in proximity to park boundary. The relationship of impala density to the park boundary should be considered in current wildlife management plans and all future impala restocking exercises at both national and local game ranch scales.

While models that included the effects of lion density received some AIC weight, the confidence interval for this effect included 1.00, indicating relatively little effect of predation risk from lions on impala distributions, but lending some support to the hypothesis that herds are constrained to areas by other factors (such as high quality forage) despite the high predation risk. That is, the risk of predation might be outweighed by the benefits for the impala in these areas. In such situations generally prey species have to make a decision that balances between nutritional benefit and the cost of predation risk (Apfelbach et al 2005). The cost of not undertaking such a balance or avoiding the risk of predation may be seen in undernourished herds or individuals with consequent negative impact on reproduction through lowered conception rate. Some studies have concluded that such energetic costs do actually cause changes not only in impala but across prey species growth, fecundity and population dynamics (Wearner & Peacor 2003; Schmitz et al 2004; cited by Preisser et al 2007). Such anti-predator responses mounted by prey have costs resulting in lowered survival, growth and reproduction as shown in the study conducted in Yellowstone National Park on elk herds (Creel et al 2005; 2007; 2008).

2.5.2. Puku

Prominent determinants of puku density were presence of lagoon, distance to river (bottom-up effects – hypothesis A (ii)) in line with prior research (Goldspink et al 1998) and predation risk (hypothesis B (v), & B (vi)). Goldspink et al (1998) found that puku was mostly confined to river floodplains, lagoons and nutrient rich grassland habitat (Spinage 1986 cited by Goldspink 1998; Rduch 2014). The top most model also included lion utilization density, indicating broadly that puku distributions are affected by a balance between bottom-up and top-down effects, and narrowly that predation risk is high near the river and lagoons in keeping with hypotheses outlined above. That puku exhibited low tolerance to water deprivation is shown by concentration of the predicted herd density to within 5 km distance from the river (see Figure 2.4). The presence of lagoons in regions within 5 km distance to river is associated with high predicted puku density, and these areas were predisposed to considerable predation risk. The data shows the puku's heavy dependency on water where sit-and-wait predators, such as lion, are common. Because of their low tolerance level to water deprivation, puku return to the areas within access to permanent water in spite of predation risk. Since the river frontage is wide, if lions persist for longer than usual in one place, puku may shift grazing to some other river frontage, or lagoon. Note that some of the lagoons are associated with fresh green lush grass well into the dry season with or without water (see Figure 2.5). It is not uncommon also to see them seeking refuge in woodland area immediately adjacent to the river, but not for extended periods before returning to more open grassland. The sensitivity of the species to water presence has important implication to potential climate change impacts. Lagoons, floodplains and rivers play a role in long term viability of the species population. If droughts resulting from climate change persist or ecosystem fragmentation from land transformation leads to unavailability of surface water the chances are that the whole balance will be upset posing a risk of loss of the species via reduced recruitment and high calf and adult mortality (Gasaway et al 1996; Dipotso et al 2006). The effect of drought might cascade to other large herbivores in the ecosystem, but would be likely to have large impacts on puku in the initial stage because of low tolerance threshold to scarcity of water. The ensuing process would ultimately end up affecting even the predators as the most readily available prey becomes less available in the long run forcing predators to go long distances in search of prey that is not easily obtainable. Puku might constitute a large proportion of lion diet because they are one of the most abundant herbivores locally and they congregate near water and grassy lagoons (Goldspinks 1998; Rduch 2014; Dipotso 2006) where sit-and-wait predators typically have a high probability of success.

2.5.3. Warthog

Factors associated with warthog distributions were complex, with a broad range of limiting effects associated with warthog density. Distance to roads and camp lodges (anthropogenic effects) showed a reduction in predicted herd density with increasing distance, contrary to the hypothesis of reduced density near human activities, but compatible with the hypothesis that tourist activities convey safety for warthogs, or that tourist activities concentrate in areas suitable for warthogs. Further, transect type warthog density was found to be higher on off-roads than seasonal and permanent tracks (roads) transects. The result is contradictory in that predicted density is high near human establishments (lodges and roads) while on the other it is somewhat low on seasonal and permanent tracks, because the tracks being referred to are the same tracks for which the distance to roads covariate was measured. Higher density was associated with off-road tracks free of anthropogenic influence (see Figure 2.6 – top left). Whereas there is a clear overlap in densities between seasonal tracks transects and off-road transects, there is none between permanent tracks transects and off-road transects. It is worth noting that the seasonal tracks consisted of man - made and animal tracks. The result shows warthog density being both high and low in proximity to human indicators, that is, in support and at the same time contradicting hypothesis C (vii). However, this apparent contradiction makes sense for the reason that KNP-North closes to tourism operation just at the onset of the rain season (mid-November to early May) because of road inaccessibility when it rains. And at the same time frequency of park patrols by law enforcement officers drop with occasional deployment of a team or two at most during the rainy season to strategic locations. Poachers seem to capitalize on scaled down anti-poaching activities with illegal hunting rampant during the rainy season. It makes plausible sense then that some tracks accessed on foot by poachers and / or predators are associated with poaching and predation activities and warthog exhibit a learned response that tends to avoid them (Alcock 1993). When the season opens (early May to mid-November) and as tourists are driven around on the game loops, the warthogs again seem to instinctively condition themselves and adjust to vehicle sound and movement that is not associated with danger. The vehicles repeatedly driven to and from camp lodges help augment this learned response such that warthog may quickly associate this with low risk resulting in none avoidance and reduced proximate distance to the tourist camp lodges (See Figure 2.6 – bottom, left and middle figures).

Warthog response to being hunted can be equated to predation risk response, with the risk emanating from poachers or hunters. One global survey estimates that humans kill adult prey the reproductive capital of most populations at 14 times higher than actual predators thus making humans the dominant predators (Darimont et al, 2015). And just as they would respond in an eco-biological setting with mounting anti-predator behavior, we suggest warthogs are reacting to either human or carnivore predation in the same way as other species do (Madsen 1998, Bregnballe et al 2004, Jayakody et al 2008, Theuekauf and Rouys 2008, Casas et al 2009, Frid & Dill 2002 - cited by Ordiz et al 2012).

Vegetation covariates showed significant limiting effects on warthog density, through grass color and height. Density was highest in green grass (2.78 fold increase of herds per km^2 relative to brown grass) followed by intermediate brown-green grass 2.45

fold increase of herds per km^2 relative to brown grass). Density was also higher in short grass (1.71 fold increase of herds per km^2 relative to intermediate grass) than tall grass (0.26 fold decrease of herds per km^2 realative to intermediate grass). The vegetation covariates present bottom-up effects operating to produce higher densities in areas with short, green grasses (hypotheses A (i), and B (iv)). High quality food patches are associated with greenness of the vegetation (Hopcraft et al, 2014; Treydte et al, 2006). Evidence shows that warthog density is higher in these quality patches of vegetation (green and brown-green grass) than in the brown patches in keeping with the two priori hypotheses. There was no overlap between the two and brown grass density. Some of the short grass had evidence of previous fires leading to fresh shoots of green grass growing. Areas remaining brown often had wilted grass and if no evidence of fire the grass height was classified as short, intermediate or tall. In addition to low dietary quality, the tall grasses posed visibility challenge for warthog and perhaps to reduce predation risk they avoided tall grasses keeping their density at the minimum as shown (see Figure 2.6, top middle) and mostly using intermediate height to short grass. Notice also that there is no overlap between these two and tall grass. Sinclair (1985) observed similar results with a larger warthog percentage mainly confined to the 10 and 25 cm tall grass and half green to green grass in the Serengeti – Mara ecosystem. Treydte et al (2006) also found that warthog preferentially foraged in or near former cattle paddock enclosures because of the high nutritional value of the grasses growing on nutrient seeded rich soils from cattle manure. Two of their hypotheses confirmed are that “warthogs select their food to maximize nutrient intake and for this reason they fed preferentially” in the former cattle holding areas with nutrient rich soils and grasses. Though in open savanna the soil and grass nutrient are not comparable to nutrient fortified former cattle paddock areas, our finding is in agreement with warthog maximizing nutrient intake in green and partially green grass areas more than in brown grass. This is evident by the higher multiplicative herd density in comparison to the brown grass areas. Implication of this in conservation is that species that defecate in middens (e.g. rhino – family *rhinocerotidae*, impala – *Aepyceros melampus*, duicker – *Sylvicapra grimmia*) play a role of enriching some patches with super concentrate of nutrients into the soil that benefit vegetation upon which ungulates graze especially in the rain season when sufficient moisture from rain trigger plant growth (Durant et al 1988; Mduma et al 1999 cited by Treydte et al, 2006).

In many ecosystems the number of herbivores is in decline due to some ecological and anthropogenic influence (Darimont et al, 2015). It is likely that the full scale impact of herbivore loss in the wild will be felt at all trophic levels because of alteration of their functional presence (absence!!) in the environment. In KNP-North, the Busanga grassland is inundated with floods that wash nutrients into the plains as water come surging from the North and North western in the rain season. This could be the main source of soil nutrients in the grassland during the wet season and that this is complemented by herbivores as they come to graze after the floods rescind.

For warthogs, predation risk from lions was included in models within 2.5 AIC units of the top model, but as for other species, the effect of predation risk was weak in comparison with bottom up or anthropogenic effects. In general, there was little evidence of top down limitation on herbivore distributions in Kafue, perhaps because, as Midlane

(2014) has suggested, large carnivore populations in Kafue has been reduced to relatively low numbers.

2.6. Conclusion

Our research shows that not all environmental covariates investigated were ranked as factors affecting density and distribution of herbivores in KNP-North. On the anthropogenic level, distance to roads, camp lodges followed by seasonal and permanent tracks featured as the main factors. Of the covariates describing edge effects, only distance to park boundary had influence on impala and not on any other species. McNaughton (1988, 1990) found that "mineral content of forages differentiated areas of high and low animal density" though "soil variables did not aid in interpreting plant variation." Our findings are in agreement in that soil pH and nutrients did not stand out as influencers of density and distribution on any one species despite having recorded some high density in lush green vegetation. Soil fertility in respect to nitrogen, sodium and phosphorous however are reported to contribute to forage mineral properties in migratory herds of the Serengeti though only magnesium levels were of significance (McNaughton, 1990). Whereas forage mineral analysis may be indicator of meeting animal needs, soil mineral analysis may not, as suggested by our observation and others (McNaughton, 1988; 1990; Nicholson, 1954). Warthog showed a sensitivity to vegetation and grass structure with high density in short (as opposed to low density in tall grass), green and green-brown grass. Water effects were exhibited by puku with high density in areas with lagoon presence and confined home range to within 5 km distance from the river.

Predation risk featured among the AIC selected models and was detected in the top most model for puku, second and fourth model for warthog. For impala predation risk featured in the second model. Overall, predation risk played a relatively minor role in the distribution and density of herbivores in KNP.

CHAPTER THREE

TOP-DOWN, BOTTOM-UP AND ANTHROPOGENIC EFFECTS ON LARGE HERBIVORE GROUP SIZES IN KAFUE NATIONAL PARK, ZAMBIA

3.1. Introduction

The evolution of group size in social species has been studied from many perspectives in many species, and a wide range of empirical and theoretical studies make it clear that group size is affected by a complex set of selection pressures (Krause & Ruxton 2002). For ungulates in particular, the primary factors affecting group sizes have typically been dichotomized into two main classes, namely bottom-up effects including the quality and quantity of food, soil nutrients and access to water, and the top-down effect of predation risk (Hopcraft et al. 2010; Mduma et al. 1999; Sinclair & Arcese 1995; Sinclair 1985). It is now widely recognized that antipredator responses often incur significant foraging costs (risk effects), an interaction that blurs the clean distinction between purely top-down and bottom-up processes (Creel & Christianson 2008). It has also become increasingly clear that human activities have strong and pervasive effects on ungulate abundance and ecology even in large, protected ecosystems (Western et al. 2009), suggesting that anthropogenic effects must now be included as a major class of importance(Sanderson et al. 2002). Finally, there are some factors that are difficult to categorize as top-down or bottom up, because they can affect optimal group size through both mechanisms. For example, both bottom-up and top-down effects may vary as a function of the extent of recent fires and / or rain, which can alter the quantity and quality of food while also changing the conditions for hunting.

The predicted effects of bottom-up factors on ungulate herd sizes are conceptually simple and parallel predictions about effects on movements and distributions (Hebblewhite et al. 2008; Hopcraft et al. 2014). By reducing competition within groups, increases in the local abundance or quality of resources (particularly food) promote increases in density and local group size. In contrast, the effect of predation risk on group size can be difficult to predict (Creel & Winnie 2005; Lima & Bednekoff 1999), because larger groups may be better able to detect or deter predators (Caro 2005; Lima & Dill 1990; Roberts 1996) and individuals in large groups benefit from dilution of risk (Hamilton 1971), but larger groups may also be more easily detected or preferentially attacked by predators (Creel & Creel 2002; Krause & Godin 1995; Uetz et al. 2002). In some species larger groups help to fortify their communal defense by challenging predators by countering attack through mobbing that usually scares the enemy to the fitness advantage of the group than if living in solitary isolation (Volka Haas 1985). Thus, while aggregation into larger groups often reduces the risk of predation for ungulates (Creel & Creel 2002) and other species (Caro 2005; Cresswell 1994; Lima & Dill 1990), commonly through dilution of risk, there are also cases in which ungulates disaggregate into smaller groups under conditions of increased predation risk (Creel & Winnie 2005), presumably to reduce the likelihood of detection (Cresswell & Quinn 2010).

Most studies of group size, including our own (Creel & Winnie 2005), have focused on a single species, and many (Kruuk 1964; Moller 1987; Okamura 1986; Petit et al 1987) have focused on testing the effect of a single factor which in effect oversimplifies by averaging out other dynamical interactions (Hassell et al 1976; McGill et al 2007) . This approach has been highly productive from the perspective of testing specific hypotheses, but does not directly address the relative importance of the selection pressures discussed above. Here, we took a broader approach, examining the relative strength of bottom-up, top-down, anthropogenic and abiotic effects on group size for the three most abundant large herbivores (impala [*Aepyceros melampus*], puku [*Kobus vardonii*) and warthog [*Phaecocerus ethiopicus*]) in Kafue National Park, Zambia. To address a common weakness of empirical studies of group size (which often rely on opportunistic observations), we temporally and spatially stratified our sampling effort to obtain representative data. By considering a comprehensive set of factors that might affect group size and comparing their effects across species, relatively broad inferences about factors affecting ungulate social organization are possible. These results are also of immediate importance for conservation, because variation in herd size contributes to variation in local ungulate density, and ungulate declines at the continental scale have become one of the most pressing conservation concerns in Africa (Bolger et al. 2008; Ripple et al. 2015; Watson et al. 2013; Western et al. 2009). In this regard, Kafue National Park is important at the national, regional and continental scales, because Kafue is a large and central component of the proposed Kavango-Zambezi Transfrontier

Conservation Area, potentially one of the most important sites for ungulate conservation in the world.

3.2. Methods

3.2.1. Study Area

Kafue National Park is located in south central Zambia (Fig. 3.1). The park covers an area of 22,840 km^2, with nine buffer zones (Game Management Areas - GMAs) spanning another 44,100 km^2 adjacent to the park, for a total area of 66,940 km^2, among the largest protected areas on the continent. The park is characterized by a dry season with no rainfall and a wet season with rainfall ranging between 600 mm to 1,200 mm. Mean maximum temperatures in the coldest month averaging 22^0 – 28^0 C and mean maximum of 31^0 - 35^0 C in the hottest month (Mwima, 2001). The Kafue River drains from the north of the park to the south with the Lufupa River as a major tributary draining from the Busanga plains in the north-west of the park into the Kafue (Fig. 3.2). Other small rivers and seasonal streams are found across the park and within the study area. The vegetation in and around the park are mainly closed and open miombo woodlands dominated by *Brachystegia* species occasionally mixed with thorny *Acacia* species in munga woodlands. Open, low bushland is also common, primarily in areas with silty black cotton soil. There are two large areas of completely open grassland plains, Busanga plains in the North and Nanzhila plains in the South.

The park is divided by the main highway from the capital city of Lusaka to Mongu in western Zambia. The study area was sited in the north-west portion of the park, with its eastern edge defined by the Kafue and Lufupa rivers, its western edge defined by the park boundary, the southern boundary defined by the Lusaka -Mongu highway, and the northern edge defined by the southern edge of the papyrus area within the Busanga Plains. The area enclosing track transects for measurement of ecological variables was approximately 480 km^2. An axis of 130 km from north to south and a variable width averaging approximately 35 km from east to the western park boundary represent approximately 4,550 km^2. Within this larger area of the study site we estimated the covariate of group size location with distance to the western park boundary.

Figure 3.1. The location of Kafue National Park within Zambia (Source: Mwima 2001).

3.2.2. Sampling Design and Observations of Group Size

To obtain spatially representative data, we established 18 approximately straight linear transects ranging in length from 2 to 16 km. All transects ran in an east-west direction, with even spacing of about 4 km intervals from north to south. This spacing was selected to ensure a low likelihood of double-counting herds, allowed an even distribution of effort over the sampled area with approximately 5 days' effort on each occasion, provided sample sizes with good statistical power, and sample across a range of conditions suitable to test the effects on group size described in the introduction. The total length of the 18 transects summed to 119.1 kilometers surveyed per sampling occasion.

Transects were driven slowly (typically 10 ~15 kilometers/h) with the driver navigating using a GPS with the transect line plotted on a moving map and two observers on the roof rack, one responsible for each side. When herbivores were detected, the vehicle was stopped and the species present and number of individuals of each species (with age-sex classifications) were recorded using binoculars, with both observers confirming the counts with assistance from the driver. The observers would then measure the distance (in meters) and bearing to the herd location using a laser range finder and compass (Model: Bushnell). The vehicle bearing was also recorded, and the sighting angle was calculated from the difference between the two bearings. With the sighting angle and distance, we calculated the perpendicular distance from the transect line to the herd location. In our statistical analysis, we analyzed herd size by species, but included a covariate identifying herds as single-species or mixed-species to account for the presence of individuals of other species.

Because the Kafue River run from north to south along one edge of the study site, each (east-west) transect sampled along a gradient of distance to permanent water and the associated vegetation types. To allow analyses of distance to the river, vegetation type and associated effects on local group size, we segmented each transect at intervals that corresponded to changes in the dominant vegetation type, or at 2 km intervals if the vegetation type remained constant. The shortest resulting segment was 0.3 km. We defined four classes of vegetation type, namely open grassland (OG – 23.4 %), open bushland (OB – 3.96 %), open woodland (OW – 50.19 %), and closed woodland (CW – 22.45 %). The midpoint of every segment was determined using a Garmin62C GPS and marked with environmentally friendly marker (green paper tape) to allow exact relocation on each sampling occasion. All data were recorded with an exact location using GPS, and by transect and segment number, with KT1.1 representing Kafue Transect number 1, segment number 1, KT1.2 representing Kafue Transect 1 & segment number 2 and so on. A total of 77 segments (and thus 77 midpoints) were established along 18 transect lines representing a distance of 119.1 km.

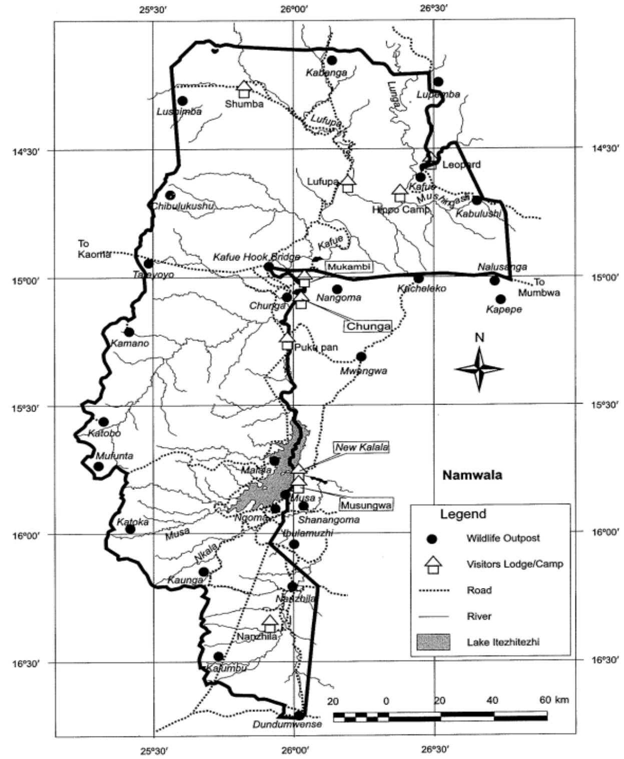

Figure 3.2. Map of Kafue National Park. KNP north is above the 15030' S line of latitude (Source: Mwima 2001).

To obtain temporal replication, we sampled the transect network on seven occasions, thus recording data for 530 segment-sampling occasion combinations (a few segments were inaccessible on a few occasions). We conducted one survey in 2012 (without soil sampling: see below). In 2013 and 2014 we carried out three surveys each year, beginning in June and ending in November when the survey lines became inaccessible due to rains. The cumulative total distance surveyed over the seven periods was 833.6 km.

Transects were conducted off-road (O - 47.55 %), following minor seasonal tracks (S – 19.06 %) and along permanent, graded dirt tracks (T – 33.4 %). The effects of distance to the nearest track and track type were considered explicitly in analysis.

3.2.3. Bottom-up Limiting Factors

We initially described the dominant vegetation type in each segment by direct observation in the field during the first round of sampling in 2012. Later, using ArcGIS 10, we created a 500 m buffer on each side of the transect segment, the area covered by the buffer was 2km long and 1km wide', and used these for determining various environmental covariates including measures of vegetation type. For analysis with distance sampling models, our animal detections were truncated at 300- 500 m, so this buffer was appropriate to describe the characteristics of ungulate locations. We used the intersect tool in ArcGIS 10 and a vegetation layer based on satellite imagery for Kafue (Midlane 2014) that classified the area into 'grassland', 'open forest', 'closed forest/woodland' to extract the proportion of each of these vegetation types on each segment. In addition, we used the perimeter tool in ArcGIS 10 to determine the density of edges between vegetation types (from the satellite imagery) within each segment, as a measure of habitat variability. Measured in this way, vegetation edge density ranged from 0 km /km^2 (uniform vegetation with no habitat type edges) to 4.34 km/km^2. The proportions of each vegetation type ranged from 0 to 0.995 for open grassland, 0 to 1 for open forest (open woodland) and 0 to 1 closed forest (closed woodland).

Vegetation biomass is often directly linked to soil nutrients and water availability (Bell 1982; Hopcraft et al. 2014; McNaughton 1985) hence soil samples were analyzed for factors that might affect plant productivity or nutritional value, including soil acidity (pH), organic matter, nitrogen (N), phosphorous (P), potassium (K), calcium (Ca), magnesium (Mg), and soil type classification. With the exception of the single survey conducted in 2012, we collected soil samples at each transect midpoint on each survey occasion, using a soil augur to a depth of 30 cm from four sub-sites within 5 m radius for laboratory measurements of pH and nutrient concentration and texture classification. The four samples were mixed thoroughly and a representative subsample of the mixture collected in a plastic zip lock bag, labelled and stored away from direct sunlight for later analysis at the soil science laboratory at University of Zambia, School of Agriculture.

At the site of each herd observation we recorded grass height (S – Short < 10 cm, 22.45 %; I – Intermediate 10 to 50 cm, 66.04 %; T - Tall > 50 cm, 11.51 %), grass color (Gr - Green, 27.36 %; BrGr-Brown - Green, 16.23 %; Br - Brown 56.42 %), burn status (C - Complete burn, 46.23 %; P - Partial burn, 35.09 %; N - No burn 18.68 %), whether semi-permanent grassy lagoons (even if currently dry) were detected within the segment

(A - Absence, 76.98 %; P – Presence, 23.02 %), and whether standing water was detected within the segment (A – Absence, 78.87 %; P – Presence 21.13%).

We determined the distance to permanent rivers using ArcGIS 10. In order to assess the effect of water other than permanent rivers on herbivore distributions we took note of presence of seasonal water within each transect segment. In the study area, grassy lagoons act as natural water catchments that can retain green grass late into the dry season.

3.2.4. Anthropogenic Limiting Factors

Anthropogenic influences on ungulate group size were assessed by incorporating effect of the distance to camp lodges within the park and distance to graded roads. These locations were mapped using GPS units in the field, except that distance to the park boundary was measured in kilometers from the edge of each buffer using ArcGIS 10 software.

3.2.5. Top-down Limiting Factors: Predation Risk from Lions

To determine whether herbivore group size were affected by spatial variation in the risk of predation, we fit a single kernel utilization distribution (Van Winkle 1975; Keating et al 2009; Worton 1989; Steiniger et al. 2013) to 24,944 lion locations collected over a period of three years (2010 to 2013) from GPS radio collars deployed in six resident lion prides and one male coalition (Midlane et al. 2013). Based on the contiguous distribution of these ranges we believe that most or all prides were sampled so that this utilization distribution provides a realistic measure of the local probability of encountering lions. We used the ‘sp’, ‘rgdal’ and ‘plyr’ packages in R to calculate the distribution of daily distance moved, which ranged from 85.85 m to 24,226.10 m, and used the mean daily distance moved as the smoothing parameter for the utilization distribution (UD), with an output grid of 300m X 300m. We fit the UD using the adehabitatHR package in R. The shape of the UD was not strongly affected by the specific kernel function used (as is typical: Silverman 1986, Calenge 2015) and the results reported here use the default (bivariate normal) kernel function for adehabitatHR.

This UD revealed substantial spatial variation in the risk of encountering lions, with the 50% isopleth (546 km^2) only covering approximately one-eighth of the 99% isopleth (4,468 km^2), and approximately one fourth of the 90% isopleth (2,336 km^2). To relate the risk of lion predation to transect data, we converted the UD from adehabitatHR to a raster using the ‘sp’ and ‘raster’ packages in R, and overlaid the raster with the buffered transects (as described above) to determine the mean lion utilization value for each transect segment.

3.3. Statistical Methods

We used generalized linear models to examine effects on herd size, with separate models fit to data for impala, puku and warthog, the three species for which data were sufficient for analysis. Because group size is an ordinal variable and a group size of zero cannot be observed, we used the *vlgm* function of the **vgam** package in R to fit zero-truncated Poisson (ZTP) models (Zuur et al. 2009). We used the *pairs.panels* function of the **psych** package to examine pairwise correlations between predictors for each data set, and where a pairwise correlation was equal or above 0.6, we dropped one predictor from consideration, using two criteria to decide which predictor to drop: (1) the magnitude of its correlation with other predictors, and (2) *a priori* expectations about the causal importance of the two effect. We confirmed that these models fit well using plots of residuals versus predicted values and residuals versus predictors, following procedures for fitting the zero-truncated Poisson model outlined by the UCLA statistical consulting group (http://www.ats.ucla.edu/stat/r/dae/ztp.htm) and Zuur et al. (2009). Cherry (pers. comm.) notes that the appropriate backtransformation of regression coefficients from the zero-truncated Poisson model is not to exponentiate the coefficients returned by *vglm (*as suggested by Zuur et al. [2009] and the UCLA statistical consulting group procedures cited above) and notes that it is possible to calculate backtransformed effects as ratios of expectations for particular covariate values, but not as a direct backtransformation of the coefficients from *vglm*. The untransformed coefficients we tabulate and the predicted values with other effects held at their observed means plotted in figures are for the ZTP model itself. The backtransformed coefficients we have tabulated are for the underlying (non-truncated) Poisson model and not the ZTP model itself. Our quantitative inferences are drawn from the untransformed coefficients and predicted values from the ZTP model. For each species, we selected our model by forward and reverse stepwise regression (with α for inclusion = 0.05) using the *add1* and *drop1* functions of the base **stats** package, confirming that both procedures yielded the same model. Where the two functions differed we settled for the simpler model identified by the forward step regression.

As described above (see Bottom-up limiting effects), soil nutrient measurements were made in two years, and all other data were available for three years. We thus compared models fit to two years' data that included soil nutrient effects, and models fit to three years' data that did not include soil nutrient effects. These comparisons showed that soil nutrients typically had little power to predict herbivore group sizes, so below we present full results for the three year analysis only.

3.4. Results

3.4.1. Impala

Mean impala herd size was 10.4 (± 0.78 S.E.), with the majority of herds holding fewer than 20 individuals but some herds approaching 80 individuals, following a distribution of typical shape (Fig. 3.3). Impala herd size was strongly associated with a broad set of bottom-up, top-down and anthropogenic effects (Table 3.1, Figure 3.4). Contrary to the expectation that larger herds may confer antipredator benefits, herd sizes were largest where lion usage was low. Consistent with their generalized diet, larger groups were found in areas with greener grazing conditions and with intermediate grass height, in areas that were at least partially burnt (and thus more likely to have green vegetation for grazing). Probably to avoid competition with puku, large groups did not form in areas with grassy lagoons (heavily used by puku). Larger groups were associated with the availability of standing water, though group size tended to increase with distance to permanent rivers (again suggesting a negative relationship with puku). Contrary to expectation, larger herds did not form in areas with more habitat edges. Anthropogenic effects were apparent with larger groups forming near the safety of camps, but smaller herds near the vehicle disturbance with higher speeds along graded permanent tracks. Among soil nutrient and soil type effects in the two-year analysis, group sizes increased on alkaline soils (backtransformed effect = 1.55, 95% CI 1.39 – 1.73), with high levels of organic matter (1.11, 1.07 – 1.14).

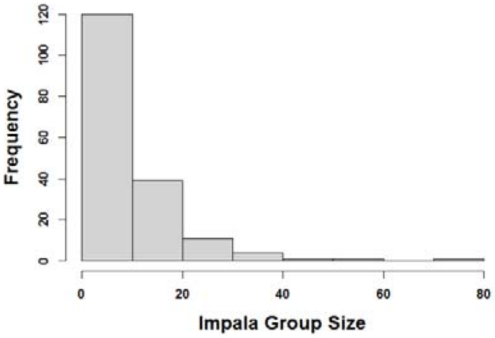

Figure 3.3. Frequency distribution of impala herd sizes.

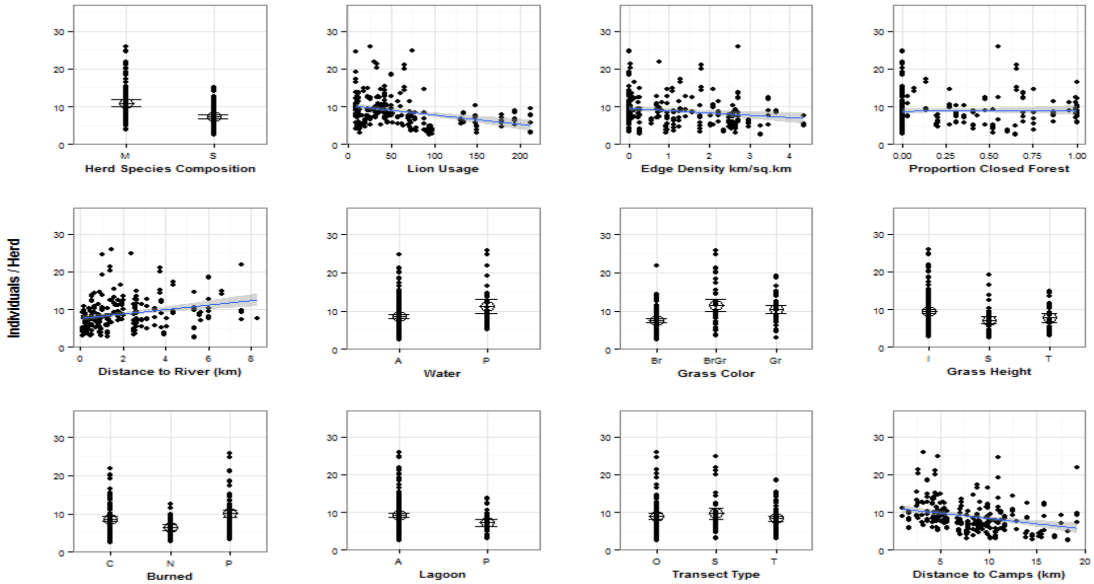

Figure 3.4. Effects on impala herd size from positive Poisson GLM. For continuous variables, the predicted values within the original data are shown, together with the linear effect and its 95% confidence limits. For categorical predictors, the mean predicted values within the original data and 95% confidence limits are shown. Level codes for this and subsequent figures: Herd Species Compostion (S) single-species, (M) mixed-species. Water (A) absent, (P) present. Grass Color (Br) brown, (Gr) green, (BrGr) mixed. Grass Height (I) intermediate, (S) short, (T) tall. Burned (C) complete, (P) partial, (N) not burned. Lagoon (A) absent, (P) present. Transect Type (O) off-track, (S) seasonal track, (T) permanent unpaved track.

Table 3.1. Effects on impala herd size from stepwise positive Poisson GLM, with coefficients and standard errors reported as additive exponential effects and back-transformed to show multiplicative effects on the original scale.

Effect	**Estimate (SE)**	**Backtransformed (95% CI)**	**Z**	**P**
Intercept	3.06 (0.13)	21.3 (16.5 – 27.5)	24.93	< 0.0001
Single species	-0.34 (0.059)	0.71 (0.63 – 0.88)	-5.69	< 0.0001
<u>Top Down</u>				
Lion use	-0.52 (0.070)	0.59 (0.52 – 0.68)	-7.44	< 0.0001
<u>Bottom Up</u>				
Grass height: short	-0.22 (0.088)	0.80 (0.68 – 0.95)	-2.49	0.013
Grass height: tall	-0.041 (0.091)	0.96 (0.80 – 1.15)	-0.47	0.66
Grass color: mixed	0.20 (0.065)	1.22 (1.14 – 1.31)	3.13	0.0017
Grass color: green	0.22 (0.070)	1.25 (1.09 – 1.43)	3.11	0.0018
Burned: no	-0.28 (0.10)	0.76 (0.62 – 0.92)	-2.74	0.0061
Burned: partial	0.052 (0.058)	1.05 (0.94 – 1.18)	0.90	0.37
Distance to river	0.052 (0.019)	1.05 (1.01 – 1.09)	2.71	0.0068
Water: present	0.52 (0.083)	1.68 (1.42 – 1.98)	6.34	< 0.0001
Habitat edge	-0.076 (0.031)	0.92 (0.87 – 0.98)	-2.46	0.014
Proportion forest	-0.24 (0.088)	0.79 (0.66 – 0.93)	-2.74	0.0061
Lagoon: present	-0.33 (0.099)	0.71 (0.59 – 0.87)	-3.30	0.001
<u>Anthropogenic</u>				
Distance to camp	-0.058 (0.009)	0.94 (0.93 – 0.96)	-6.70	< 0.0001
Track type: Seasonal	0.43 (0.094)	1.54 (1.28 – 1.85)	4.58	< 0.0001
Track type: Permanent	-0.24 (0.078)	0.78 (0.68 – 0.92)	-3.06	0.0022

3.4.2. Puku

Mean puku herd size was 7.49 ± 1.11 (S.E.), with most herds holding fewer than 10 individuals and the largest groups approaching 70 individuals (Fig.3.5). Puku herd size was associated with fewer variables than was seen for impala (Table 3.2, Fig.3.6), primarily bottom-up effects related to the quality and quantity of grass, and anthropogenic effects.

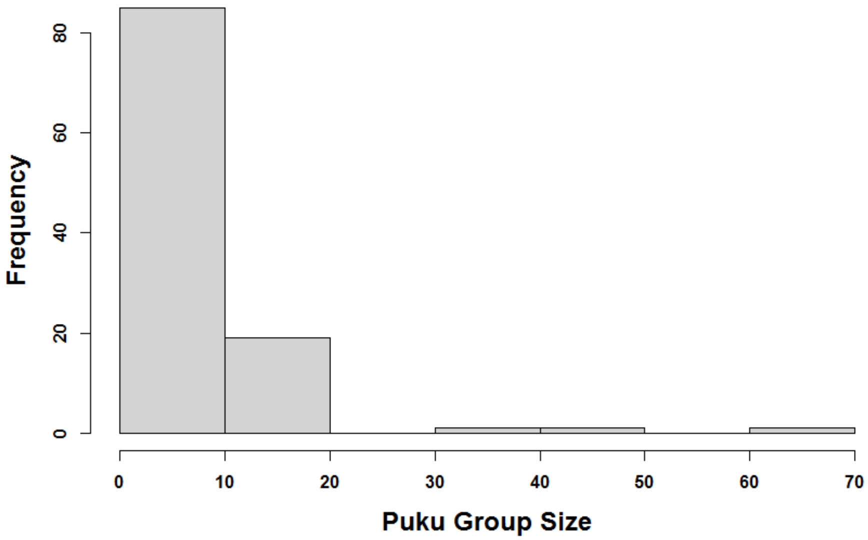

Figure 3.5. Frequency distribution of puku herd sizes.

As would be expected from the foraging ecology of puku, much larger herds were found in areas with a high proportion of open grassland, which on our study site were primarily open long grass plains immediately adjacent to riverine corridors, and grassy lagoons that formed around areas that held standing water for portions of the year. It is initially surprising to note that herds were smaller in areas with primarily green grasses, and largest in areas with a mixture of brown and green grazing patches. Anthropogenic effects on puku were quite different from those seen for impala, with larger herds forming farther from roads, but no detectable association between herd size and proximity to camps. Despite this basic result, herds were larger on transects along permanent tracks than on off-track transects, and largest along seasonal tracks, so that road effects are difficult to interpret for puku. Also unlike the result for impala, we found no top-down effect of lion usage on puku herd size. No effects of soil nutrients or soil type on puku herd size were detected in the two-year analysis.

Table 3.2 Effects on puku herd size from stepwise positive Poisson GLM, with coefficients and standard errors reported as additive exponential effects and back-transformed to show multiplicative effects on the original scale.

Effect	**Estimate (SE)**	**Backtransformed (95% CI)**	**Z**	**P**
Intercept	2.00 (0.18)	7.39 (5.19 – 10.51)	11.34	< 0.0001
Top Down	**--**	**---**	**---**	**---**
Bottom Up				
Grass color: mixed	0.47 (0.10)	1.60 (1.32 – 1.95)	4.67	< 0.0001
Grass color: green	-0.54 (0.12)	0.58 (0.46 – 0.74)	-4.44	< 0.0001
Proportion grassland	0.68 (0.14)	1.97 (1.50 – 2.60)	4.88	< 0.0001
Anthropogenic				
Distance to roads	0.15 (0.053)	1.16 (1.05 – 1.29)	2.76	0.0059
Track type: Seasonal	0.42 (0.14)	1.52 (1.16 – 2.00)	3.02	0.0025
Track type: Permanent	0.23 (0.14)	1.26 (0.96 – 1.66)	1.70	0.089

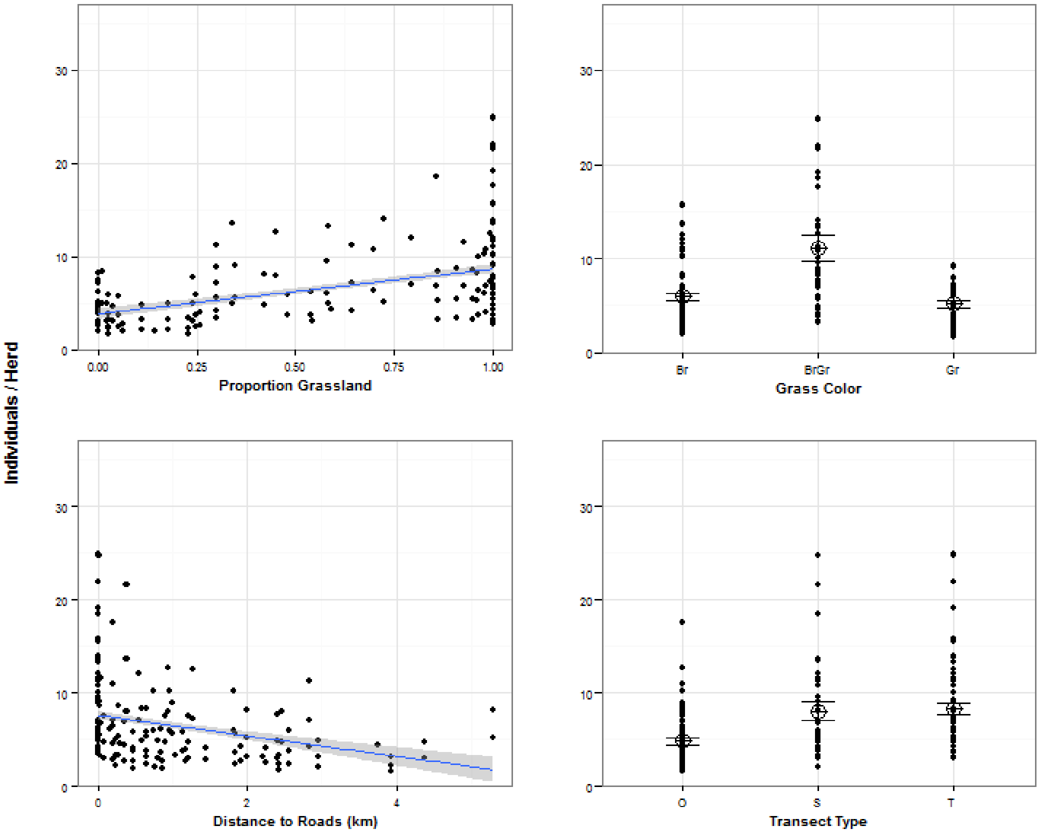

Figure 3.6 Effects on puku herd size from positive Poisson GLM. For continuous variables, the predicted values within the original data are shown, together with the linear effect and its 95% confidence limits. For categorical predictors, the mean predicted values within the original data and 95% confidence limits are shown. (See Figure 4 for level codes.)

3.4.3. Warthog

Because warthogs live in family groups, their group sizes were relatively small (3.52 ± 0.25 S.E.), with the modal group size being one, and no groups larger than 10 individuals (Fig. 3.7).

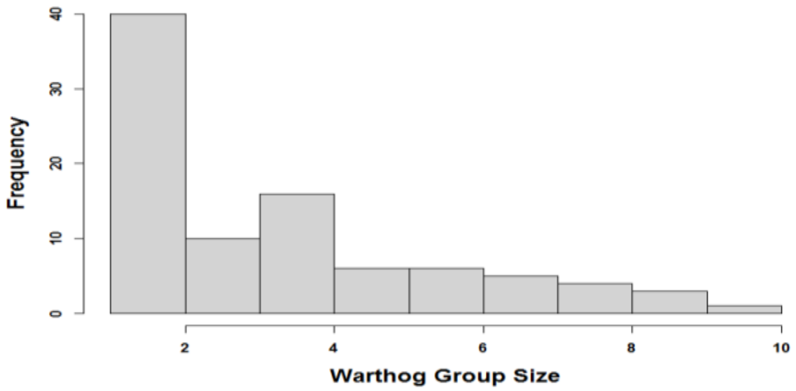

Figure 3.7. Frequency distribution of warthog group sizes.

Table 3.3. Effects on warthog group size from stepwise positive Poisson GLM, with coefficients and standard errors reported as additive exponential effects and back-transformed to show multiplicative effects on the original scale.

Effect	**Estimate (SE)**	**Backtransformed (95% CI)**	**Z**	**P**
Intercept	1.29 (0.15)	3.63 (2.71 – 4.87)	8.68	< 0.0001
Top Down				
Lion use	-0.58 (0.19)	0.56 (0.39 – 0.81)	-3.06	0.0025
Bottom Up				
Burned: no	-0.55 (0.24)	0.58 (0.36 – 0.92)	-2.29	0.022
Burned: partial	0.17 (0.13)	1.19 (0.92 – 1.53)	1.26	0.21
Water: present	0.55 (0.14)	1.73 (1.31 – 2.28)	4.09	< 0.0001
Habitat edge	-0.16 (0.077)	0.85 (0.73 – 0.99)	-2.04	0.041
Anthropogenic	**---**	**---**	**---**	**---**

Warthog group size was associated with top-down and bottom-up effects, but no antrhopogenic effects were detected (Table 3.3, Fig. 3.8). With respect to top-down effects, warthogs groups were smaller in areas that were heavily used by lions, contrary to the hypothesis that grouping provides antipredator benefits, as was observed for impala. Fewer bottom-up effects were observed for warthog than for impala, but those that were observed were very similar, namely larger groups in partially burned areas, larger groups in areas with water, and larger groups in areas with low habitat edge density. Warthog and impala are commonly found in association with one another, so the fact that similar patterns were observed is not surprising. Though the result that groups were larger in uniform areas with low habitat edge density was not anticipated (for either species), it may be a manifestation of grouping as an antipredator response in areas with high probability of detection, because open grasslands have low edge density. The only effect of soil nutrients on warthog group size in the two year analysis was an association with high soil phosphorous (backtransformed effect = 1.04, 95% CI 1.01 1.09).

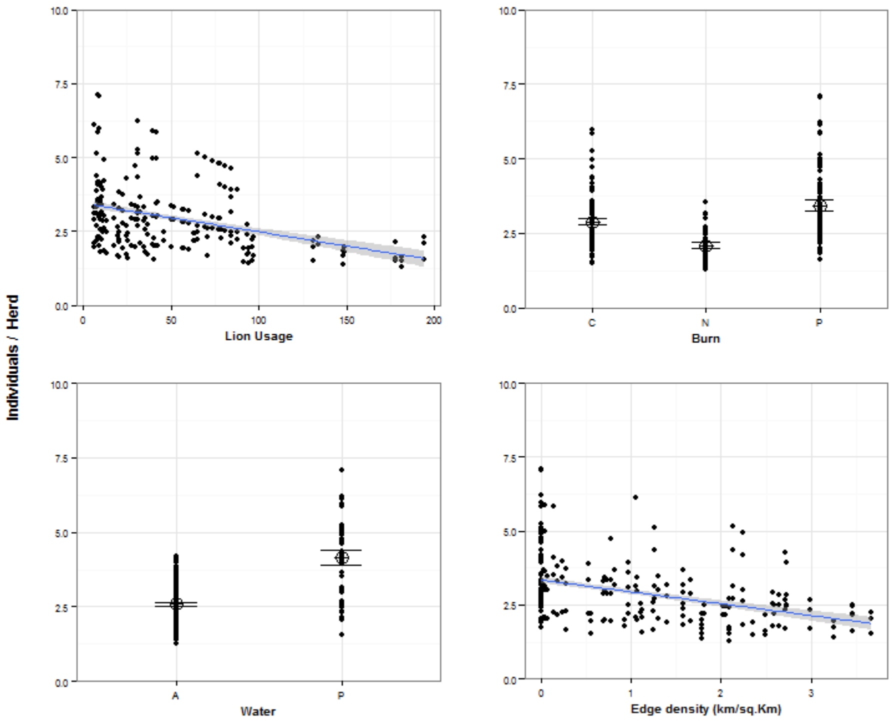

Figure 3.8. Effects on warthog group size from positive Poisson GLM. For continuous variables, the predicted values within the original data are shown, together with the linear effect and its 95% confidence limits. For categorical predictors, the mean predicted values within the original data and 95% confidence limits are shown. (See Figure 4 for level codes.)

3.5. Discussion

By comparing the factors affecting group size for the three most abundant members of a large herbivore community, our analysis reveals that top-down, bottom-up and anthropogenic factors all had strong effects, but their relative strength varied substantially among species. Even for a single guild within a single ecosystem, group size responds to widely varying ecological controls.

The top-down effect of predation risk from lions was strong for impala and warthogs, but did not detectably affect puku. Contrary to the hypothesis that larger groups provide antipredator benefits, we found that group sizes were smaller in areas with heavier use by lions, similar to the responses of elk to wolves in some systems (Creel & Winnie 2005). Increased attack rates by predators are associated with increased prey group size in some systems (Cresswell & Quinn 2010; Cresswell & Quinn 2011), and attack abatement could explain this result.

Like top-down effects, anthropogenic effects were apparent for two of the three species, puku and impala. Groups were larger near camps, consistent with a hypothesis of aggregation in areas likely to be avoided by illegal hunters. Though there was an overlap, impala group size was higher in seasonal track transects with predicted 9.64 [95 % CI: 8.92 to 11.01] than permanent track transect 8.32 [95 % CI: 7.61 to 9.02] and slightly higher than off-road transects with predicted 8.93 [95 % CI: 8.15 to 9.71]. Herd sizes were lower along permanent tracks with higher vehicle speeds and traffic unrelated to game viewing, relative to seasonal tracks that do not allow high speeds and are used almost exclusively for low-speed game viewing. Herd sizes along low-speed seasonal tracks were in fact higher than we observed in off-track transects, probably because seasonal tracks are intentionally sited in areas that provide good concentrations of animals. However, these interpretations are undermined by results for puku, for which herd sizes decreased with increasing distance to roads. This result may be an artefact of the preference of puku for open grasslands adjacent to riverine corridors along permanent water, within which many of Kafue's major tracks run.

Herd size was related to bottom-up effects for all three species, confirming the general importance for large herbivore ecology of aggregation in areas with adequate access to food and water (Hopcraft et al. 2014; Mduma et al. 1999; Sinclair 1985). The strongest bottom-up effects varied among species, but in aggregate showed effects of forage quantity (as exemplified by the positive effect of proportion grassland on puku), forage quality and its trade-off with quantity (as exemplified by the related effects of grass color, grass height and burning on all of the species), access to water (as exemplified by the effect of presence of standing water on impala) and habitat structure (as exemplified by the effects of habitat edge density).

As noted in the Methods, we examined the potential effects of soil type and soil nutrients for a two-year subset of the data and found that they had little influence. Of 24 effects tested across the three species, only three (soil pH, organic matter and phosphorous) effects had confidence intervals that did not overlap zero, no variables affected all three species, and puku herd sizes were not associated with any of these measures. Overall, these results suggest that congregation on soil nutrient hotspots, which influences herbivore movements and aggregation patterns in some systems, particularly those with migration (Augustine et al. 2003; McNaughton 1985), is not a major driver in this system.

Broadly, our results show that herbivore group sizes respond to a wide range of top-down, bottom-up and anthropogenic effects. Grouping patterns in these species are not a simple response to predation risk, resources or anthropogenic effects, but represent a balanced response to all of these limiting forces. This result confirms the importance of trade-offs between responses to predation and access to resources for large herbivores. Viewed in more detail, there are pronounced differences among these three species in the type, magnitude and sign of effects on group size. This result suggests that general, predictive rules about the form of trade-offs between top down and bottom up effects (Creel 2011; Heithaus et al. 2009) are likely to remain elusive.

CHAPTER FOUR

COMPARATIVE ANALYSIS OF ECOLOGICAL AND ANTHROPOGENIC VARIABLES AFFECTING DISTRIBUTION AND SIZE OF LARGE HERBIVORES IN KAFUE NATIONAL PARK, ZAMBIA.

4.1. Introduction

From the perspective of population ecology, there has been considerable interest in the balance between top-down and bottom-up forces in the regulation of ungulate populations, in large part due to seminal studies of ungulate dynamics in East Africa (Sinclair 1985, Sinclair & Arcese 1995, Hopcraft et al. 2010, 2015). More recently, continent-scale declines in the distribution and abundance of large herbivores have led to increased concern about anthropogenic effects on their dynamics (Bolger et al. 2008, Western et al. 2009, Watson et al. 2013). In the three years of research I have investigated environmental and anthropogenic variables affecting the density and distribution of herds and their size for impala, puku and warthog, the three most abundant large herbivores in Kafue National Park. Here, I present comparative results for the two analyses reported in chapters 2 and 3, which examined effects on the distribution of herds and the size of herds, respectively. By comparing these analyses, one can elucidate what factors act synergistically on both processes, what factors act in opposition, and what factors act on only one process.

Such findings help conservation and management when managers, planners and policy makers are informed by research findings to focus on factors with predictable negative or positive impact. Maintenance of biodiversity and increase in number of herbivores is achieved by putting in place measures that mitigate identified limiting environmental factors (Geldmann et al 2013). With regard to management of large herbivores in African national parks, there is some tendency to assume that actions that benefit one species will benefit all species, but this gambit may not succeed if factors limiting distribution and abundance differ appreciably among species (Cardillo et al 2005). Management of African large herbivores is also typically centered on data from aerial censuses that provide estimates of population size but little information on the ecological or anthropogenic drivers of population dynamics and spatial distributions. The lack of such information can impede or delay response in mitigating intervention. In developing countries like Zambia where the study was conducted this usually results from delays in analysis of animal count data / surveys that may further be subjected to lengthy bureaucratic process of reviewing through hierarchies before final approval. In a sense by the time technocrats resolve to put prompt intervention measures there is a time lag which can disadvantage conservation. The strength of our study is that density, herd size and environmental covariates affecting the three species reported are analyzed simultaneously. This way factors identified may be applied as early warning tools for assessing habitat integrity.

Determining “spatially detailed assessment of species numbers and distribution” has also become key to sustaining species conservation alongside reporting their drivers (Woody et al 2003).

4.2. Comparison of Effects on Herd Distribution and Herd Sizes

Table 4.1 summarizes the primary results from chapters 2 and 3. The comparative results presented in Table 4.1 are based on the three year data, analyzed without inclusion of the effect of soil nutrients as these were found to be uniformly weak in analysis restricted to data for two years.

In Chapter 2 I used distance sampling models to identify the covariates with the largest influence on herd density and distribution, and to estimate their effects. In Chapter 3 I used zero truncated Poisson generalized linear models to identify the covariates with the largest influence on group size, and to estimate their effects. The data for both analyses was based on the same covariates recorded under the same transect segments, because the data on group sizes was recorded at the same time of conducting herd counts at transect level. The fundamental partition was that we used two different analytical approaches with herds per square kilometer as response variable for distance sampling regression and individual numbers per herd as response variable for the zero truncated Poisson regression analysis.

The comparative results (Table 4.1) show that there were more covariates of herd size detected for impala and puku than were detected for herd density (13 for impala, 9 for puku as opposed to 1 and 2, respectively). This is interpreted to mean we have more environmental factors detected to account for the influence on herd size than herd density in the two species. We have more variables associated with herd size effect than with where herds are distributed, and the two response variables are not controlled by the same ecological and anthropogenic effects. For warthogs, the opposite pattern was observed, with more covariates associated with herd density than with herd size (7 verses 4 only). This difference can perhaps be explained by noting that mean group size is appreciably smaller and less variable for warthogs (which typically live in family groups) than for the other two species (which form larger and socially more diffuse herds).

While herds with several of these species are commonly observed together, for example close to water or food resources, our analyses reveal that the species really do differ appreciably in their ecological responses to specific selection pressures and occupy distinct niches. For instance, if we examine the effect of lagoon presence on impala herd density and distribution we detect no effect, but for puku we find a 1.96 fold increase for herd density in areas with lagoon presence. No effect of distance from rivers was found in the impala herd density model, but puku were sensitive to this effect, with 0.5 fold decline in herd density for each kilometer away from the river. Both of these effects support a general inference that niche partitioning has promoted mechanisms that reduce competition between puku and impala.

Somewhat contrary to this inference, impala herd size however increased by a factor of 1.05 for each kilometer away from river, and puku increased by a factor of 1.14 , revealing similar effects on both species in this case. Distance to river is the only covariate with antagonistic negative effect on herd density and a positive effect on herd size for puku. There was an increase in vegetation edge density away from the river, and predation risk is often suggested to be high at habitat edges. If this suggestion is correct, then the observed increase in herd size lends support to the hypothesis that this aggregation might abate predation by the dilution effect (Fryxell J. M. 1991). If this explanation is correct, it is not surprising that the effect would operate similarly for impala and puku, because both would benefit from such an effect.

Another major contrast is observed when testing for the effect of water presence in natural catchment areas and springs apart from the river. Here we saw no effect on the density and distribution of impala, puku and warthog, but did find a 1.69 fold increase for impala herd size, supporting the idea that increased impala herd size is frequently associated with watering points that are not heavily used by puku and warthog.

There was no detectable effect of vegetation and grass structure on impala and puku herd density. These variables did affect herd size in both species though not in a uniform pattern. Short grass had a negative effect on impala with 0.8 fold reductions in herd size relative to intermediate or tall grass, and puku herd sizes did not respond to grass height. Grass of mixed color had a positive effect on herd sizes of both species with a 1.22 fold increase for impala and 1.59 fold increase for puku. Grass of green color had a positive effect on impala herd size with 1.24 fold increase but had a negative influence for puku with 0.59 fold reduction. Thus, there were complex differences between species in these effects of forage quality and quantity.

Though puku were associated with lagoons often laced with green grass, bigger herd size seem to favor grass of mixed color between green and brown. Preference for a mixed color suggests a trade-off between forage quantity and quality, or alternatively, dietary needs for dry roughage. Why this is so is a matter of conceivable speculation. Perhaps a diet consisting of entirely fresh green grass is not well tolerated and predisposes to veterinary conditions such as bloat, a digestive disorder characterized by distention of the first two compartments of the ruminant stomach due to accumulation of gas. The condition is reported in domestic herbivores and is attributed to ingestion of protein rich grasses that interact with ruminal microbes producing gas that is not easily expelled through the mouth. This condition causes intra-abdominal pressure that is often fatal if unattended in domestic stock (Wang et al 2012; Bartley et al 1983; Berg et al 2000). In the wild where intervention is unlikely, selection will tend to favor a diet that avoids this condition. Considering that the herd size for puku increased 1.97 fold in locations with a high proportion of grassland, it is logical that this grass proportion is of mixed color between brown and green in keeping with my speculation. Grass proportion had no effect on impala herd size.

Herd size also increased by 1.18 fold in areas with increased habitat edge density for puku but no effect was detected on impala. Areas with no evidence of having been burnt had negative effect on impala herd size (0.75 fold reduction) but no effect on puku herd size. Recall that impala showed an increase of herd size in mixed color grass and green grass; because areas not burnt are typically brown, this result is consistent with the patterns described above.

Bottom up effects on warthog were rather different than those just described for impala and puku, with a similar number of effects on herd density (4) and herd size (3). Short grass showed a positive effect on herd density, with a 1.71 fold increase (71 %). Given their notably short stature, short grass may be favored by warthog because of both high forage quality and good visibility providing for early detection of predator approach and hence allow for quick escape. A similar effect is evident in the negative effect tall grass with 0.26 fold reduction (74 %) of herd density. Warthog had a significant multiplicative effect from mixed grass color and green grass with 2.45 and 2.78 fold increases on herd density, again suggesting selection of areas with high forage quality. What is perhaps surprising is that these factors affecting herd density did not affect herd size: as noted previously, warthogs typically live in family groups, so that group size is less affected by ecological conditions, relative to puku and impala. However, we did detect a negative effect of habitat edge density (0.86 fold decrease), areas not burnt (0.57 fold decrease) on warthog group size. Vegetation with partial burn status showed a 1.19 fold increase (19 %) in warthog herd size. This is in agreement with levels of improved visibility and perhaps presence of new shoots of grass attractive for grazing. Just as some vegetation effects on herd density were not detected on herd size, the last three stated vegetation effects on warthog herd size were not detected on herd density. Collectively, these data are compatible with the hypothesis that warthog groups disaggregate in areas with a combination of high predation risk (poor visibility, many habitat edges) and low forage quality.

Of the five anthropogenic variables, effect of distance to park boundary was detected on impala herd density with a 1.08 fold increase of herds away from park boundary. I attribute this effect to high traffic of human activity near the park boundary. Distance to camp lodges for impala had a negative effect on herd size with a 0.94 fold decrease with increasing distance, suggesting some level of safety or protection in proximity to camp lodges. Seasonal tracks less associated with heavy human presence had a positive effect on herd size with 1.54 fold increase. In contrast, permanent tracks had a negative effect on herd size, with a 0.79 fold decrease, possibly because of suspected high traffic on these better maintained tracks. Anecdotally, it is also possible the permanent tracks could be associated with predation as we observed lion spoors on permanent tracks often. Another possibility is that illegal hunters use the routes more so off-season when anti-poaching teams are less active. Distance to road for puku showed a positive effect on herd size with 1.16 fold increase for each kilometer away from roads, but no effect on herd density. Unlike impala both seasonal tracks transect type and permanent tracks showed a positive effect on puku herd size with 1.52 and 1.26 fold increases respectively. These patterns do not lend themselves to clear interpretation, because the effects of distance from roads and track type tend to oppose one another.

For puku, distance to camp lodges showed that herd size decreased with increasing distance (0.89 fold decrease) but no effect on herd density. As with impala, this pattern is compatible with the suggestion that lodges confer some degree of safety.

For warthog, herd density decreased with increasing distance to roads and camp lodges with 0.87 and 0.88 fold decreases (i.e. 13 % and 12 % reduction). Transect type on seasonal tracks had a negative effect on warthog herd density with 0.76 fold reduction (24 %), suggesting a diminished occurrence of herds on seasonal tracks. These results again show a degree of herbivore attraction to tourist camps may be due to derived benefit of protection, though general inferences about effects of roads and tracks remain elusive.

Lion usage had little effect on both herd size and herd density for all the three species, suggesting that in this ecosystem, bottom-up an anthropogenic effects currently play stronger roles than top-down effects. Midlane (2014) recently suggested that the lion population of Kafue is far below the expected carrying capacity for such an ecosystem, which provide a possible explanation for their relatively small effects in these analyses. Predation risk is perhaps seen to play some defining role when interacting with other ecological variables as shown in some models.

Table 4.1. Summary of effects on the density of distribution of herds (HD) and herd size (HS) for impala, puku and warthog, based on data from 3 years.

	Impala		**Puku**		**Warthog**	
Top – down effect	**HD**	**HS**	**HD**	**HS**	**HD**	**HS**
Predation risk						
Lion usage	-	0.59	-	-	-	0.56
Single (S) species herd	-	0.72	-	-	-	-
Bottom – up effect						
Water						
Distance to river	-	1.05	0.50	1.14	-	-
Lagoon presence	-	0.72	1.96	-	-	-
Water presence	-	1.69	-	-	-	-
Vegetation and grass structure						
Grass height (short)	-	0.80	-	-	1.71	-
Grass height (Tall)	-	-	-	-	0.26	-
Grass color (BrownGreen)	-	1.22	-	1.59	2.45	-
Grass color (Green)	-	1.24	-	0.59	2.78	-
Grass proportion	-	-	-	1.97	-	-
Closed forest proportion	-	0.79	-	-	-	-
Edge density	-	-	-	1.18	-	0.86
Burn status (Not burnt)	-	0.75	-	-	-	0.57
Burn status (Partial burn)	-	-	-	-	-	1.19
Anthropogenic effect						
Distance to roads	-	-	-	1.16	0.87	-
Distance to camp lodges	-	0.94	-	0.89	0.88	-
Distance to park boundary	1.08	-	-	-	-	-
Transect type (seasonal tracks)	-	1.54	-	1.52	0.76	0
Transect type (permanent tracks)	-	0.79	-	1.26	-	-

Note: Dashes denote effects not included in the model. Predation risk on herd density was noted with weak evidence with coefficient in the order of 0.999 (close to 1)

4.3. Summary of Findings

The primary findings of this study are that:

- The most abundant large herbivores in KNP are impala, puku and warthog.
- The drivers of herd density are not the same as those driving herd sizes.
- The drivers of herd density and herd size differ substantially for the three species, reducing the likelihood that 'one size fits all' strategies will conserve all of the species equally well.
- Fire plays a role in shaping some ungulate herd sizes as noted for warthog and impala.
- For impala, density and distribution are driven primarily by anthropogenic activities while herd size is driven by access to permanent rivers and other alternate sources of water, vegetation structure and anthropogenic effect.
- Puku density and distribution is driven by proximity to rivers and presence of lagoons, whereas herd size is driven by proximity to river, vegetation / grass structure and anthropogenic activities.
- Warthog density is driven by vegetation / grass structure and so is herd size, but the details of these variables are not the same for the two response variables.
- The presence of tourist camps in KNP north may enhance conservation by providing areas of safety.

4.4. Conclusion

The take home message from the findings is that even though we have the grouping of herbivores, management approach may not be uniform in that the environmental factors prevailing may affect them in unique ways. If we are to manage and conserve different species of large herbivores successfully, it is necessary to identify and differentiate the ecological and anthropogenic effects on individual species. This will help managers and conservationists assess for purpose of prioritizing effects in order of importance. This is especially critical in cost effective resource allocation and utilization as emphasis is placed tackling important matters first targeting areas with rapid biodiversity decline (Woody et al 2003). On rather a practical note, qualitative assessment for suitability of conservancies and other protected area designate can draw parallels from the reported findings.

Perhaps one final point among many to appreciate on the variance and non-uniform response to environmental and ecological drivers on impala, puku and warthog is that the variation is important in bringing about biodiversity.

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APPENDIX A

DEDICATION

I dedicate this dissertation to my father Mr. John Sikavizya Matandiko, who upon learning of my admission to University of Zambia for undergraduate degree abandoned all plans to pursue his degree. His rationale at the time was to give me undivided support without stretching his already thin financial base to beyond limit. I have fulfilled attending undergraduate and graduate school on his behalf. His words still echo in my ears, “Son, if you attend University, it is as good as I having attended.” He is and will always be a hero in the shadows who never celebrated my academic achievement in order not to pave way for complacency on my part.

I also wish to dedicate the dissertation to my mother Rosemary Nakanyika Matandiko, for reassuring me that one day I will complete the course no matter how long it was going to take and for not whining over lack of financial support from her first born son in graduate school.

I dedicate this to my five children Taizya Natasha, Lamuka Lorraine,Wigganson (Jr) Twalola, Keegan Twatemwa and Cynthia Bupe Sadowski, for enduring my prolonged absence. I did promise that it was for their good, and I am on the homestretch to fulfil that promise. I dedicate this to you all so that you start aiming higher than I have attained. Do not aim at the sky, aim at the universe!

Finally, I wish to dedicate this to Georgina for holding the fort and keeping the children together during the period I was an absent Dad. I appreciate and love you!