

TESTING THE EFFECTS OF ANTHROPOGENIC PRESSURES ON AFRICAN LIONS AND
THEIR PREY IN THE GREATER KAFUE ECOSYSTEM, ZAMBIA

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Fish & Wildlife Management

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2020

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ACKNOWLEDGEMENTS

I would like to sincerely thank my advisor Dr. Scott Creel for providing mentorship, inspiration, and the motivation to become a better scientist. I also want to sincerely thank both of my committee members Dr. Matthew Becker and Dr. Jay Rotella for their guidance, support, and inspiration throughout this process. Many thanks are also in order to the numerous co-authors on both of these chapters for their hard work and input towards these collaborative research efforts. I would not have been able to complete this work without the dedication, hard work, and perseverance from all of my co-workers from the Zambian Carnivore Programme, and I extend many thanks to them as well. I would also like to officially thank the Zambia Department of National Parks and Wildlife for permission to conduct this research, and for their collaborative efforts to help monitor, manage, and conserve these herbivore and carnivore populations. Naturally, I would not be here without the love and support of my friends and family. I truly appreciate all those unique individuals in my life, and I am very grateful for all that you have done for me.

FUNDING ACKNOWLEDGEMENTS

This research was supported and made possible by the National Science Foundation, National Geographic Society Big Cats Initiative, Gemfields Inc., World Wildlife Fund – Netherlands & Zambia, The Bennink Foundation, Wilderness Wildlife Trust, Panthera, Ntengu Safaris, Elephant Charge, and IUCN Save Our Species/European Union.

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ABSTRACT

Rapid human population growth across Africa has put tremendous pressure on large herbivore and large carnivore populations, and most of these large terrestrial species are now limited to residing within or adjacent to protected area (PA) networks. However, high rates of human encroachment and associated activities around and within PAs are jeopardizing their effectiveness and have become a major conservation concern. High rates of illegal harvest are linked to human encroachment and can have devastating effects on large herbivore and large carnivore populations. Large herbivore declines are often greatest in areas with high rates of illegal offtake and ensuing prey depletion can be a primary driver of large carnivore declines. Kafue National Park (KNP) of central Zambia supports a diverse large herbivore community and the country's second largest lion population. However, KNP is thought to be experiencing human-caused wildlife declines, providing a unique opportunity to evaluate anthropogenic effects on both the large herbivores and large carnivores of this system. Here, we evaluated the status and major anthropogenic and environmental drivers of KNP's large herbivore populations and lion population. First, we estimated population densities and distribution of the ten most abundant large herbivore species using stratified ground-based surveys conducted from 2012 – 2018. These data indicated that population densities were consistently low across species and areas, though there was ecologically important variation among species and size classes. Moreover, densities of larger-bodied herbivores were greatly depressed relative to smaller species. Second, we evaluated population density, survival rates, and demography for the KNP lion population from 2013 – 2018. These data indicated that age- and sex-specific survival rates for settled individuals were generally high, and factors known to correlate with local prey density had small effects on lion survival. In contrast, average lion density was low and recruitment of cubs was poor. These findings suggest that low recruitment might be a better signal of low prey density than survival. Overall, large herbivores and lions appear to be limited by human activities in KNP. Increased resource protection and reducing the underlying drivers of prey depletion are urgent conservation needs to facilitate the recovery of these economically and ecologically valuable species.

CHAPTER ONE

INTRODUCTION TO THESIS

Overview of Thesis

Current extinction rates are drastic and unprecedented in human history (Ceballos et al. 2015). Both large herbivores and large carnivores fall within the most affected taxa (Ceballos and Ehrlich 2002), and many of these species are now declining rapidly across the globe (Estes et al. 2011, Terborgh and Estes 2013, Ripple et al. 2014). Large carnivores are some of the world's most iconic and valued species, yet 77% of the world's large carnivore species are experiencing population declines, and 61% are threatened under the International Union for the Conservation of Nature (IUCN; Ripple et al., 2014). Likewise, approximately 60% of the world's large terrestrial herbivore species are listed as threatened under the IUCN, and 58% are experiencing population declines (Ripple et al. 2015). Many of these species are found in developing countries, predominantly on the African, South American, and Asian continents.

The African continent harbors 29% of the world's large carnivore species and 43% of the world's large herbivore species (Ripple et al. 2014, 2015). Rapid human population growth across Africa has put tremendous pressure on these large terrestrial species, and most are now limited to residing within or adjacent to protected areas (PAs) (Ripple et al. 2014). PAs are an important tool to protect wildlife from human activities, and are often encompassed by buffer zones with lower levels of protection (Geldmann et al. 2013). These buffers establish a physical gradient aimed to minimize edge effects

(Woodroffe and Ginsberg 1998) and source-sink dynamics (Pulliam 1988).

Unfortunately, rural human population growth across Africa is highest around PAs (Wittemyer et al. 2008). Consequently, high rates of human encroachment and associated activities around and within these PAs is jeopardizing the effectiveness of these buffer zones and has become a major conservation concern (Watson et al. 2013, 2015).

High rates of illegal harvest are linked to human encroachment (Watson et al. 2013, 2015) and can have a devastating effect on large herbivore and large carnivore populations ((Rosenblatt et al. 2016, 2019). Large herbivore declines are often greatest in areas with high rates of illegally harvested wild game consumption (Brashares et al. 2011, Lindsey et al. 2013, Ripple et al. 2015). Prey depletion directly linked to illegal offtake, is now widely suspected to be a primary driver of large carnivore declines (Midlane 2013, Rosenblatt et al. 2014, 2016, Creel et al. 2018). Illegal harvest of wild game in west and central Africa is increasing due to human population growth, increased access to protected areas through developing road networks, increased hunting pressure, and the rise of more efficient hunting methods (Fa et al. 2005). Until recently, the illegal wild game trade and its effects on large herbivore and large carnivore populations received little attention in the savannas of eastern and southern Africa (Lindsey et al., 2013), though it is likely to have strong negative effects on ecosystem structure and function (Estes et al. 2011, Ripple et al. 2014, 2015, Creel et al. 2018).

Illegal harvest of wild game in Zambia has been identified as a major threat to wildlife (Barnett 2000), and its growth and commercialization drives negative ecological, social, and economic impacts (Lindsey et al. 2013, Creel et al. 2018). Central Zambia's

Greater Kafue Ecosystem (GKE) is comprised of Kafue National Park (KNP) and nine adjacent Game Management Areas (GMAs), which were established as buffer zones between the park and human settlement. The GKE supports a diverse large herbivore community of 27 species (Mwima 2001) suspected to suffer from long-term population declines due to illegal harvest (Lindsey et al. 2014, Overton et al. 2017, Creel et al. 2018). As a consequence, prey depletion is expected to negatively impact population dynamics and demography for an intact large carnivore guild (Midlane 2013, Creel et al. 2018). Depletion of ungulate prey is widely-recognized as a major driver of lion (*Panthera leo*) population declines (Becker et al., 2013; Midlane, O’Riain, Balme, Robinson, & Hunter, 2014; Rosenblatt et al., 2014), and expected given the close association between lion population density and prey abundance (Schaller 1972, Van Orsdol et al. 1985, Hayward et al. 2007).

Little work has directly quantified the direct effects of anthropogenic pressures on large herbivore populations, and as a consequence these effects remain poorly described in most of the systems experiencing large herbivore declines. Likewise, the effects of prey depletion on lion demography are rarely tested, though prey depletion is considered a major threat to lions. The GKE presents a unique study system to evaluate both the anthropogenic pressures on the local large herbivore guild, as well as determine the extent to which lions are limited by prey depletion.

The GKE large herbivore guild is facing extensive human pressure, and densities have long been thought to be well below carrying capacity (Midlane 2013, Lindsey et al. 2014, Overton et al. 2017, Creel et al. 2018). Therefore, in chapter 2, I used distance-

sampling models fit to 7 years of ground-based survey data to measure density and distribution of the ten most abundant large herbivore species in KNP. I conclude this chapter by highlighting that KNP is indeed affected by prey depletion and emphasize the direct and indirect effects on large carnivore populations, with broad implications for the ecotourism and trophy hunting industries.

The GKE lion population faces negative anthropogenic pressure from the illegal wild game trade, which has led to the loss of preferred ungulate prey (Midlane 2013, Overton et al. 2017, Creel et al. 2018). Therefore, in chapter 3, I used mark-resight models fit to six years of data from known individuals to measure lion density, demography, and test the factors that affect survival. I conclude this chapter by highlighting the negative impacts of prey depletion on lion demography and suggest a simple and effective method of initially evaluating whether a lion population is affected by prey depletion.

Finally, in chapter 4, I provided general conclusions and discuss how this work can contribute to our efforts to conserve large herbivore and carnivore populations in the face of growing anthropogenic pressures. I also explored how these methods can be improved and expanded for monitoring continent wide large herbivore and lion populations important for regional conservation efforts.

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CHAPTER TWO

TESTING THE EFFECTS OF ANTHROPOGENIC PRESSURES ON A DIVERSE AFRICAN HERBIVORE COMMUNITY

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Manuscript Information

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Ecosphere

Status of Manuscript:

- ☐ Prepared for submission to a peer-reviewed journal
- ☐ Officially submitted to a peer-review journal
- ☐ Accepted by a peer-reviewed journal
- ☒ Published in a peer-reviewed journal

Published by Wiley & Sons

In Volume 11, Issue 3, Article e03067, doi: 10.1002/ecs2.3067 (2020)

Abstract

Large herbivore communities around the world have declined steeply in recent decades. Although illegal harvest of wild game is thought to be the primary cause of herbivore declines in many ecosystems, the direct effects of anthropogenic pressures on large herbivore populations remain poorly described in most of the systems experiencing decline. To test the extent to which large herbivores are impacted by ecological and anthropogenic factors in a protected area (PA) thought to be experiencing human-caused decline, we fit distance sampling models to seven years of data from systematic ground-based surveys in Kafue National Park (KNP) to estimate the population densities and distributions of 10 species of large herbivores, and to test what factors affect these parameters. Population densities of the ten most abundant large herbivores in KNP were substantially lower than those reported for an ecologically similar PA with less poaching pressure. Low densities were consistent across species and areas, though there was ecologically important variation among species and size classes. Densities of larger-bodied herbivores were greatly depressed relative to smaller species. This pattern has direct and indirect effects on large carnivore populations, with broad implications for the ecotourism and trophy hunting industries. Statistically and methodologically rigorous methods to test the effects of anthropogenic and environmental variables on density and distribution exist, but are rarely applied to large herbivores. To quantify trends in herbivore populations and evaluate the effectiveness of conservation actions, our results show that distance sampling with stratified ground-based monitoring is an efficient and effective method. In the Greater Kafue Ecosystem (GKE) continued increases in resource

protection are needed to facilitate the recovery of an economically and ecologically important large herbivore guild. More broadly, our results confirm that anthropogenic effects on large herbivore distribution and abundance can be strong over wide areas for all species (particularly the larger members of the guild), even in very large PAs.

Keywords: Prey depletion, large herbivore, poaching, distance sampling, protected areas, anthropogenic, Kafue

Introduction

Large terrestrial herbivore populations are facing dramatic population declines and range contractions globally (Ripple et al. 2015). Approximately 60% of these species are listed as threatened under the International Union of the Conservation of Nature (IUCN), and 58% are experiencing population declines (Ripple et al. 2015). Large herbivore communities in Protected Areas (PAs) have undergone declines comparable to populations in unprotected areas (Western et al. 2009, Craigie et al. 2010). These declines are of concern for two major reasons. First, large herbivores have strong effects on most terrestrial ecosystems (Bowen-Jones and Entwistle 2002, Danell et al. 2006) by mediating both top-down and bottom-up effects on ecosystem structure and function (Gordon et al. 2004, Estes et al. 2011). Through a combination of their abundance and position in the food web, these species can have strong, direct effects on plant and carnivore ecology (Sinclair and Norton-Griffiths 1979, Sinclair and Arcese 1995). As a consequence, large herbivore communities are often a focal point for ecosystem conservation and management, and are flagship species for many protected areas

(Sinclair and Norton-Griffiths 1979, Sinclair and Arcese 1995, Bowen-Jones and Entwistle 2002). Second, large herbivores provide significant economic and societal value to rural communities, particularly through wildlife-based economies utilizing tourism, trophy hunting, and game ranching (Gordon et al. 2004, Krüger 2005, Lindsey et al. 2007).

Anthropogenic activities are thought to be the strongest driver of recent large herbivore declines (Bolger et al. 2008, Wittemyer et al. 2008, Watson et al. 2014). As with other species, herbivore declines are often greatest in areas with high rates of illegally harvested wild game consumption (Brashares et al. 2011, Lindsey et al. 2013, Ripple et al. 2015). Illegally harvested herbivore populations show consistent declines in density, sometimes leading to local extirpation (Robinson and Bodmer 1999). Despite this pattern, few studies have tested how anthropogenic pressures affect the density and distribution of each species within the large herbivore guild. Herbivore declines affect both plant and large carnivore populations, so that cascading effects on ecosystem structure and function are of concern (Estes et al. 2011, Ripple et al. 2014, 2015, Creel et al. 2018). Large-bodied herbivores are often the first species to disappear from disturbed landscapes, and by monitoring their populations managers can quantify the anthropogenic impacts on PAs (Colinvaux 1979, Ripple et al. 2014, 2015, Schuette et al. 2016, 2018).

Until recently, the illegal wild game trade and its effects received little attention in the savannas of eastern and southern Africa (Lindsey et al. 2013), though prey depletion due to illegal offtake is widely suspected to be a serious problem in eastern and southern African PAs (Midlane et al. 2014, Rosenblatt et al. 2016, 2019, Creel et al. 2018). As

elsewhere, illegal offtake in Zambia has been identified as a major threat to wildlife (Barnett 2000), and its growth and commercialization drives negative ecological, social, and economic impacts (Lindsey et al. 2013, Midlane 2013, Overton et al. 2017, Creel et al. 2018).

Central Zambia's Greater Kafue Ecosystem (GKE) is comprised of Kafue National Park (KNP) and nine adjacent Game Management Areas (GMAs), which were established as buffer zones between the park and human settlement. There has been little direct study of the density and trends of the GKE large herbivore populations, although the GKE supports a diverse herbivore community of 27 species (Mwima 2001) and thus provides a good system to evaluate the effects of anthropogenic pressures on a large herbivore guild suspected to suffer from long-term population declines (Creel et al. 2018).

Understanding the limiting factors and drivers of large herbivore densities and distribution is crucial for successful conservation of African PAs, but assessing these factors and drivers is logistically difficult (Schuette et al. 2018). Several methods to describe the distribution and abundance of large herbivores exist, but they vary in their ease of use, spatial coverage, precision, and bias (Buckland et al. 2001, Jachmann 2002, Hayward et al. 2015, Schuette et al. 2018, Rosenblatt et al. 2019). Ideally, large herbivores should be monitored with methods that: (1) provide an estimate of the uncertainty associated with population estimates, (2) provide estimates with sufficient precision to allow detection of population trends before they are extreme, and (3) avoid biased estimates by accounting for imperfect detection (Caughley 1974, Jachmann 2002).

Ground-based distance sampling is a well-established method to obtain unbiased estimates that account for imperfect detection when assessing distribution and density of species (Buckland et al. 2001, Royle et al. 2004). This method provides better precision, at lower cost, than aerial surveys (Jachmann 2002). Although it is logistically difficult to conduct ground-based surveys over large areas, vehicle and foot based distance sampling surveys with stratified sampling have been successfully implemented in several sub-Saharan African PAs (Schuette et al. 2016, 2018, M'soka et al. 2017, Rosenblatt et al. 2019).

Here, we used stratified ground-based surveys and distance sampling models to estimate population densities and distribution of ten herbivore species in KNP (which collectively comprise the prey base for an intact carnivore guild: Creel et al. 2018). We then use model selection to determine what biotic, abiotic, and anthropogenic factors have the strongest relationships with these local densities and distributions, thereby providing a direct test of the extent to which large herbivores are affected by natural and anthropogenic factors in KNP.

Materials and Methods

Study area

Our study was conducted in the GKE with a focus on KNP, the largest National Park in Zambia and the 5th largest in Africa. The park encompasses 22,319 km² dominated by miombo woodland (*Brachystegia* and *Julbernardia sp.*), and includes a mixture of savannah grassland, riverine woodland, mixed acacia woodland, termitaria

woodland, and seasonally inundated grasslands. The surrounding GMAs encompass another 44,000 km², so that the GKE exceeds 66,000 km². Our core study area for this analysis was within northern KNP, north of the M9 road, west of the Kafue River, and south of the papyrus swamps of the Busanga floodplain (Fig. 1) and was representative of the park with respect to vegetation types. Mean annual rainfall in northern KNP is 1,020 mm (Midlane 2013), which is comparable to other miombo woodland ecosystems (Creel and Creel 2002, Gillingham and Lee 2003). Though our data were collected in KNP, our qualitative inferences likely also pertain to the entire GKE, which collectively is facing more human pressure than the park (Watson et al. 2014, Overton et al. 2017).

Study design

We used line transects and distance sampling (Buckland et al. 2001) to estimate herd density (herds/km²), herd size (individuals/herd), and individual density (individuals/km²) for 10 herbivore species across northern KNP. We surveyed eighteen approximately linear transects, ranging in length from 2 - 16 km, for a total distance of 121.2 km (Fig. 1). The majority of transects were oriented in an east-west direction, with even spacing at 4 km intervals from north to south. Spacing was selected to ensure a low likelihood of introducing bias from counting the same groups multiple times (Buckland et al. 2001), and transect orientation was selected to mitigate sampling bias in productive areas along major rivers. Furthermore, the design allowed for constant effort over the sampled area with an approximate 5 days of sampling effort on each occasion. Each transect was segmented based on changes in dominant vegetation type, or at 2 km intervals if the vegetation type remained constant, establishing a total of 77 segments.

Covariate values for herbivore group observations were measured at both the segment level and observation level as required by our analysis, described below.

Transects were sampled on 15 occasions between 2012-2018. Surveys were conducted during daylight hours (0900-1700) at the beginning (June-July) and end (September-October) of the dry season (May-November). An additional survey was conducted in the middle (August) of the dry season in 2014 and 2015. The wet season (Dec-April) made the study area inaccessible and prevented surveys. Each transect was sampled by vehicle traveling at 10-15 kph, with the driver maintaining the transect via a handheld Global Positioning System (GPS) with a moving map, and two rooftop observers scanning for herbivores. When a group was detected, observers recorded the distance and azimuth to the group (Buckland et al. 2001), its size and species composition, and a set of environmental covariates (described below). For each group observation, some additional segment level covariates (also described below) were calculated using QGIS 2.14.3 and the *sf* package in R (www.qgis.org, Pebesma 2018) with data layers from the Zambia Department of National Parks and Wildlife (DNPW).

Covariates of herbivore density

We measured a broad set of environmental and anthropogenic variables hypothesized to be drivers of herbivore distributions and herd sizes across KNP. Variables were either directly recorded during surveys or derived from existing GIS layers, and were measured at the segment level. We categorized variables into three classes, namely abiotic, bottom-up, and anthropogenic. In a subsequent paper we will examine how these variables affect the density and demography of carnivores,

particularly lions (*Panthera leo*), because variation in lion density is strongly correlated with prey density (Schaller 1972, Van Orsdol et al. 1985).

Anthropogenic variables considered in this analysis included: (1) distance from each segment midpoint to the nearest permanent road, (2) distance to the park boundary, (3) distance to the nearest safari lodge, and (4) distance to the nearest traditional fishing camp. These variables were the most direct measures of human activity across our core study area, and have been examined and their relevance explained in prior studies in KNP (Matandiko 2016, Schuette et al. 2018).

Abiotic variables included: (1) distance from the segment midpoint to the nearest perennial river, (2) presence or absence of any standing water, (3) presence or absence of a semi-permanent lagoon, and (4) presence or absence of burned areas. The year and season of each survey were included to account for potential temporal variation in density and herd size. All continuous distance variables were measured using QGIS 2.14.3 and the *sf* package in R (www.qgis.org, Pebesma 2018), using base maps of roads, administrative boundaries, major vegetation types, and permanent rivers from the Zambia DNPW.

Bottom-up variables included several measures of vegetation composition and structure. Directly recorded variables included vegetation type, presence or absence of green grass, and three categories of grass height (short: <10cm, intermediate: 10-100cm, tall: >100cm). We calculated the percent cover of the three dominant vegetation types (grassland, open woodland, and closed woodland) within a 500 m buffer across each segment using QGIS 2.14.3 (Midlane 2013, Matandiko 2016, www.qgis.org). We used

the perimeter tool in QGIS 2.14.3 to determine the density of edges between the three vegetation types within this buffer as a metric for habitat variability (Matandiko 2016, www.qgis.org). Specific covariates were dropped throughout the modeling process due to collinearity, with one member of each pair of predictors with Pearson correlation ≥ 0.6 discarded.

Herd density estimation

We used a multinomial generalized distance sampling model to estimate superpopulation size (λ) for each of the 10 species within each segment across all transects, while accounting for variation in availability for detection (ϕ) at the time of the survey and the probability of detection (p) if available (Chandler et al. 2011). We used this extension of Royle et al.'s (2004) multinomial-poisson mixture model because this model does not assume that repeated surveys are independent, it accounts for variation in availability of herds at the time of sampling, and it does not assume perfect detection on the transect. We used the *gdistsamp* function in the *unmarked* package in R to fit candidate models for each species (Fiske and Chandler 2011). Where sample size permitted, we identified a truncation distance for each species to exclude outlier distances that would compromise estimation of detection probability (150 m for common duiker (*Sylvicapra grimmia*); 250 m for reedbuck (*Redunca arundinum*); 300 m for puku (*Kobus vardonii*), impala (*Aepyceros melampus*), warthog (*Phacochoerus africanus*) and hartebeest (*Alcelaphus buselaphus ssp. lichtensteinii*); 350 m for waterbuck (*Kobus ellipsiprymnus ssp. defassa*); 700 m for roan (*Hippotragus equinus*); 900 m for zebra (*Equus quagga*); 1000 m for wildebeest (*Connochaetes taurinus*)).

We used Akaike's Information Criteria (AIC) to identify the best-supported models of herd density. Model selection followed a four-step method developed for analysis of similar data from South Luangwa Valley, Zambia (Rosenblatt et al. 2019): (1) We used AIC scores to select a model for detection (p) as a function of the perpendicular distance between the animal and transect, or as a function of both perpendicular distance and dominant vegetation type (Matandiko 2016). For each of these models we assessed uniform, half-normal, and hazard detection functions to describe the relationship between detection probability and perpendicular distance (Buckland et al. 2001). (2) Using this detection model we identified the best-supported model for availability for detection (ϕ) by testing effects of all combinations of year and season. (3) We then used the models of detection (p) and availability (ϕ) identified in steps 1 & 2, and used AIC scores to identify the best-supported combination of variables within each of the three classes of effects on the superpopulation (λ) of herds: bottom-up, abiotic, and anthropogenic. Continuous variables were allowed to appear as linear, logarithmic, or 2nd degree polynomial functions. (4) Finally, we selected our final herd density model by using AIC scores to compare all possible combinations of the best-supported models for each of the three classes of effects on the super-population (λ) of herds identified in step 3. This multi-stage approach was necessary to limit the number of models compared and thus computation time. We examined model fit for each species' top herd density model(s) using deviance goodness-of-fit tests, and by examining the relationship between fitted detection functions and the observed histogram of herds detected in a set of distance bins (Schuette et al. 2016, Rosenblatt et al. 2019).

We used our final best supported model to estimate herd superpopulation size (λ) and availability (ϕ) with the *predict* function in R, and derive herd density estimates ($\hat{D}$) as the product of these two parameter estimates divided by the total sampling area (Chandler et al. 2011).

Herd size estimation

We fit zero-truncated Negative Binomial (ZTNB) and zero-truncated Poisson (ZTP) regression models using the *vglm* function in the *VGAM* package in R to estimate transect-specific mean herd size for the ten focal herbivore species, and to determine effects on herd size for each species (Yee and Wild 1996, Yee 2015). Prior to fitting full models of herd size, we used a simplified ZTNB/ZTP model, with herd size as a function of distance to the transect, to test whether observed herd size was affected by distance to the transect. If the model yielded a p-value less than 0.15 we used observed herd size on the transect (distance of 0 m) to fit our herd size models. For species with limited observations and where herd size was not affected by distance to the transect, we fit our herd size model to the full data set. We used forward step-wise likelihood ratio tests, starting with an intercept-only model, to determine the best model of herd size for each of the 10 species. We fit an intercept-only ZTP model to estimate common duiker herd size, since this species is generally solitary and group size values were predominately one. We examined goodness of fit for each species' top herd size model with rootograms using the *countreg* package in R (Kleiber and Zeileis 2016).

Individual population density

Because distance sampling estimates the density of herds (not individuals), we multiplied the predicted segment-specific herd density by the predicted segment-specific herd size from our best-supported ZTNB and ZTP models to predict segment-specific individual density, which is the variable of primary interest, for all 10 focal species. Overall, these methods allowed us to estimate the mean and variance of the densities of the 10 most abundant herbivore species in KNP, determine environmental and anthropogenic effects on them, and map their predicted distributions as functions of those effects.

Results

Herd density and herd size

Ten herbivore species (out of 19 detected and 27 recorded for the GKE) were recorded sufficiently often on transects ($n \geq 40$) to model herd density and herd size. The ten species included five small-bodied herbivores (puku, impala, warthog, common duiker, reedbuck) and five large-bodied herbivores (Lichtenstein's hartebeest, blue wildebeest, roan antelope, zebra, waterbuck), following Creel et al.'s (2018) size classification for KNP. Final sample sizes for analysis were 511 puku herds, 350 impala herds, 158 warthog herds, 59 common duiker individuals, 59 blue wildebeest herds, 57 Lichtenstein's hartebeest herds, 46 roan antelope herds, 45 reedbuck herds, 41 zebra herds, and 40 waterbuck herds.

The top generalized distance sampling models for lambda (λ), phi (ϕ), and detection probability (p) varied across species (Tables 1 and 2), as did ZTNB models of herd size (Table 3). Despite this variation, there was substantial overlap across species in the variables that affected density, particularly the anthropogenic variables that were of primary interest (Tables 1 and 2).

Population density

Mean density varied considerably across the ten focal species. The most abundant large herbivore in KNP was puku, with a mean density of 11.54 animals/km² (95% CI: 10.27 - 12.82; Table 4). The second and third most abundant large herbivores were impala and warthog, with mean densities of 6.25 animals/km² (95% CI: 5.99 – 6.51) and 2.51 animals/km² (95% CI: 2.36-2.67), respectively (Table 4). Hartebeest, reedbuck, common duiker, roan, waterbuck, and zebra were all found at densities < 1 animal/km² (Table 4). The three most abundant herbivores in KNP (puku, impala, and warthog) all fell within the small size class, whereas the least abundant herbivores (zebra, and waterbuck) both fell within the larger size class.

Abiotic and biotic effects

Distance to permanent rivers had the largest effect on the densities of puku, warthog, and common duiker (Fig. 2). Vegetation composition and the density of edges between the three vegetation types affected the densities of puku, impala, warthog, reedbuck, hartebeest, and zebra, with varying strength and sign of effects (Table 2). Puku density was highest in areas with a low proportion of closed woodland (Table 2).

Conversely, hartebeest density was highest in areas with a large proportion of closed woodland (Table 2). Warthog density was highest in areas with a low proportion of open woodland (Table 2). Impala and zebra densities were positively associated with the proportion of open woodland, and zebra density was highest in areas where half of the vegetation composition was dominated by open woodland (Table 2). Reedbuck was the only species whose density was affected (positively) by the density of edges between the three vegetation types, indicating that they prefer areas with high habitat variability (Table 2).

Anthropogenic effects

Anthropogenic variables affected the densities of all species, with distance to the nearest permanent road, to the nearest park boundary, and to the nearest traditional fishing camp being the most consistent drivers. Distance to the nearest park boundary was an important correlate of density in the majority of our top models, but the strength and direction of these effects varied across species (Fig. 3). Distance to the nearest road was included in the top model for most species, with densities higher near roads and dropping off as distance increased (Fig. 4). Distance to the nearest traditional fishing camp was also in the top model for each species and had a consistent but uniquely-shaped relationship with density across species (Fig. 5). Densities were consistently highest in close proximity to traditional fishing camps.

Anthropogenic drivers were the only variables consistently included in the top density models for wildebeest, roan, and waterbuck, suggesting that these species are particularly associated with anthropogenic activity in KNP. In general, the models that

best explained density and distribution of the ten most abundant large herbivores in KNP were complex, including several environmental and anthropogenic variables.

Temporal effects

There were sufficient data to estimate variation in density across years for puku, impala, warthog, and zebra (Fig. 6). Confidence intervals overlapped substantially and we did not see clear trends in population density for puku, warthog, impala or zebra, suggesting that populations for these species were relatively stable over the years of sampling.

Mapping distributions

We mapped the densities of the three most abundant herbivore species (puku, impala, warthog), using predicted values from top herd density and herd size models (Fig. 7). Additionally, we aggregated herd density estimates for the five small-bodied herbivore species and the five large-bodied herbivore species and mapped these densities to describe broad, general patterns (Fig. 8). We chose to map herd density instead of individual density for comparison of larger versus smaller prey distribution because herd density has been suggested as a measure of hunting opportunities for large carnivores (Fryxell et al. 2007, Mosser et al. 2009). These figures reveal relatively high densities in the north-central portion of the study area, with important variation between the concentrations of different size classes (Figs. 7 and 8); in particular, puku densities were highest in proximity to major rivers (Fig. 7A).

Discussion

Large herbivore communities across Africa are rarely monitored in a manner that provides unbiased estimates of population density and distribution with sufficient precision to evaluate drivers. Here, stratified, systematic ground-based transects accounting for differences in detection proved valuable to test the extent to which anthropogenic activities affect large herbivore densities, and to test whether KNP is affected by prey depletion. This information is of use to guide conservation strategies for these economically, socially, and ecologically important species (Schuette et al. 2016, 2018, M'soka et al. 2017, Rosenblatt et al. 2019). Our results also demonstrate the value of long term monitoring (15 surveys over 7 years), which allowed us to examine a broader set of species and potential drivers of density and distribution than could be examined in prior analyses for this ecosystem (Matandiko 2016, Schuette et al. 2018).

To further evaluate whether large herbivore densities in KNP are low as previously suggested (Midlane 2013, Overton et al. 2017, Creel et al. 2018), we compared mean density estimates from this study to historical estimates from Selous Game Reserve (SGR), Tanzania, where anti poaching efforts were strong in the early 1960's (Rodgers 1979). Like Kafue, the Selous is a miombo-dominated ecosystem that is similar in vegetation type and rainfall, and thus provides the best available point of comparison (Creel and Creel 2002, Gillingham and Lee 2003). Moreover, Rodgers (1979) derived large herbivore density estimates using comparable distance sampling methods, with surveys conducted during the dry season, like ours. The current densities of impala, warthog, hartebeest, wildebeest, and zebra in KNP were 4.6-fold, 2.5-fold, 5.4-

fold, 24.7-fold, and 42.9-fold lower respectively than their densities in Selous (Fig. 9).

Two of the three most abundant herbivores from past data in Selous (wildebeest and zebra) were in the large size class, but the three most abundant herbivores in KNP (puku, impala, and warthog), were all in the small size class.

Broadly, this comparison indicates that the population densities of the most abundant large herbivores in KNP are lower than has been reported historically in miombo woodland ecosystems with less poaching pressure (Rodgers 1979). This observation provides empirical support to the suggestion that the GKE is affected by prey depletion (Midlane 2013, Creel et al. 2018). Low densities are consistent across species, although there is ecologically important variation among species and size classes (Figs. 7 and 8). Importantly, we observed considerable variation between the densities of large versus small herbivores, with plausible implications for the distributions of large carnivores in the system, and competition among them (Fig. 8). Puku, impala, and warthog densities were higher than previous findings from a short-term study spanning the entire park (Schuette et al. 2018), but very low in comparison to historical data from an intact miombo herbivore guild (Rodgers 1979). In particular, the densities of larger-bodied herbivores (hartebeest, wildebeest, waterbuck, and zebra) are considerably depressed.

Our results support previous research that found lower wildlife densities in areas with less protection (Caro et al. 1998, Stoner et al. 2007, Ogutu et al. 2009, 2011, Schuette et al. 2016, Rosenblatt et al. 2019). However, these areas have generally been adjacent to national parks (Becker et al. 2013a, Rosenblatt et al. 2016, 2019), and prey

depletion within the national park itself is notable in this case. Depletion of large herbivores in KNP is linked to long-term illegal harvest at unsustainable levels (Overton et al. 2017). A prior study, conducted at a broader spatial scale but a shorter time scale, also found low herbivore densities across the entire park (Schuette et al. 2018), and the rate of illegal harvest is consistent throughout the GKE (Overton et al. 2017). Illegal offtake is strongly correlated with human encroachment, which is increasing in the area surrounding KNP (Watson et al., 2013, 2014).

Separating effects of poaching from environmental variables is difficult, because poaching efforts are non-random and correlated with both anthropogenic and environmental variables (Watson et al., 2013). Anthropogenic variables were important correlates of density for all 10 species, but we caution against inferring causation due to the confounding of environmental and anthropogenic variables (Ogutu et al. 2010, M'soka et al. 2017). With that caveat, we found a non-linear relationship between herbivore density and distance to fishing camps that was constant across species, suggesting that these camps are consistently sited in areas with relatively high herbivore density. Human presence around traditional fishing camps could be providing some level of refuge for herbivores (Reid 2012) and this logic might also explain higher herbivore densities in proximity to roads. We consider this explanation unlikely given our understanding of large carnivore movements around traditional fishing camps and roads (unpublished observations and GPS collar data). Rather, we suggest that relatively high herbivore densities near traditional fishing camps simply reflects the fact that these camps are predominantly located within the Busanga flood plain, which is one of the most

productive areas in Kafue and the epicenter of tourism for the park. Consequently, this area has a high capacity to maintain herbivores, and high tourism operator presence and anti-poaching efforts locally deter poaching. Similarly, we suggest that the positive effect of proximity to roads on herbivore densities reflects that roads are located in high quality habitat to facilitate animal sightings for tourism operators.

Effects of traditional fishing camps are consistent at small distances, and based on many data points. Although effects for this variable are also consistent at large distances, these effects are based on far fewer points. Additionally, the ubiquitous increase in density at large distances from traditional fishing camps is due to only two transects, located in the most southern part of our study area (Fig. 1). Park regulations allow 17 fishing weirs to be operational seasonally along the Lufupa River in northern KNP (Mwima 2001). Thirty active weirs and 20 associated camps are currently documented in this area (Midlane 2013, *Zambian Carnivore Programme*, unpublished). Given the increase in fishing pressure beyond current regulations, increased resources for enforcement are recommended to both protect important wildlife areas and to protect traditional users with legitimate fishing rights from being encroached by illegal fishing operations. These illegal operations can also pose a poaching threat.

The ubiquitous low density of large herbivore populations in KNP has two major conservation implications. First, it is likely to negatively impact the ecotourism and trophy hunting industries. The GKE supports a unique herbivore community with 27 documented species. This diverse herbivore community and the associated large carnivore guild drive ecotourism across the GKE. Declines in ecotourism would further

limit tourism-based employment, negatively impacting local communities (Lindsey et al., 2013). Sustainable trophy hunting is another conservation tool with the potential to provide benefits to local communities (Lindsey et al. 2007, Di Minin et al. 2016), but this industry is often financially unviable in areas with high rates of wild game poaching (Lindsey et al. 2012). Second, the decline of large herbivores will likely alter density and demography of large carnivores. Prey depletion is a major global threat facing many large carnivore populations and is widely recognized to be a strong driver of carnivore declines (Midlane et al. 2014, Ripple et al. 2014, Rosenblatt et al. 2016). In KNP, a comparison of carnivore diets now and 50 years ago showed that the importance of relatively abundant small-bodied herbivores has increased, whereas the importance of large-bodied herbivores has decreased (Creel et al. 2018). Consequently, prey depletion and niche compression will have likely direct and indirect effects on carnivore populations. We will directly test the effect of low prey density on African lion density, survival, and population structure in a forthcoming paper.

As large herbivore population declines continue across Africa, precise population level estimates will be critical to detect population declines, to determine their causes, and to guide adaptive management and conservation action. Such measures will be particularly crucial to the conservation success of KNP, the GKE, and Kavango - Zambezi Transfrontier Conservation Area (KAZA). These findings reflect how large herbivore communities might be affected in other ecosystems experiencing high rates of illegal harvest (Midlane 2013, Overton et al. 2017, Creel et al. 2018). The effect of wild game poaching is evident and expected to rise with growing human populations (Watson

et al., 2013, 2014). In order to detect trends in herbivore populations, and to implement constructive conservation measures against illegal offtake and evaluate their effectiveness, we emphasize that stratified ground-based monitoring continue to be conducted and expanded. Moreover, continued increases in resource protection are needed across the GKE to mitigate anthropogenic pressures and facilitate the recovery of an economically and ecologically important large herbivore guild.

Acknowledgements

Our thanks to the Zambia Department of National Parks and Wildlife for permission to conduct this research, and for collaborative efforts to help monitor, manage and conserve these herbivore populations. Funding: this research was supported by the National Science Foundation (IOS1145749), National Geographic Society Big Cats Initiative, Gemfields Inc., World Wildlife Fund– Netherlands & Zambia, The Bennink Foundation, Wilderness Wildlife Trust, Panthera, Ntengu Safaris, Elephant Charge, and IUCN Save Our Species/European Union.

Table 2.1: Model selection results for distance sampling models estimating herd density for the 10 herbivore species of interest. We made model-averaged predictions using models within 1 delta AIC score of the top model; we used top models if there were no closely competing models. Continuous covariates may appear in models as a linear, logarithmic (log), or 2nd-order polynomial (poly) association with the parameter.

Model - λ	Model - ϕ	Model - p	k	Δ AIC	AIC Weight
Puku					
~Dist to Bound + poly(Dist to FC) + %CW + poly(Dist to Riv)	~Sea	~Veg	15	0	0.48
~Dist to Bound + poly(Dist to FC) + %CW + poly(Dist to Riv) + Edge D	~Sea	~Veg	16	0.43	0.39
Impala					
~Dist to Bound + log(Dist to FC) + log(Dist to Rd) + %OW	~Yr + Sea	~1	15	0	0.61
~Dist to Bound + log(Dist to FC) + log(Dist to Rd) + %OW + Edge D	~Yr + Sea	~1	16	1.76	0.25
Warthog					
~Dist to Bound + poly(Dist to FC) + Dist to Rd + poly(Dist to Riv)	~Sea	~1	12	0	0.26
~Dist to Bound + poly(Dist to FC) + Dist to Rd + %OW + poly(Dist to Riv)	~Sea	~1	13	0.93	0.17
~Dist to Bound + poly(Dist to FC) + Dist to Rd	~Sea	~1	10	0.95	0.16
~Dist to Bound + poly(Dist to FC) + Dist to Rd + %OW	~Sea	~1	11	1.36	0.13
~Dist to Bound + poly(Dist to FC) + Dist to Rd + poly(Dist to Riv) + Edge D	~Sea	~1	13	1.99	0.097
Common Duiker					
~poly(Dist to FC) + log(Dist to Rd) + poly(Dist to Riv)	~1	~1	8	0	0.49
~poly(Dist to FC) + log(Dist to Rd) + %CW + poly(Dist to Riv)	~1	~1	9	1.76	0.2
~poly(Dist to FC) + log(Dist to Rd) + poly(Dist to Riv) + Edge D	~1	~1	9	1.77	0.2
Reedbuck					
~Dist to Bound + poly(Dist to FC) + log(Dist to Rd) + Edge D	~Sea	~1	10	0	0.45
~Dist to Bound + poly(Dist to FC) + log(Dist to Rd) + Dist to Riv + Edge D	~Sea	~1	11	1.96	0.17
Hartebeest					
~poly(Dist to FC) + log(Dist Rd) + %CW	~Yr + Sea	~1	15	0	0.46
~poly(Dist to FC) + log(Dist Rd) + %CW + Edge D	~Yr + Sea	~1	16	1.83	0.18

~poly(Dist to FC) + log(Dist Rd) + %CW + Dist to Riv	~Yr + Sea	~1	16	1.98	0.17
Wildebeest					
~Dist to Bound + poly(Dist to FC)	~Yr + Sea	~1	19	0	0.45
~Dist to Bound + poly(Dist to FC) + %CW	~Yr + Sea	~1	20	1.66	0.2
Roan					
~Dist to Bound + poly(Dist to FC) + log(Dist to Rd)	~1	~1	7	0	0.29
~Dist to Bound + poly(Dist to FC) + log(Dist to Rd) + log(Dist to Riv)	~1	~1	8	1.21	0.16
~Dist to Bound + poly(Dist to FC) + log(Dist to Rd) + Edge D	~1	~1	8	1.3	0.15
~Dist to Bound + poly(Dist to FC) + log(Dist to Rd) + %CW	~1	~1	8	1.68	0.13
Zebra					
~Dist to Bound + poly(Dist to FC) + Dist to Lodge + poly(%OW) + poly(%CW)	~1	~1	11	0	0.52
~Dist to Bound + poly(Dist to FC) + Dist to Lodge + poly(%OW) + poly(%CW) + Edge D	~1	~1	12	1.66	0.23
Waterbuck					
~Dist to Bound + poly(Dist to FC) + log(Dist to Rd)	~1	~1	7	0	0.36
~Dist to Bound + poly(Dist to FC) + log(Dist to Rd) + log(Dist to Riv)	~1	~1	8	1.56	0.16
~Dist to Bound + poly(Dist to FC) + log(Dist to Rd) + %CW	~1	~1	8	1.86	0.14
~Dist to Bound + poly(Dist to FC) + log(Dist to Rd) + Edge D	~1	~1	8	1.94	0.13

Notes: Dist to Bound = Distance to park boundary; Dist to FC = Distance to nearest traditional fishing camp; Dist to Riv = Distance to nearest permanent river; Dist to Rd = Distance to nearest road; Edge D = Density of edges between dominant vegetation types; Dist to Lodge = distance to nearest safari lodge; Yr = Study year of survey; Sea = Season of survey; Veg = Dominant vegetation type.

Table 2.2: Coefficient estimates and standard errors from each species' top herd density model. Coefficient estimates with p-values <0.05 are indicated (*). Covariates included in model averaging for puku and warthog but not in the top model are also indicated (+).

	Puku	Impala	Warthog	Duiker	Reedbuck	Hartebeest	Wildebeest	Roan	Zebra	Waterbuck
λ - Covariates	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)
Intercept	1.52 (0.31)*	2.93 (0.46)*	2.17 (0.43)*	0.44 (0.58) -0.58	-6.45 (2.36)*	0.57 -0.69	-7.62 (2.00)*	-1.80 (-1.28)	-21.65 (8.04)*	-0.33 (3.43)
Edge Density	+	-	-	-	0.34 (0.16)*	-	-	-	-	-
% OW	-	0.01 (0.003)*	+	-	-	-	-	-	2.90 (3.85)	-
% OW ²	-	-	-	-	-	-	-	-	3.37 (2.26)	-
% CW	-0.01 (0.003)*	-	-	-	-	0.01 (0.004)*	-	-	-2.35 (4.45)	-
% CW ²	-	-	-	-	-	-	-	-	-6.27 (2.30)*	-
% OG	-	-	-	-	-	-	-	-	-	-
% OG ²	-	-	-	-	-	-	-	-	-	-
Distance to Road	-	-	-0.12 (0.10)	-	-	-	-	-	-	-
log(Distance to Road)	-	-0.05 (0.04)	-	0.23 (0.11)*	0.29 (0.11)*	0.12 (0.11)	0.17 (0.10)	0.23 (0.09)*	-	0.22 (0.10)*
Distance to Fishing Camp	-7.00	-	-6.76	-5.50	5.53	-5.73	3.54	-1.34	20.85	-0.97

	(1.02)*		(1.17)*	(1.68)*	(3.04)	(1.53)*	(2.88)	(2.18)	(10.28)*	(2.10)
Distance to Fishing Camp ²	10.53	-	4.45	14.52	23.93	14.51	23.43	19.30	42.33	15.67
	(1.33)*		(1.27)*	(2.83)*	(4.64)*	(2.58)*	(4.27)*	(2.96)*	(12.55)*	(2.61)*
log(Distance to Fishing Camp)	-	-0.47 (0.10)*	-	-	-	-	-	-	-	-
Distance to Safari Lodge	-	-	-	-	-	-	-	-	-0.31 (0.16)	-
Distance to Park Boundary	-0.05 (0.01)*	-0.06 (0.01)*	-0.05 (0.01)*	-	0.25 (0.07)*	-	0.2 (0.06)*	0.08 (0.04)*	0.71 (0.26)*	0.06 (0.03)
Distance to River	2.39 (0.92)*	-	0.52 (0.91)	3.97 (1.88)*	-	-	-	-	-	-
Distance to River ²	0.88 (0.73)	-	1.76 (0.83)*	2.78 (1.33)*	-	-	-	-	-	-

φ - Covariates	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)
Intercept	-0.83 (0.16)*	-0.26 (0.40)	-1.73 (0.61)*	-	-5.14 (0.52)*	-5.06 (1.16)*	-	-	-	-
Year2013	-	-0.54 (0.37)	-	-	-	-0.23 (1.15)	-	-	-	-
Year2014	-	-0.78 (0.38)*	-	-	-	0.66 (1.10)	-	-	-	-
Year2015	-	-0.48 (0.38)	-	-	-	1.26 (1.07)	-	-	-	-
Year2016	-	-0.93 (0.39)*	-	-	-	0.85 (1.10)	-	-	-	-
Year2017	-	-0.90 (0.38)*	-	-	-	0.67 (1.11)	-	-	-	-
Year2018	-	-0.26	-	-	-	2.03	-	-	-	-

		(0.38)				(1.04)				
SeasonLate	0.60	0.31	0.47	-	0.66	-0.45	-	-	-	-
	(0.14)*	(0.17)	(0.22)*		(0.35)	(0.31)				
SeasonMid	0.33	0.37	0.7	-	0.41	0.86	-	-	-	-
	(0.20)	(0.27)	(0.31)*		(0.50)	(0.51)				
Estimate	-	-	-	-2.40	-	-	-2.21	-4.63	-3.77	-4.67
				(0.53)*			(0.52)*	(0.54)	(0.34)	(3.19)
<i>p</i> - Covariates	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)	β Estimate (SE)
Intercept	-1.77 (0.10)*	-	-	-	-	-	-	-	-	-
Flooded Grassland	-0.39 (0.12)*	-	-	-	-	-	-	-	-	-
Open Bushland	-0.41 (0.16)*	-	-	-	-	-	-	-	-	-
Open Grassland	-0.29 (0.13)*	-	-	-	-	-	-	-	-	-
Open Woodland	-0.45 (0.11)*	-	-	-	-	-	-	-	-	-
Detection Estimate	-	-2.26 (0.04)*	-3.67 (0.88)*	-3.04 (0.10)	-2.07 (0.17)	-2.18 (0.11)	-1.52 (0.11)*	-1.34 (0.12)	-1.11 (0.13)	-2.01 (0.14)
Hazard Detection Function	-	-	0.08 (0.27)	-	-	-	-	-	-	-

Table 2.3: Coefficient estimates and standard errors from final ZTNB and ZTP group size models. Covariates not included in the final models are indicated as either dropped during model refinement (+) or excluded from model refinement due to high collinearity, or Hauck-Donner effects (-). Coefficient estimates with p-values <0.05 are indicated (*).

	Puku	Impala	Warthog	Duiker	Reedbuck	Hartebeest	Wildebeest	Roan	Zebra	Waterbuck
Covariate	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)	Estimate (SE)
Intercept:1 (mean)	0.21 (0.54)	2.13 (0.28)*	0.82 (0.33)*	-1.35 (0.35)*	1.48 (0.35)*	0.99 (0.26)*	3.18 (0.49)*	2.75 (0.45)*	1.99 (0.37)*	1.18 (0.16)*
Intercept:2 (over dispersion)	-0.12 (0.39)	-0.51 (0.17)*	2.30 (0.49)*	NA	1.41 (0.70)*	0.55 (0.37)	-1.28 (0.60)*	-0.63 (0.55)	2.15 (0.47)*	1.46 (0.74)*
Edge Density	+	+	+	+	0.31 (0.17)	+	-	+	+	+
% CW	+	+	-0.004 (0.002)*	-	-	0.01 (0.004)*	-	-	-	+
% OW	+	+	+	-	+	0.01 (0.004)*	-0.03 (0.01)	+	+	-
% OG	+	-	-	-	+	-	-	+	-	-
Lagoon:Present	+	-0.42 (0.19)*	-	+	-	+	-	-	-	-
Water:Present	+	+	+	-	-	+	-	+	+	+
Grass Height : Short	+	+	0.36 (0.15)*	-	-0.59 (0.45)	+	+	-1.67 (0.70)*	+	0.17 (0.29)
Grass Height : Tall	+	+	0.17 (0.36)	-	-1.63 (0.72)*	+	+	-2.02 (0.98)*	+	-1.84 (0.75)*
Grass Color : Green	+	+	+	+	+	+	+	+	+	+

Distance to Road	+	-0.16 -0.09	+	-	+	+	+	-0.65 (0.34)	-	+
Distance to Lodge	+	+	-0.04 (0.02)*	-	-	+	-	-	-0.07 (0.02)*	+
Distance to Park Boundary	-	-	-	+	+	-	-	+	+	+
Distance to Fishing Camp	+	+	-0.02 (0.007)*	+	-0.03 (0.02)*	+	-0.12 (0.04)*	-0.05 (0.02)*	+	-
Distance to River	+	+	+	+	-0.17 (0.08)*	+	+	-	+	-
Mixed Herd	0.99 (0.39)*	+	+	+	+	+	+	+	+	+
Season Late	+	-0.53 (0.16)*	0.31 (0.14)*	-	+	+	+	+	+	+
Season Mid	+	-0.43 (0.24)	0.36 (0.18)*	-	+	+	-	+	+	+
Year2013	1.83 (0.63)*	0.21 (0.29)	0.61 (0.31)*	+	-	+	-	+	0.54 (0.42)	-
Year2014	2.07 (0.72)*	0.60 (0.30)*	0.73 (0.30)*	+	-	+	-	+	0.36 (0.35)	-
Year2015	1.58 (0.96)	0.51 (0.30)	0.92 (0.30)*	+	-	+	-	+	0.59 (0.36)	-
Year2016	0.6 (0.67)	-0.09 (0.32)	0.82 (0.32)*	+	-	+	-	+	0.51 (0.38)	-
Year2017	1.2 (0.87)	0.36 (0.32)	1.10 (0.32)*	+	-	+	-	+	0.76 (0.41)	-
Year2018	2.73	0.31	0.69	+	-	+	-	+	1.41	-

	(0.39)*	(0.29)	(0.32)*						(0.33)*	
Burn:Present	+	-	+	+	+	+	-	+	+	+

Table 2.4: Estimates and range across segments of herd density and individual density. Mean herd density estimates are mean values for 1,155 model estimates (77 segments surveyed on 15 occasions between 2012 and 2018) based on each species' top herd density model. Mean individual density estimates reported are mean values of the 1,155 model estimates of herd density multiplied by the estimated herd size from each species top herd size model at each one of the 77 segments. 95% CIs are listed for each density estimate, and ranges coincide with the max and min densities across all segments.

Species	Mean Herd Density (herds/km2)	Range Across Segments	Mean Individual Density (animals/km2)	Range Across Segments
Puku	1.31 (1.20 - 1.42)	(0.01 - 5.04)	11.54 (10.27 - 12.82)	(0.04 – 101.37)
Impala	0.74 (0.72 - 0.77)	(0.13 - 3.47)	6.25 (5.99 – 6.51)	(0.54 – 33.61)
Warthog	0.66 (0.63 - 0.70)	(0.04 - 2.68)	2.51 (2.36 - 2.67)	(0.10- 16.55)
Reedbuck	0.09 (0.08 - 0.10)	(0.00 - 1.02)	0.40 (0.33 - 0.46)	(0.00 – 9.59)
Common Duiker	0.31 (0.29 - 0.34)	(0.00 - 1.84)	0.36 (0.33 - 0.39)	(0.00 - 2.10)
Wildebeest	0.07 (0.06 - 0.07)	(0.00 - 0.53)	1.06 (0.90 – 1.22)	(0.00 - 15.30)
Hartebeest	0.13 (0.11 - 0.15)	(0.00 - 3.32)	0.76 (0.64 - 0.88)	(0.00 – 24.40)
Roan	0.04 (0.04 - 0.05)	(0.00 - 0.32)	0.37 (0.31 - 0.42)	(0.00 - 4.97)
Waterbuck	0.07 (0.07 - 0.08)	(0.00 - 0.43)	0.24 (0.22 - 0.27)	(0.00 - 1.76)
Zebra	0.03 (0.03 - 0.04)	(0.00 - 0.56)	0.25 (0.21 - 0.30)	(0.00 - 9.60)

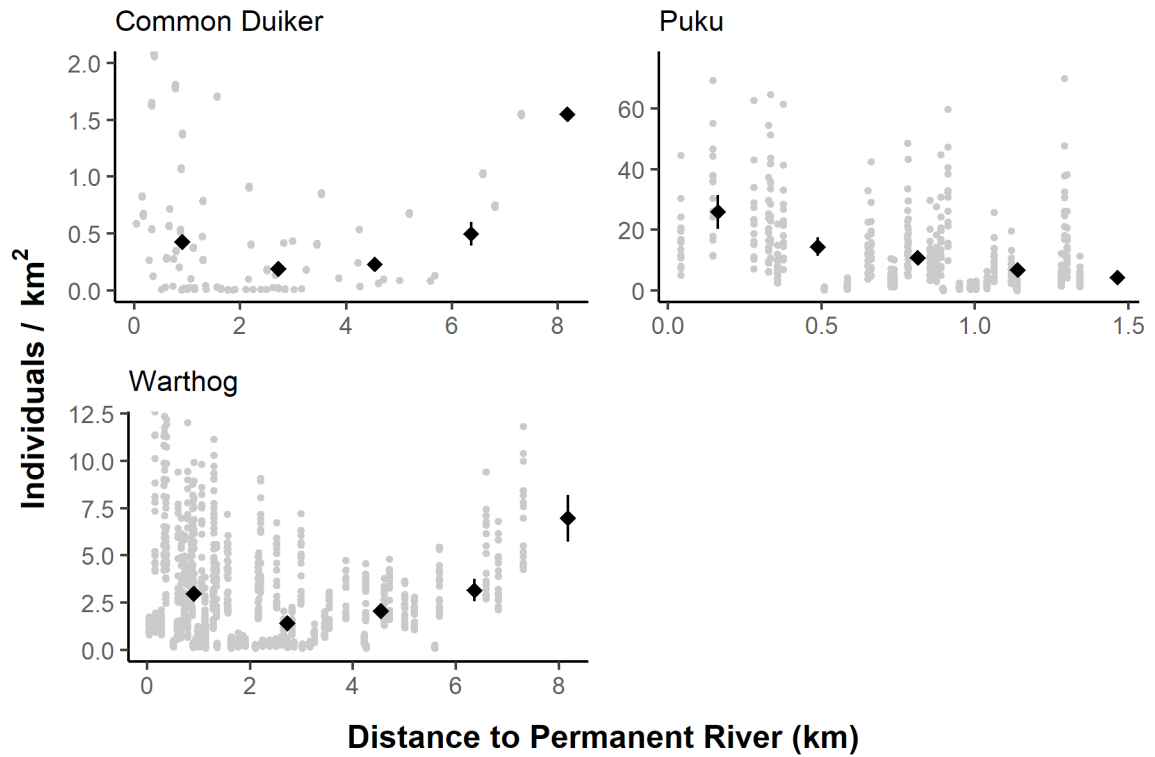


Figure 2.2: Effect of distance to permanent rivers on population densities for three small herbivore species in KNP. Grey points are segment-specific density estimates across the six-year study. Black diamonds depict mean density estimates across binned distances, along with 95% CIs. Y-axes were truncated to clearly display variation in the effect across species.

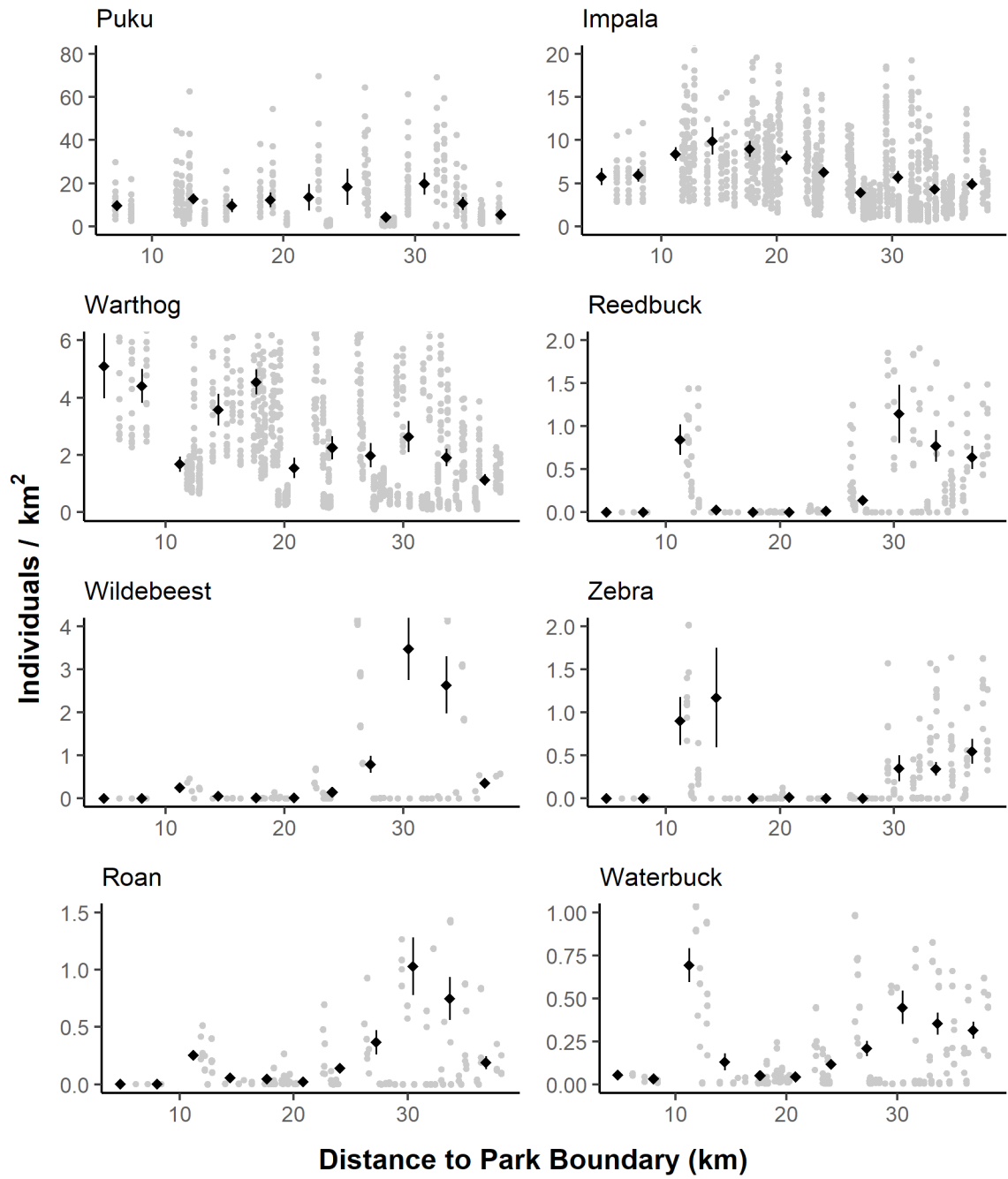


Figure 2.3: Effect of distance to park boundary on population densities for eight herbivore species in KNP. Grey points are segment-specific density estimates across the six-year study. Black diamonds depict average density estimates across binned distances, along with 95% CIs. Y-axes were truncated to clearly display variation in the effect across species.

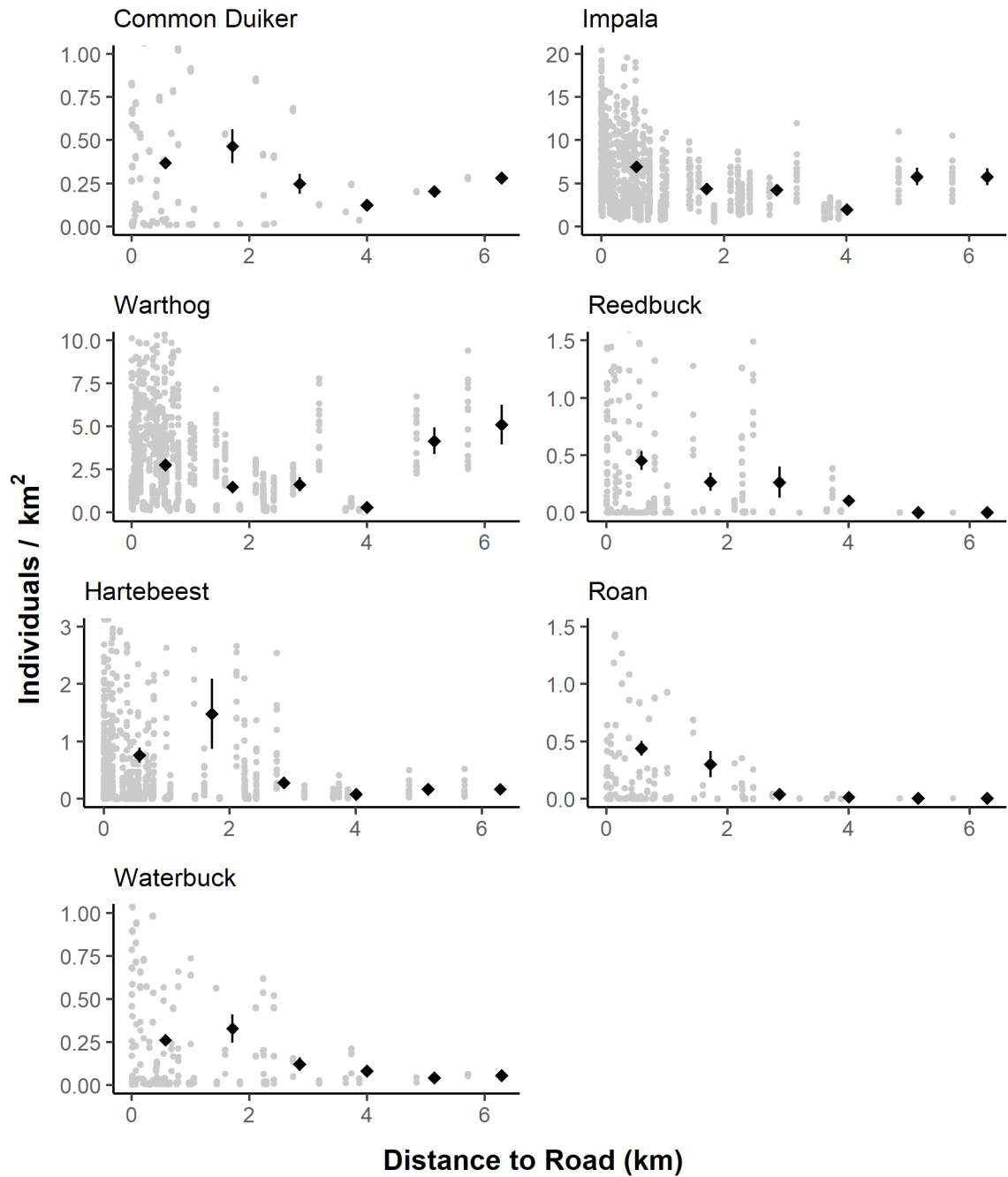


Figure 2.4: Effect of distance to road on population densities for seven herbivore species in KNP. Grey points are segment-specific density estimates across the six-year study. Black diamonds depict average density estimates across binned distances, along with 95% CIs. Y-axes were truncated to clearly display variation in the effect across species.

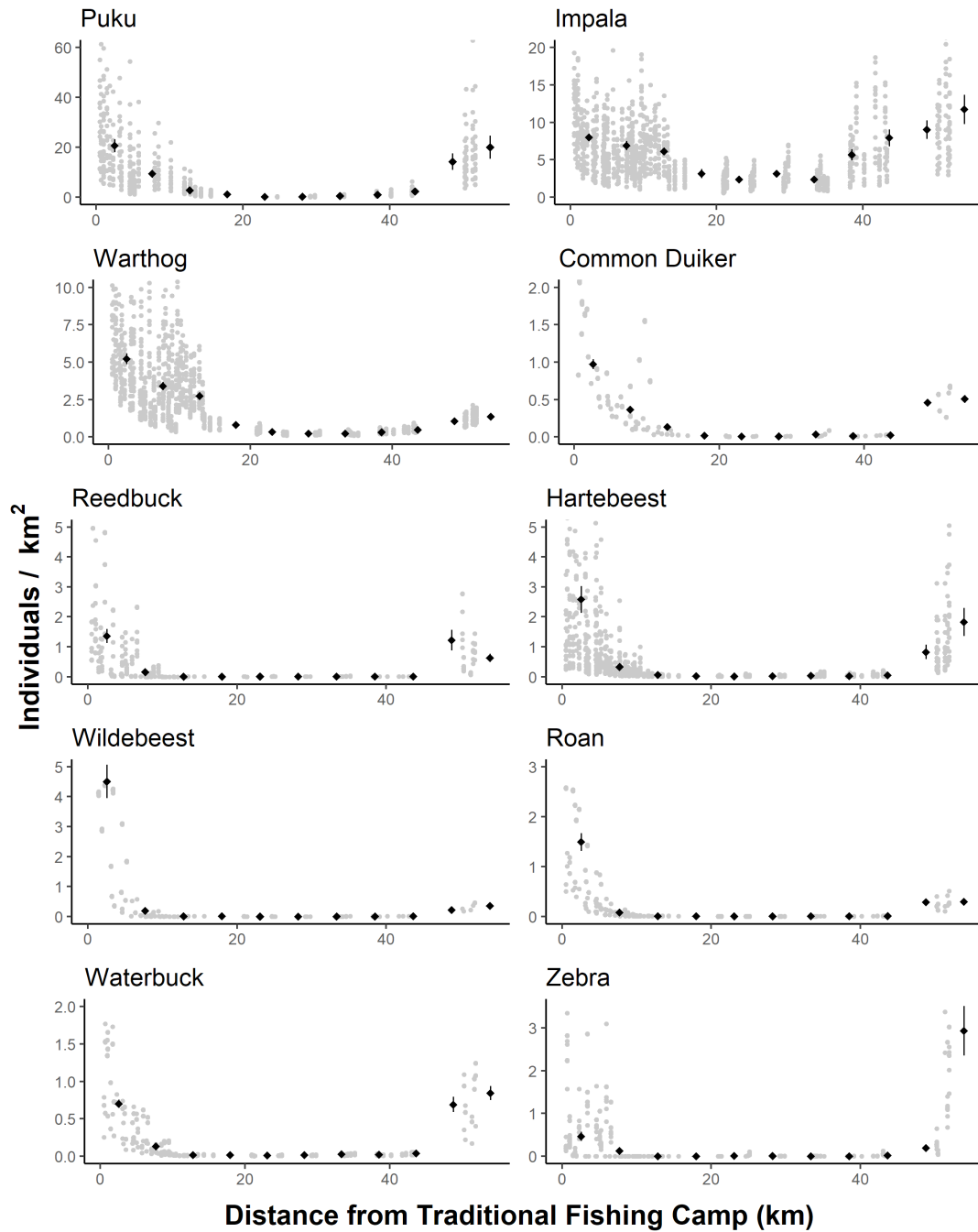


Figure 2.5: Effect of distance to traditional fishing camp on population densities for all ten herbivore species in KNP. Grey points are segment-specific density estimates across the six-year study. Black diamonds depict average density estimates across binned distances, along with 95% CIs. Y-axes were truncated to clearly display variation in the effect across species.

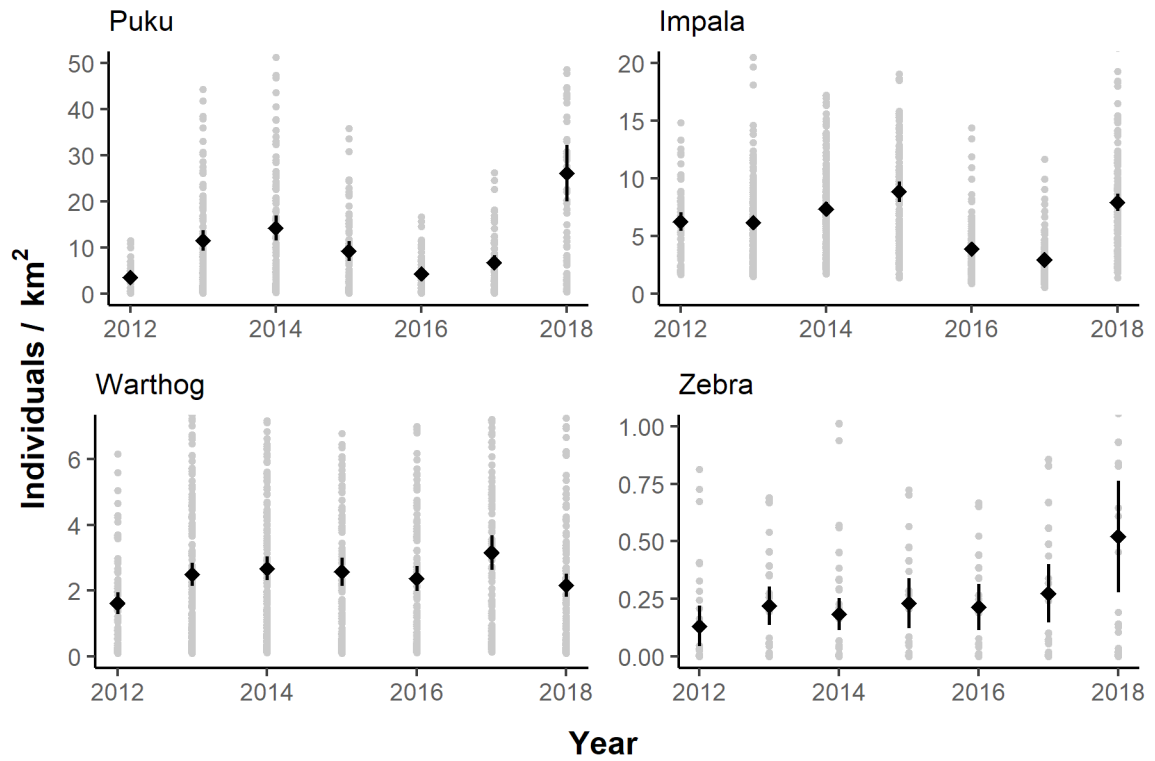


Figure 2.6: Temporal effects on population density for 4 herbivore species in KNP. Grey points are segment-specific density estimates across the six year study, overlaid with average annual densities (black diamonds) and 95% CIs. Y-axes were truncated to clearly display variation between annual averages.

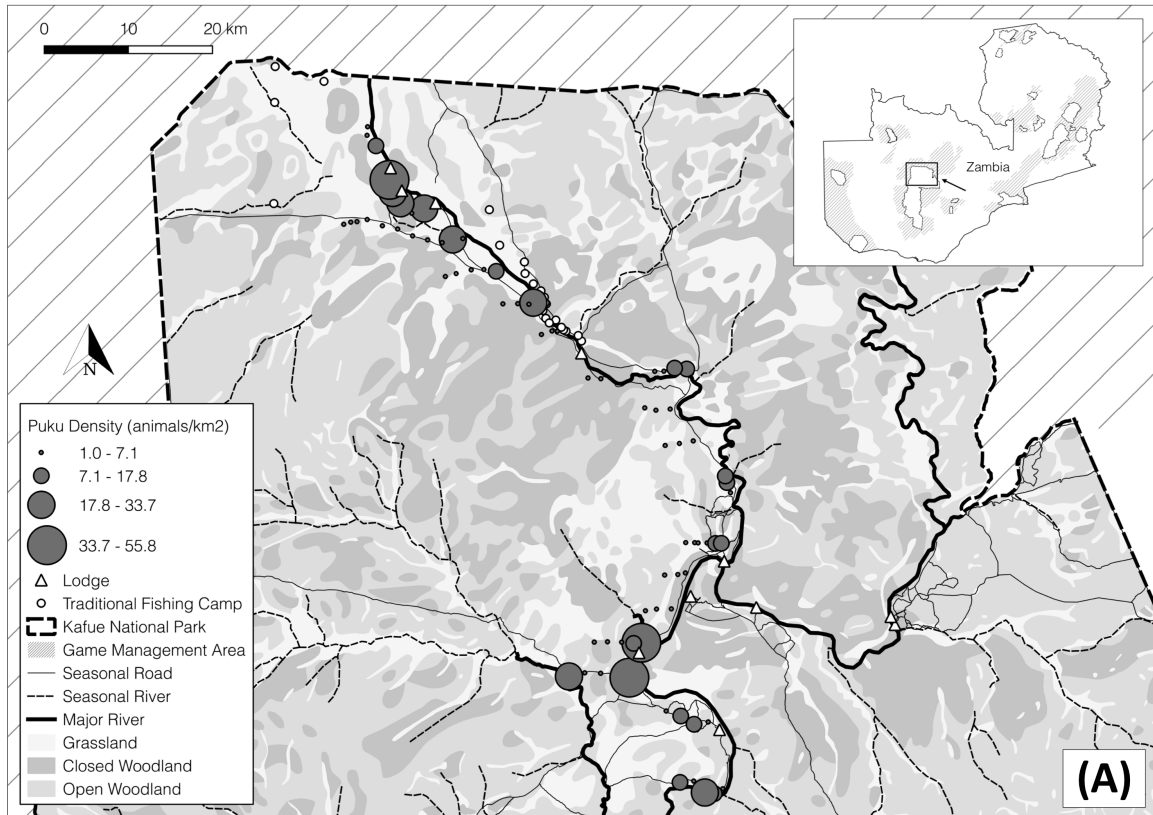


Figure 2.7: Predicted distribution of population density (animals/km²) for puku (A) across each surveyed transect segment using ground-based distance sampling methods in northern Kafue National Park, Zambia. Estimates are based on the top herd density and herd size models.

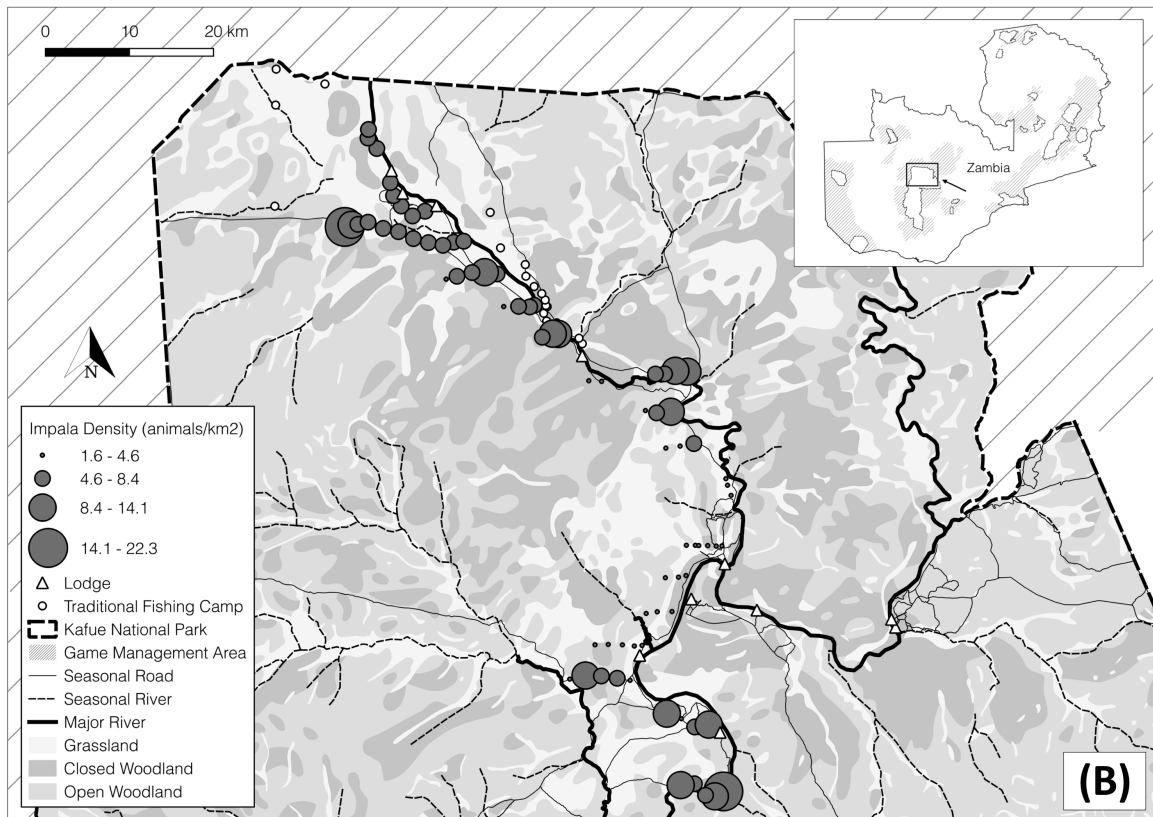


Figure 2.8: Predicted distribution of population density (animals/km²) for impala (B), across each surveyed transect segment using ground-based distance sampling methods in northern Kafue National Park, Zambia. Estimates are based on the top herd density and herd size models.

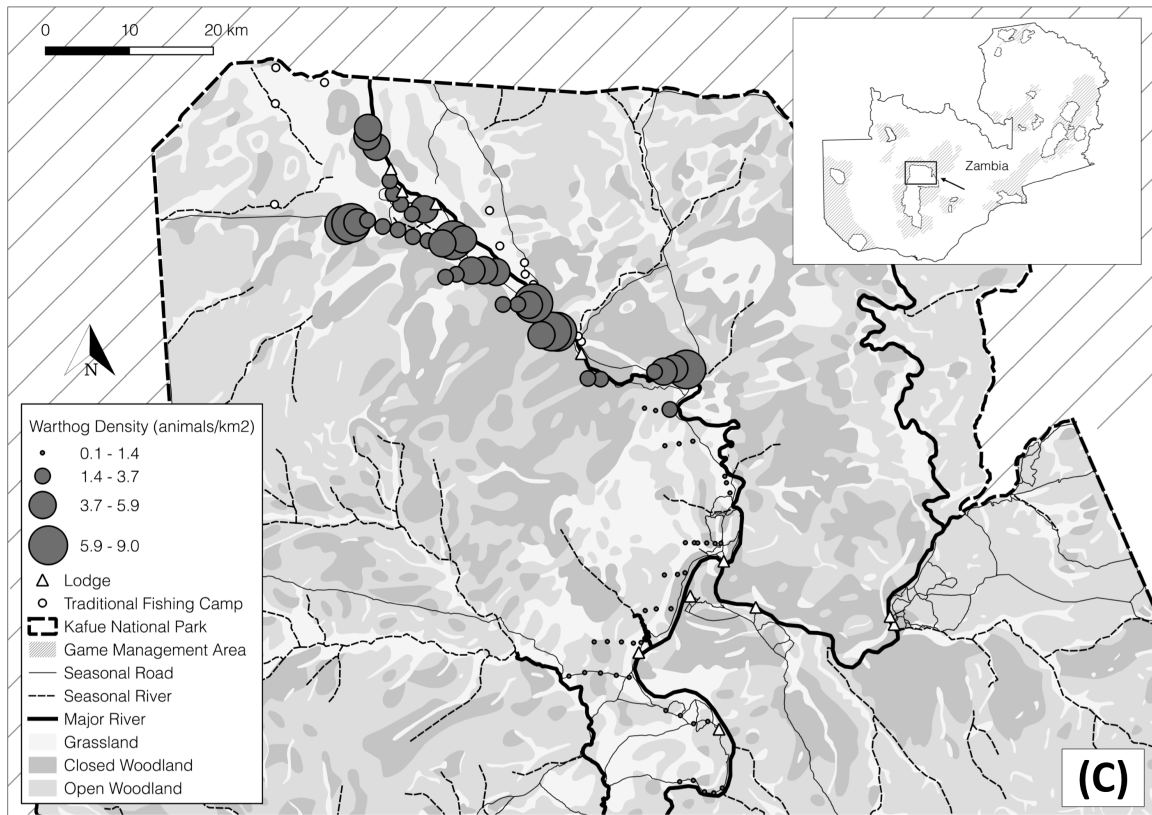


Figure 2.9: Predicted distribution of population density (animals/km²) for warthog (C), across each surveyed transect segment using ground-based distance sampling methods in northern Kafue National Park, Zambia. Estimates are based on the top herd density and herd size models.

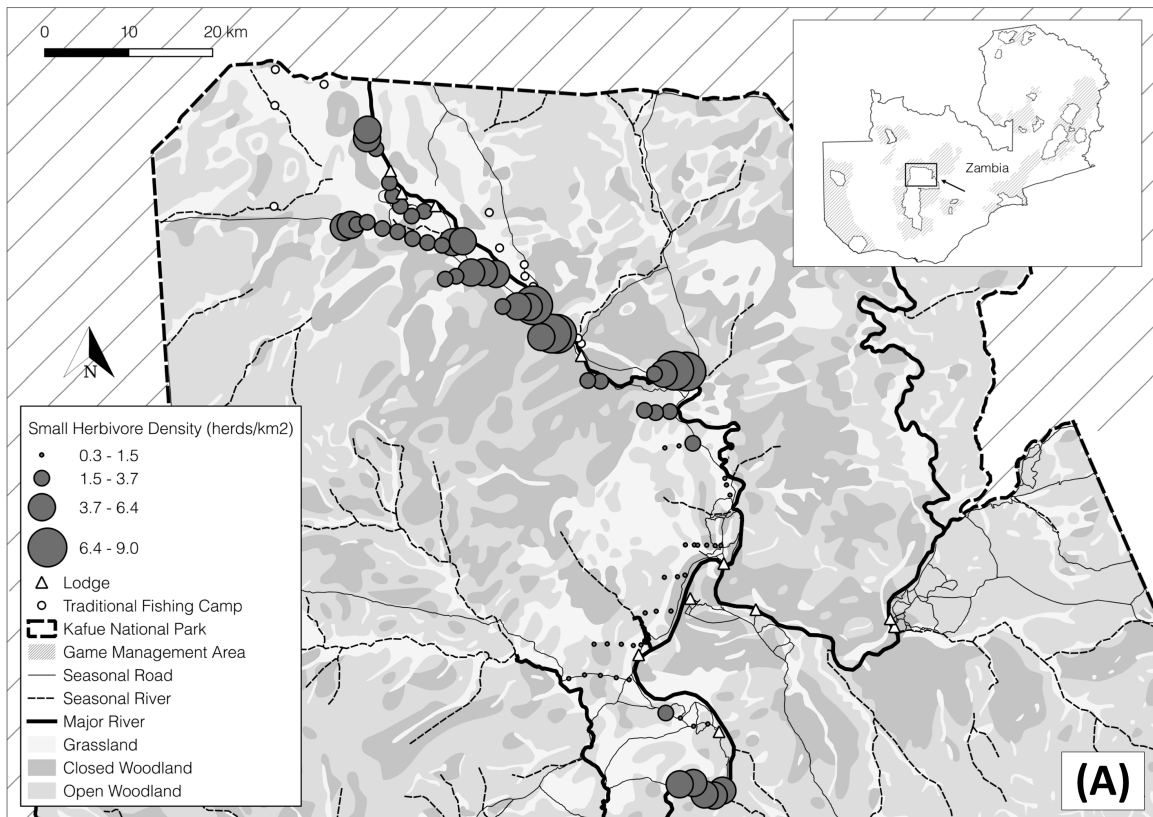


Figure 2.10: Predicted distribution of combined small-bodied (A) herbivore density (herds/km²) across each surveyed transect segment using ground-based distance sampling methods in northern Kafue National Park, Zambia. Estimates are based on the top herd density and herd size models.

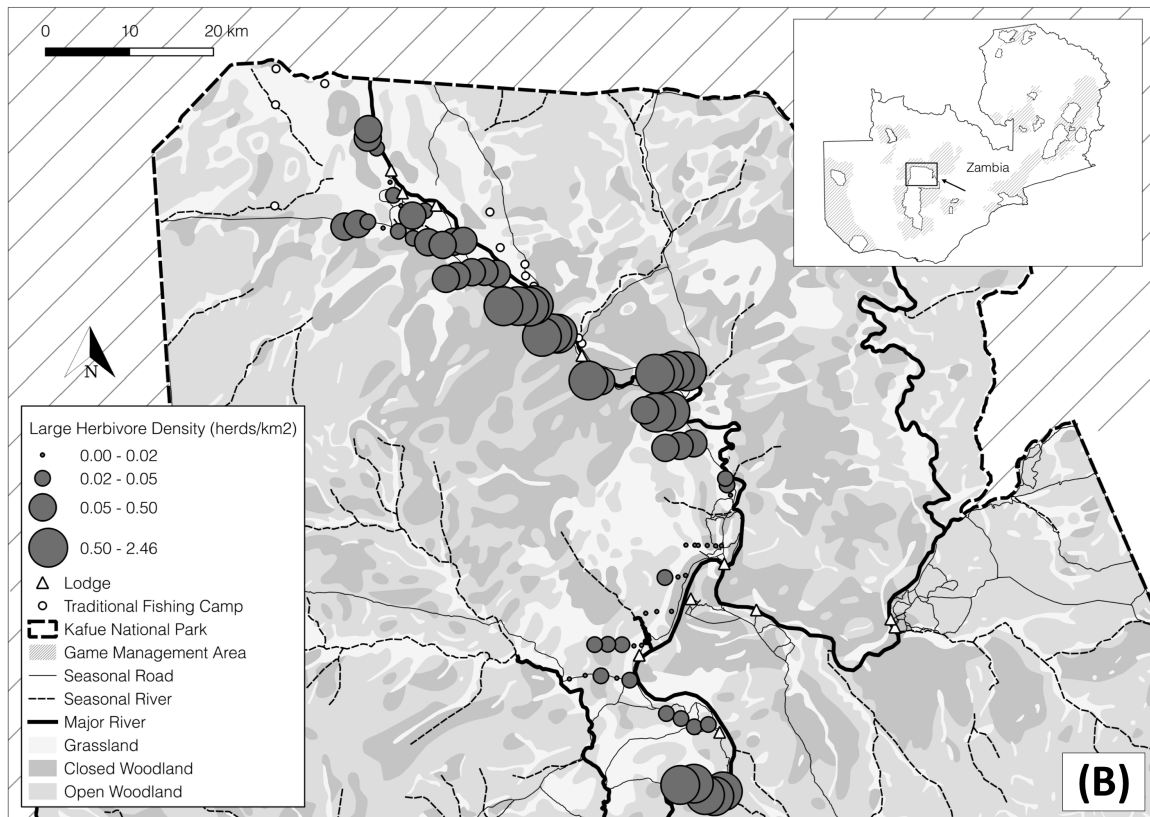


Figure 2.11: Predicted distribution of combined large-bodied (B) herbivore density (herds/km²) across each surveyed transect segment using ground-based distance sampling methods in northern Kafue National Park, Zambia. Estimates are based on the top herd density and herd size models.

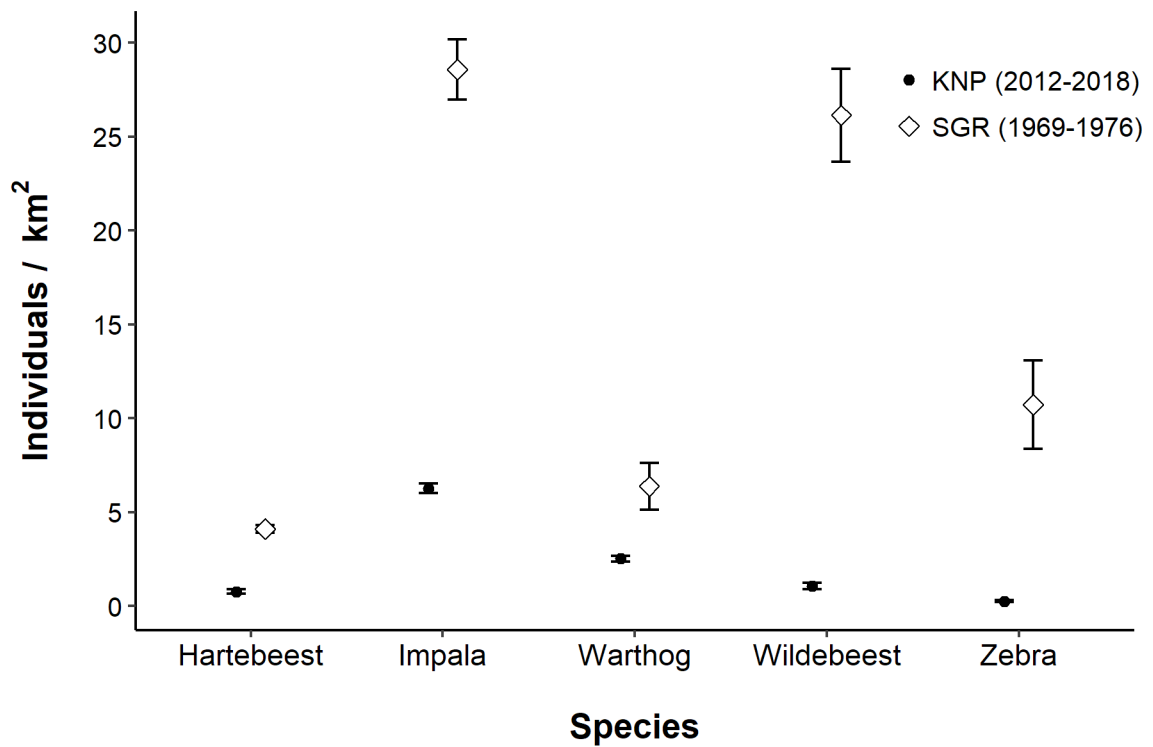


Figure 2.12: Comparison of herbivore densities between two ecologically similar miombo ecosystems. White diamonds depict mean densities in Selous Game Reserve (SGR) from 1969-1976. Black circles depict mean densities in Kafue National Park (KNP) from 2012-2018. Error bars depict 95% confidence intervals. Both sets of estimates were generated using ground-based distance sampling methods.

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CHAPTER THREE

RESPONSE OF LION DEMOGRAPHY AND DYNAMICS TO THE LOSS OF PREY AND CHANGES IN PREY COMMUNITY COMPOSITION

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Ecological Applications

Status of Manuscript:

- ☐ Prepared for submission to a peer-reviewed journal
☒ Officially submitted to a peer-review journal
☐ Accepted by a peer-reviewed journal
☐ Published in a peer-reviewed journal

Date submitted: 22 March, 2020

Abstract

Large carnivores are experiencing range contraction and population declines globally. Prey depletion due to illegal offtake is considered a major contributor, but the effects of prey depletion on large carnivore demography are rarely tested. We measured African lion density and tested the factors that affect survival using mark-recapture models fit to six years of data from known individuals in Kafue National Park (KNP), Zambia. KNP is affected by prey depletion, particularly for large herbivores that were preferred prey for KNP lions a half-century ago. This provides a unique opportunity to test whether variables that explain local prey density also affect lion survival. Average lion density within our study area was 3.43 individuals per 100 km² (95% CI: 2.79 – 4.23), which was much lower than the lion density reported for another miombo ecosystem with similar vegetation structure and rainfall that was less affected by prey depletion. Despite this, comparison to other lion populations showed that age- and sex-specific survival rates for KNP lions (settled individuals) were generally good, and factors known to correlate with local prey density had small effects on lion survival. In contrast, recruitment of cubs was poor. In particular, the proportion of the population comprised of 2nd year cubs was low, indicating that few cubs are recruited into the sub adult age class. Our findings suggest that low recruitment might be a better signal of low prey density than survival. Thus, describing a lion population's age structure may be a simple and effective method of initially evaluating whether a lion population is affected by prey depletion. These dynamics should be evaluated for other lion populations and other large carnivore species. Increased resource protection and reducing the underlying

drivers of prey depletion are urgent conservation needs for lions and other large carnivores as their conservation is increasingly threatened by range contraction and population declines.

Keywords: African lion, prey depletion, population density, survival, recruitment, anthropogenic, Kafue

Introduction

Large carnivores are experiencing substantial declines in numbers and geographic distribution (Estes et al. 2011). Of the 31 species within this group, 61% are considered threatened under the International Union for the Conservation of Nature (IUCN), and 77% are experiencing population declines (Ripple et al. 2014). Declines are driven mainly by anthropogenic pressures, particularly habitat loss and degradation, direct persecution, human utilization, and prey depletion (Ripple et al. 2014). Prey depletion is thought to be a particular problem for large carnivores in South America, Africa, and Asia, yet surprisingly little work has directly evaluated the effects of prey depletion on carnivore demography and population density in these systems.

African lions provide a good opportunity to evaluate the effects of prey depletion on large carnivore ecology because they are relatively easy to study, widely distributed, exhibit a strong positive association between population density and prey density, and have experienced high but variable rates of prey depletion across their range (Schaller 1972, Van Orsdol et al. 1985, Riggio et al. 2013, Bauer et al. 2015). African lions have lost more than ninety percent of their historical range, and few countries currently possess

strong evidence for stable populations (Riggio et al. 2013, 2016, Bauer et al. 2015), with impending consequences for the photo tourism and trophy hunting industries (Lindsey et al. 2012, Rogan et al. 2017), and for ecosystem function (Estes et al. 2011). Prey depletion is widely cited as a driver of lion population declines in southern Africa (Becker et al., 2013; Midlane et al., 2014; Rosenblatt et al., 2014), yet little work has directly quantified the effects of prey depletion on lion population demography.

Prey depletion is apparent in many ecosystems heavily affected by poaching (Bolger et al. 2008, Fa and Brown 2009, Western et al. 2009, Ripple et al. 2015). Rates of illegal harvest in west and central Africa is increasing due to human population growth, increased access to protected areas through developing road networks, increased hunting pressure, and the rise of more efficient hunting methods (Fa et al. 2005). The rise in illegal harvest and consequent prey depletion are likely to have strong negative effects on ecosystem structure and function (Estes et al. 2011, Ripple et al. 2014, 2015b, Creel et al. 2018). Until recently, the illegal trade of wild game and its effects received less attention in the savannas of eastern and southern Africa (Lindsey et al., 2013), but prey depletion is now widely suspected to be a driver of carnivore declines in eastern and southern African Protected Areas (PAs; Midlane et al., 2014; Rosenblatt et al., 2016; Creel et al., 2018).

Central Zambia's Greater Kafue Ecosystem (GKE), comprised of Kafue National Park (KNP) and surrounding Game Management Areas (GMAs), is a potential lion population stronghold, although prey depletion has already altered the diets of large carnivores, particularly lions, in this system (Midlane et al. 2014, Creel et al. 2018, Vinks et al. 2020). A long-term decline of large prey species in the GKE has led to niche

compression and increased dietary niche overlap between lions and other large carnivores, with implications for the ecology of the carnivore guild (Creel et al. 2018). The consequences of these changes for carnivore conservation cannot be evaluated without data on population dynamics and demography. Here, we used data from a six-year study of lions in KNP to provide rigorous estimates of population density, vital rates, and the factors that affect them.

Specifically, we fit mark-recapture models to data from intensive monitoring of known individual lions in KNP and parts of the surrounding GMAs between 2013 and 2018, providing precise estimates of population size and annual survival while accounting for imperfect detection. We have previously used extensive data from ground-based distance sampling (over the same period) to identify the drivers of large herbivore densities on this site (Vinks et al. 2020), presenting a unique opportunity to test whether the environmental and anthropogenic variables that predict prey density also predict lion survival. Similar data have been successfully used to guide conservation and management of lions in other systems (Loveridge et al. 2007, 2016, Packer et al. 2011, Rosenblatt et al. 2014, Mweetwa et al. 2018), and by comparing our estimates of density, survival, and age structure to similar data from other populations, we further evaluate the consequences of prey depletion (Overton et al. 2017, Creel et al. 2018).

Materials and Methods

Study area

The 2,364 km² study area was located in central and northern KNP on both the western and eastern sides of the Lufupa and Kafue rivers (Fig. 1). KNP lies in western Zambia (S14.5394 and E26.0782), and is the country's largest PA at 22,319 km². Together, KNP and the surrounding GMAs comprise the 66,000 km² GKE. This system is dominated by miombo woodland (*Brachystegia* and *Julbernardia spp.*), and includes a mosaic of savannah grassland, riverine woodland, mixed acacia woodland, termitaria woodland, and seasonally inundated grasslands. The region experiences a rainy season with extensive flooding from December through April and a dry season from May through November. Mean annual rainfall in northern KNP is 1,020 mm (Midlane 2013), which is comparable to other miombo woodland ecosystems (Creel and Creel 2002, Gillingham and Lee 2003). The GKE represents 13% (520, 000 km²) of the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA), which spans the borders of Angola, Botswana, Namibia, Zambia and Zimbabwe. KNP is impacted by prey depletion, and densities of larger-bodied herbivores are particularly depressed relative to smaller species (Vinks et al. 2020). Though the majority of our data was collected in KNP, some of our inferences likely also pertain to the entire GKE, most of which is facing more human pressure than our study site (Overton et al., 2017; Watson et al., 2014).

Data collection

We recorded all sightings ($n = 2,689$) from intensive monitoring of known lions ($n = 170$) in 16 prides and 16 male coalitions between 2013 and 2018. Male coalitions associated with multiple prides throughout the study, and for the purpose of analysis we considered them as independent groups. Individuals were uniquely identified by whisker-spot patterns, nose-pigmentation patterns, scarring, and tooth wear (Pennycuick and Rudnai 1970) using a digital photo-ID database. Individual ages were estimated using calibrated standards for nose-pigmentation pattern, tooth wear and coloration, and facial scarring (Pennycuick and Rudnai 1970, Whitman et al. 2004, Whitman and Packer 2006). We validated the accuracy of these standards with known-age individuals in this population and in a longer-running study of another Zambian population (Mweetwa et al. 2018). Radio-collars were deployed to assist with individual, pride, and coalition detection. At least one adult female lion was radio-collared in 9 of 16 monitored prides throughout the study (and the presence of collared lions within a group was included as a covariate in models of detection probability, see below). In addition, we radio-collared one adult male lion in a three male coalition between 2013 and 2017. Lions were collared with a combination of VHF, GPS store on board, and Iridium Satellite GPS collars (all Telonics Inc., Mesa, Arizona, USA). A licensed wildlife veterinarian deployed all collars in collaboration with the Department of National Parks and Wildlife (DNPW). Because lions live in stable social groups, regular sightings of non-collared pride members were obtained by tracking collared lions. Opportunistic sightings of un-collared prides and

male coalitions, and sightings with photographs from commercial guides, professional hunters, conservation partners, and tourists provided additional detections of known lions.

Measuring covariates of lion survival

To test whether prey density affects lion survival, we could have treated the predicted density of prey from distance sampling models (Vinks et al. 2020) as an independent variable in this analysis. While that approach is intuitively appealing and has precedent, it treats the output of a model as though it were empirical data. To avoid this problem, we tested whether the set of abiotic, bottom-up, and anthropogenic variables that were previously found to affect the local density of primary lion prey (Creel et al. 2018, Vinks et al. 2020) also affected lion survival. Because location-specific estimates of prey density from our distance sampling models are derived from these predictors (hereafter referred to as prey density covariates), our test is functionally equivalent to a test of the relationship between lion survival and the best available estimates of prey density (accounting for variation in detection of prey: Vinks et al. 2020). Some covariates of prey density were dropped from our analyses due to collinearity, with one member of each pair of predictors with Pearson correlation ≥ 0.6 discarded, yielding the following set of anthropogenic/abiotic predictors: (1) the distance from the center of a lion's core range to the nearest traditional fishing camp, and (2) the distance from the center of a lion's core range to the nearest perennial river. Bottom-up predictors were: (3) the percent cover of two dominant vegetation types (open woodland and closed woodland) within the lion's core range, and (4) the density of edges (km) between all three dominant

vegetation types (open woodland, closed woodland, open grassland) within the lion's core range, as a measure of habitat variability (Matandiko 2016). A summary of primary lion prey densities in KNP, species-specific variables driving density, and species-specific proportions of the KNP lion diet is compiled in Table 1 (Creel et al. 2018, Vinks et al. 2020).

We defined the core of a pride's range as the 50th percentile isopleth of a kernel utilization distribution (KUD) fit to all fixes for a pride. We used the *adehabitatHR* package in R (Calenge 2006) to calculate 50% KUDs for prides with available GPS data (7 prides). We calculated the centroid of each 50% KUD in QGIS to represent the geometric center of a lion's core range (www.qgis.org). For VHF-collared and uncollared prides/coalitions we determined the centroid of opportunistic locations in QGIS and used a fixed radius to identify an area centered on that point that was equal to the mean core range of GPS collared pride of females and one VHF collared coalition of males (www.qgis.org). With core ranges identified, we used the *sf* package in R (Pebesma 2018) to calculate the proportion of open woodland, closed woodland, and edge density (km) within each lion's core range, and the distance from the center of each lion's core range to the nearest traditional fishing camp and the nearest perennial river. Each lion was also categorized in each year as being associated with a pride with or without at least one radio collar (primarily to control for effects on the probability of detection). Finally, we categorized the general location (south, central, north) of a lion's core range within the study area to test for broad spatial variation in survival.

Modeling survival

We used 6 years (2013 – 2018) of detection records for 170 unique lions with 2,689 detections to fit Cormack-Jolly-Seber (CJS) models of age- and sex-specific annual survival rates (ϕ), detection probability (p), and to test what factors affect survival, after accounting for individual heterogeneity in detection (Pledger et al. 2010). As in a prior analysis for lions in Zambia (Rosenblatt et al. 2014), age was categorized into five biologically meaningful age classes: 1st year cub (0 – 0.99 years old), 2nd year cub (1 – 1.99 years old), sub-adult (2 – 3.99 years old), sexually mature young adult (4 – 5.99 years old), prime adult (6 – 7.99 years old), and old adult (≥ 8 years old). Detections were binned into three occasions per year (May through October), each of two months duration, so that the detection (1) or non-detection (0) of each individual in each two-month period yielded a potential 18-occasion encounter history for each individual over the 6-year study. The CJS model estimates survival conditional on being released after the first detection, accounting for staggered entry of individuals over the study. Because most of the GKE is seasonally inaccessible during the rainy season, we restricted analysis to 6 months per year when conditions allowed monitoring across the entire study site and yielded a probability of detection high enough for precise estimates of survival rates (see Results). We excluded individuals known to have died during the study from this analysis because they were not a substantial portion of the sample ($n = 6$) and including them would require a combination of recovery and recapture models that also estimate a site fidelity parameter for each age and sex class (Burnham 1993, Rosenblatt et al. 2014).

CJS analysis fits one sub-model for survival and one sub-model for detection, and allows an overlapping set of variables to affect each of these parameters. We used the

RMark package in R and program MARK (White and Burnam 1999) to identify the best-supported CJS model in two stages of model selection, following the process of Mweetwa et al. (2018) for very similar data from lions in South Luangwa Valley, Zambia. First, we identified the best model for detection (p) using a single model of survival with effects of age class and sex. At this stage, the candidate models tested for effects on p of age class, sex, sampling year, and presence/absence of a radio collar. We also considered a detection model with a discrete mixture of individuals with 2 detection categories (p -high or p -low) and a probability of falling into either category of π or $1-\pi$, respectively (Pledger et al. 2010). Because there was both spatial and temporal variation in our sampling effort, we tested for variation in detection among years, to avoid the possibility that higher detection rates during periods of better sampling effort would bias estimation of the mixing parameter (Pledger et al. 2010, Mweetwa et al. 2018). We identified the best model of detection by comparing Akaike's Information Criterion scores with correction for small sample size (AICc) for the models just described.

Having identified the best model of detection, we identified the best-supported model for survival (ϕ) by testing effects of all combinations of age class, sex, group size, location of a lion's core range, and prey density covariates (the effects of primary interest), fitting each survival model with the top detection covariates identified in the first stage of the analysis. We also considered the effect of pride identity on survival, but models with this effect did not converge (probably because small pride sizes provide relatively little replication within prides). As in the first stage, we used AICc scores to

identify the strength of support for each model. We compared models to an intercept-only model and used Fletcher's $c\text{-hat}$ to test for overdispersion (Fletcher 2012).

Estimating abundance and density

Following methods applied to similar data for another Zambian lion population (Mweetwa et al. 2018), we used closed mark-resight models to estimate lion abundance in each year, accounting for individual and temporal heterogeneity in detection (Huggins 1989). We fit a Huggins model with individual heterogeneity in detectability to estimate the probability of initial detection, subsequent detection, and population size using RMark and program MARK (Mweetwa et al. 2018). To mimic the parameterization of the detection process from the top CJS survival model, we constrained detection by assuming no difference between the likelihood of initial detection (p) and subsequent detection (c). This constraint kept abundance estimation consistent with the CJS framework, which conditions the likelihood on first capture, and is justified by repeated observations of the tolerant animals in our study (Mweetwa et al. 2018). Consistent with the survival analysis, we incorporated a mixing parameter (π) to account for individual heterogeneity in detection. This parameter was fixed at its model-averaged estimate from the top two CJS survival models to maintain consistency in model structure through time (Williams et al. 2002). We used the same detection covariates from the top CJS survival model to also model population size (Mweetwa et al. 2018), complementing the time varying effect of study year with occasion. Analyzing each year's data separately, we split detection records into the same three, two-month occasions per year as the survival detection records. The detection (1) or non-detection (0) of each individual was recorded

for each two-month period (May through October) resulting in a potential 3-occasion encounter history for each individual each year. We excluded detection histories for lions known to have died during the study but added these individuals to the population estimate for the year that they died.

We focused our inferences about population density on the data for 2018, because 2018 had the highest and most consistent sampling effort across the entire study area. This decision was intended to avoid making incorrect inferences about population trends if our models of detection were not equally good for all years. We converted the estimate of population size in 2018 to density by dividing the estimated population size (excluding cubs < 1 years old) by the area of the 80th percentile isopleth of a KUD (Worton 1989) fit to all GPS locations from adult female lions using the `adehabitatHR` package in R (Calenge 2006). GPS data was not available for all lions in this study, but the distribution of lion sightings confirms that this is a reasonable description of the area used by the sampled lion population, i.e., that it provides a reasonable trade-off between excluding areas with some use by the sampled lions and including areas used by lions not included in the sampled population (and the detection probability from our population model accounts for individuals resident but missed during the study). Finally, we compared our estimate of population density to estimates from other PAs across Africa with established lion populations.

Results

Lion population structure

We identified 170 individual lions from 16 prides and 16 male coalitions in our study area between 2013 and 2018. Six of these individuals were known to have died during the study, all from unknown causes, and were excluded from mark-resight analysis but included in population size estimates. Pride size ranged from 1 to 5 adult females with a mean of 2.89 (95% CI: 2.62 – 3.15), and male coalitions ranged from 1 to 3 sub-adult and adult males with a mean size of 1.95 (95% CI: 1.56 – 2.35). Second year cubs were the least common age class, comprising an average of 10% (95% CI: 0.04 – 0.16) of the population (Fig. 2). Combined, first- and second-year cubs never comprised more than 38% of the population, and on average these age classes comprised 28% (95% CI: 0.21 – 0.34) of the total population (Fig. 2-3). In contrast, cubs comprised 33.4% (95% CI: 27.3 - 39.4) of Zambia's Luangwa Valley lion population between 2008 and 2015, and 42.0 % (95% CI: 34.4 - 49.5) during a trophy-hunting moratorium between 2013 and 2015 when the Luangwa population was growing (Mweetwa et al. 2018). Cubs comprised 33.7% (95% CI: 31.0 - 36.4) of the total lion population in an ecologically similar miombo ecosystem, Tanzania's Selous Game Reserve (SGR; Brink et al. 2013).

The number of litters of 1st year cubs directly observed for 9 collared prides within the detection window (May – October) ranged from 2 to 5 between 2013 and 2018, with a mean of 3.33 (95% CI: 2.24 – 4.43). Litter sizes ranged from 1 to 8 cubs across years, but the average between 2013 and 2018 was 2.63 cubs/litter (95% CI: 1.69 – 3.58). The sex ratio (females: males) of adult lions (> 2 years old) ranged from a low of 1.20 in 2016 to a high of 1.83 in 2014, with a mean of 1.57 (95% CI: 1.36 – 1.78).

Survival rates and detection probabilities

Detection models that incorporated individual heterogeneity in detection (modeled as 2 classes of detection, p -high and p -low, with probability π and $1 - \pi$, respectively) performed better than any of the models without individual heterogeneity. The top detection model included the main effects of detection class, year, and the presence/absence of at least one radio collar within the pride (radio-collared prides were better monitored), plus an interaction between detection class and year, and an interaction between detection class and the presence/absence of at least one radio collar (Tables 2 and 3).

Only one model of survival fell within 2 AICc units of the top model (Table 2). Effects on survival of age class, sex, plus an interaction between age class and sex were included in both of these models (Table 2). Estimated survival was lower in males than in females for all age classes > 2 years old (Fig. 4). Estimated survival rates for sub-adult males (2 – 3.99 years old) and young adult males (4 – 5.99 years old) were the lowest rates for any sex x age-class combination: 0.42 (95% CI: 0.25 – 0.61) and 0.53 (95% CI: 0.24 – 0.80), respectively (Fig. 4). Survival for prime adults (6 – 7.99 years old) was the highest at 0.94 (95% CI: 0.66 – 0.99) for prime adult females and 0.90 (95% CI: 0.52 – 0.98) for prime adult males (Fig. 4). Survival of young adult females (4 – 5.99 years old) was comparable to the estimated rate for prime adult males at 0.90 (95% CI: 0.69 – 0.97; Fig. 4). For females, old adults had the lowest survival at 0.64 (95% CI: 0.41 – 0.82; Fig. 4).

The detectability of young cubs was low during the first 4 years of the study due to sampling limitations, likely leading to many cubs potentially dying without ever being

detected. Hence, our models would overestimate cub survival rates, which we consequently do not report.

The variables previously shown to predict the local density of lion prey (Vinks et al. 2020) had little ability to predict lion survival. The second-best model included an effect of distance to a perennial river, but the effects across age classes and sexes were small, with overlapping confidence intervals. None of the top candidate survival models incorporated an effect of the location or vegetation composition of a lion's core range.

Population density

The estimated population size (excluding cubs < 1 years old) in 2018 was 81 lions (95% CI: 66 – 100) over an area of 2,364 km² centered along the Kafue and Lufupa rivers (Fig. 1). This yields an estimated density of 3.43 lions per 100 km² (95% CI: 2.79 – 4.23 lions per 100 km²). Lion density estimates for 18 other protected areas across Western, Eastern, and Southern Africa are compiled in Table 4. Lion density in KNP is comparable to the low lion densities in arid systems with low prey densities. Estimated lion density in KNP is lower than what has been reported for most other savanna-woodland ecosystems, including miombo-dominated systems.

Discussion

The effect of prey depletion on the survival and reproduction of lions is still little-studied, even though prey depletion is thought to be a primary cause of continental lion population declines and continues to pose a serious threat to conservation of wildlife species across African savannas (Fa, Peres, & Meeuwig, 2002; Lindsey et al., 2013;

Ripple et al., 2014). Estimated lion density in KNP is 3.2-fold lower than has been reported for miombo woodland with higher prey density and less poaching pressure (Rodgers 1979, Creel and Creel 1997, Brink et al. 2013), providing empirical support for what has been suspected to be a problem (Midlane et al. 2014, Creel et al. 2018, Vinks et al. 2020). This estimate pertains to a productive portion of KNP with higher levels of activity by tourists and park personnel than other portions of the GKE (Vinks et al. 2020). Consequently, lion density is likely lower outside our core study area, which collectively is facing more human pressure (Watson et al. 2015, Overton et al. 2017). Nonetheless, given that densities of preferred lion prey in KNP are low (Vinks et al. 2020), and given the strong positive association between prey density and lion density (Schaller 1972, Van Orsdol et al. 1985, Packer et al. 2005), our results confirm that low prey abundance, specifically low densities of large to very-large bodied prey, is associated with relatively low lion density in this system (Bauer et al. 2008, Hayward and Kerley 2009).

Counter to our predictions, drivers of prey density were not strongly associated with survival, and low prey abundance did not lead to low lion survival (Blackburn et al. 2016). Overall, we infer that prey depletion decreases lion density by lowering carrying capacity without reducing survival. This result is consistent with findings from a comparison of leopards inside and outside of South Luangwa National Park (Rosenblatt et al. 2016) and suggests that survival rates may not be a sensitive tool to evaluate the effects of prey depletion on large carnivore populations. Female survival rates (> 2 years old) in KNP were comparable to rates reported for a high-density, stable population in Zambia's Luangwa Valley (Rosenblatt et al. 2014, Mweetwa et al. 2018), with the

exception of rates for females > 8 years old (which exhibited signs of senescence). Our estimates of survival rates for sub adult males and young adult males were appreciably lower than those that have been recorded in high density, stable lion populations (Rosenblatt et al. 2014), suggesting that survival for dispersal age males not associated with a settled pride could be reduced by prey depletion. However, high survival across female age classes (> 2 years old) and high survival for prime adult males show that survival for settled individuals was not reduced in this system (Fig. 4).

Mechanisms other than prey depletion might also cause low apparent survival in young males, including targeted poaching which has been recorded across the GKE (Overton et al. 2017) and is an emerging threat in southern Africa (Everatt et al. 2019). Although legal trophy hunting was not a known source of lion mortality during this study, effects of trophy hunting on lion survival are well demonstrated (Loveridge et al., 2007, 2016; Packer et al., 2010; Rosenblatt et al., 2014; Mweetwa et al., 2018), and male depletion in the GMAs due to either legal or illegal harvest could be causing a vacuum effect (Loveridge et al. 2007). Because the CJS model framework cannot distinguish between permanent emigration and mortality, this vacuum effect could partially explain lower observed survival for younger males (2 – 5.99 years old) and older males (> 8 years old), if there is net emigration by these age classes from our core study area into vacant territories in adjacent GMAs or within the park. We were not able to directly test for effects of proximity to the park boundary on adult male survival because male movement patterns were not well described (because we monitored males by collaring the females with whom they associated). Wire snaring, which is prevalent in the GKE

(Overton et al. 2018), is a well known source of mortality for sub-adult and adult male lions (Becker et al., 2013a; Becker et al., 2013b). Eighty percent of snared lions observed in our study (immobilized for snare-removal and successfully treated for injuries; $n = 5$) were young males. Undetected snaring by-catch could have significant impacts on lion dynamics throughout the GKE, and would further explain lower observed survival for younger and older males. Younger and older males, without established territories, would be expected to range wider (Elliot et al. 2014), and thus presumably encounter more snares (Becker et al., 2013a).

As was first described 36 years ago, resource limitation plays an important role in infant mortality in lions through abandonment and starvation (Packer and Pusey 1984, 1995). Although our data do not allow direct estimates of 1st and 2nd year cub survival, the proportion of cubs within this population was low in comparison to data from two lion population strongholds (Brink et al. 2013, Mweetwa et al. 2018). This comparison is particularly cogent for lions in KNP and the Selous Game Reserve, which is very similar in vegetation structure and rainfall, which predict prey density well in the absence of strong anthropogenic effects (East 1984). Notably, second year cubs were the smallest age class in the KNP population, indicating that few cubs are recruited into the sub adult age class, and we consider it very unlikely that individuals in monitored prides could go undetected in their second year.

Our results suggest that poor recruitment is a ‘demographic signature’ of prey depletion in this system, and is supported by previous findings linking poor cub survival to low prey availability (Bertram 1973, Eloff 1980, Van Orsdol et al. 1985, Van Vuuren

et al. 2005). The low density of preferred large-bodied prey in Kafue (Vinks et al. 2020, Creel et al., 2018) could decrease foraging success, increase the costs of hunting, and increase within-group feeding competition, all of which would be expected to reduce the likelihood of producing and raising cubs (VanderWaal et al. 2009). Low lion density is expected to reduce intergroup competition (and the observed pride sizes match those optimal for recruitment (VanderWaal et al. 2009, Mosser et al. 2015)), but our results nonetheless suggest that poor recruitment is associated with low prey density. In a long-lived, iteroparous species, life history theory predicts that limited resources should affect reproduction before survival (Gaillard et al. 1998), and this expectation is supported by the high survival rate we observed for adult females.

Low recruitment could also be due in part to infanticide following turnover in male coalitions (Bertram 1975, Packer and Pusey 1984, 1995). However, survival for prime adult males was relatively high, which reduces the likelihood of turnover and weakens this explanation, which remains a plausible explanation for low recruitment in other ecosystems (Rosenblatt et al., 2014).

Regardless of the mechanism that links low prey density to poor recruitment, our results suggest that low recruitment is a better signal of low prey density than survival in this system. Thus, describing a lion population's age structure may provide a simple and useful method to initially evaluate whether a lion population is likely to be suffering the effects of prey depletion. Given the very difficult, ongoing problem of developing monitoring methods that are accurate, sensitive, and applicable over large areas, this method warrants investigation in other lion populations.

Female prides and male coalitions were both small, averaging <3 adult females and <2 adult males. A decrease in group size has previously been identified as a probable consequence of prey depletion (Creel et al., 2018). Our results confirm an association between low prey density and small groups (Bauer et al. 2008), which may provide another indirect tool to assess whether prey depletion is a concern. Home range configuration can also be affected by prey abundance and a decreases in lion density could be due to larger home ranges (Macdonald 1989, Valeix et al. 2012): a detailed understanding of the mechanisms that link prey depletion to recruitment is beyond the scope of our data, but warrants further investigation.

The effects of prey depletion are likely occurring in many ecosystems experiencing high rates of illegal harvest, with serious implications for conservation of large carnivores (Wolf and Ripple 2016). The current status of lions in the GKE could affect the ecotourism and trophy hunting industries (Lindsey et al. 2007, 2012, Rogan et al. 2017), highlighting the economic impacts of prey depletion, in addition to a myriad of ecological impacts (Ripple et al. 2015). Addressing the consequences of prey depletion by evaluating direct effects on population demography, increasing resource protection, and addressing underlying drivers of illegal offtake are urgent conservation needs for lions and other large carnivores now experiencing rapid decline across their ranges.

Acknowledgements

Our thanks to the Zambia Department of National Parks and Wildlife for permission to conduct this research, and for collaborative efforts to help monitor, manage

and conserve these herbivore and carnivore populations. Funding: this research was supported by the National Science Foundation (IOS1145749); National Geographic Society Big Cats Initiative; Gemfields Inc., World Wildlife Fund– Netherlands & Zambia; The Bennink Foundation, Wilderness Wildlife Trust, Panthera, Ntengu Safaris, Elephant Charge, and IUCN Save Our Species/European Union.

Table 3.1: Primary lion prey densities in KNP, species-specific variables driving density, and species-specific proportions of the KNP lion diet.

	Species	Density (individuals/km ²)	Density Covariates	Proportion of Lion Diet
			Dist to Bound, Dist to FC, %CW, Dist to Riv,	
	Puku	11.54 (10.27 - 12.82)	Edge D	0.15
	Impala	6.25 (5.99 - 6.51)	Dist to Bound, Dist to FC, Dist to Rd, %OW	0.04
Small-			Dist to Bound, Dist to FC, Dist to Rd, Dist to	
bodied	Warthog	2.51 (2.36 - 2.67)	Riv, %OW	0.15
	Reedbuck	0.40 (0.33 - 0.46)	Dist to Bound, Dist to FC, Dist to Rd, Edge D	0.00
	Common Duiker	0.36 (0.33 - 0.39)	Dist to FC, Dist to Rd, Dist to Riv	0.00
	Wildebeest	1.06 (0.90 - 1.22)	Dist to Bound + poly(Dist to FC)	0.03
	Hartebeest	0.76 (0.64 - 0.88)	Dist to FC, Dist Rd, %CW	0.01
Large-	Roan	0.37 (0.31 - 0.42)	Dist to Bound, Dist to FC, Dist to Rd	0.03
bodied			Dist to Bound, Dist to FC, Dist to Lodge, %OW,	
	Zebra	0.25 (0.21 - 0.30)	%CW	0.02
	Waterbuck	0.24 (0.22 - 0.27)	Dist to Bound, Dist to FC, Dist to Rd	0.03
Source:		Vinks et al. 2020	Vinks et al. 2020	Creel et al. 2018

Notes: Dist to Bound = Distance to park boundary; Dist to FC = Distance to nearest traditional fishing camp; Dist to Riv = Distance to nearest perennial river; Dist to Rd = Distance to nearest road; Edge D = Density of edges between dominant vegetation types; Dist to Lodge = distance to nearest safari lodge; Yr = Study year of survey; Sea = Season of survey; Veg = Dominant vegetation types.

Table 3.2: The three best-supported Cormack Jolly Seber models of survival, as determined by AICc scores.

Model	k	ΔAICc	weight
$\phi(\sim\text{Age class} * \text{Sex}), p(\sim\text{detection class} * \text{study year} + \text{detection class} * \text{radio collar}), \pi(.)$	25	0	0.194
$\phi(\sim\text{Age class} * \text{Sex} + \text{River}), p(\sim\text{detection class} * \text{study year} + \text{detection class} * \text{radio collar}), \pi(.)$	26	1.663	0.084
$\phi(\sim\text{Age class} * \text{Sex} + \text{CW}), p(\sim\text{detection class} * \text{study year} + \text{detection class} * \text{radio collar}), \pi(.)$	26	2.088	0.068

Table 3.3: Coefficient estimates from the best-supported Cormack–Jolly–Seber model, which included effects of age, sex, plus an interaction between age and sex on apparent survival (ϕ), and effects of detection class, year, and the presence/absence of at least one radio collar within the pride, plus an interaction between detection class and year, and an interaction between detection class and the presence/absence of at least one radio collar on detection (p).

β	Effect of	Parameter affected	Estimate	SE	95% LCL	95% UCL
1	Intercept	π	-0.785	0.320	-1.412	-0.158
2	Intercept	ϕ	0.450	0.450	-0.431	1.332
3	Sub adult	ϕ	1.299	0.734	-0.139	2.737
4	Young adult	ϕ	1.705	0.835	0.069	3.341
5	Prime adult	ϕ	2.382	1.188	0.054	4.710
6	Old adult	ϕ	0.122	0.651	-1.154	1.398
7	Sex male	ϕ	1.013	0.657	-0.276	2.302
8	Sub adult * Sex male	ϕ	-3.083	0.981	-5.005	-1.161
9	Young adult * Sex male	ϕ	-3.046	1.160	-5.319	-0.773
10	Prime adult * Sex male	ϕ	-1.686	1.665	-4.950	1.579
11	Old adult * Sex male	ϕ	-1.053	0.971	-2.957	0.851
12	Intercept	p	2.538	1.278	0.033	5.043
13	Mixture (2)	p	-2.456	1.832	-6.048	1.136
14	Study Year [2014, 2015]	p	-1.682	1.287	-4.204	0.840
15	Study Year [2015, 2016]	p	-3.065	1.381	-5.771	-0.359
16	Study Year [2016, 2017]	p	-3.652	1.341	-6.281	-1.022
17	Study Year [2017, 2018]	p	-1.486	1.237	-3.910	0.938
18	Study Year [2018, 2019]	p	0.175	1.351	-2.473	2.824
19	Collar Present	p	-1.138	0.672	-2.455	0.178
20	Mixture (2) * study year [2014, 2015]	p	-0.920	1.832	-4.510	2.671
21	Mixture (2) * study year [2015, 2016]	p	2.994	1.925	-0.779	6.766
22	Mixture (2) * study year [2016, 2017]	p	1.327	1.833	-2.267	4.920
23	Mixture (2) * study year [2017, 2018]	p	-0.229	1.767	-3.692	3.234
24	Mixture (2) * study year [2018, 2019]	p	-2.058	1.884	-5.750	1.634
25	Mixture (2) * collar present	p	4.340	0.842	2.689	5.991

Table 3.4: Comparison of lion densities across 18 African Protected Areas. Densities are listed from lowest to highest, along with the year of each estimate, the survey method, and its source.

PA	Protected Area Designation	Lion Density (individuals / 100 km ²)	Year	Survey Method	Source
Kalahari					
Gemsbok	National Park	1.46	1977	Lincoln Index	Mills et al. 1978
Gonarezhou	National Park	1.46	2010	Calling-Stations	Groom et al. 2014
Etosha	National Park	1.8	1989	Known Individuals	Stander 1991
Bénoué Complex	National Park	1.81	2007, 2008 & 2010	Track Index Surveys	Croes et al. 2011
Kafue	National Park	3.43	2018	Mark-Recapture Known	This study
Zakouma	National Park	3.9	2006	Individuals/Calling- Stations	Vanherle 2005
Hwange	National Park	4.3	2012	Mark-Recapture	Loveridge et al. 2016
Moremi	Game Reserve	5.8	2010	Calling-Stations	Cozzi et al. 2013
Tarangire	National Park	6.43	2010	Known Individuals	Packer et al. 2011
Serengetti	National Park	7.54	2010	Known Individuals	Packer et al. 2011
Kruger	National Park	9.55	2006	Calling-Stations	Ferreira and Funston 2010
South Luangwa	National Park	10.4	2012	Mark-Recapture Known	Rosenblatt et al. 2014
Selous	Game Reserve	11	1995 & 2009	Individuals/Calling- Stations	Creel and Creel 1997, Brink et al. 2012
Ngorongoro Crater	Conservation Area	11.26	2010	Known Individuals	Packer et al. 2011
Masai Mara	Game Reserve	11.87	2013	Known Individuals	Blackburn et al. 2016
Olkiramatian and Shompole	Game Ranches	13.6	2010	Known Individuals	Schuette et al. 2013

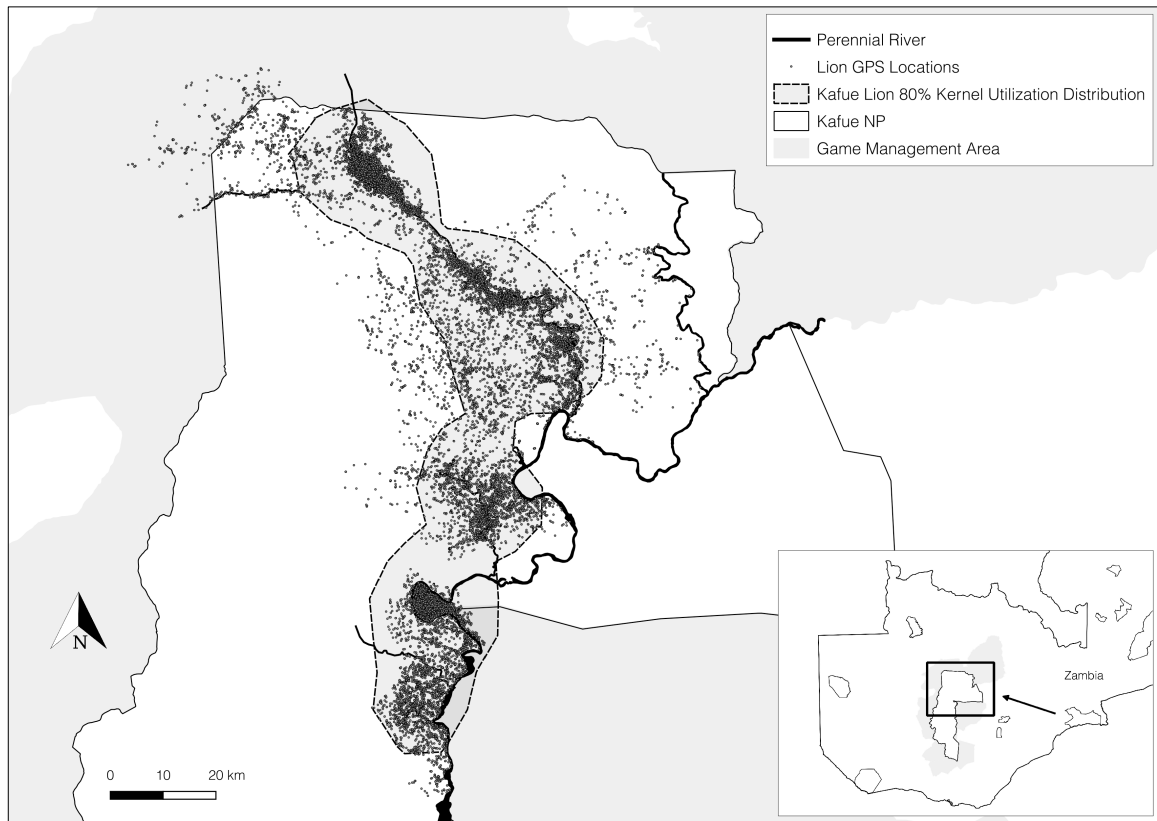


Figure 3.1: Our intensive study area in Kafue National Park, Zambia (S14.5394 E26.0782). An 80th percentile isopleth of a kernel utilization distribution identifies the core study area (2,364 km²). This area was further used as the denominator to estimate the density for the KNP lion population.

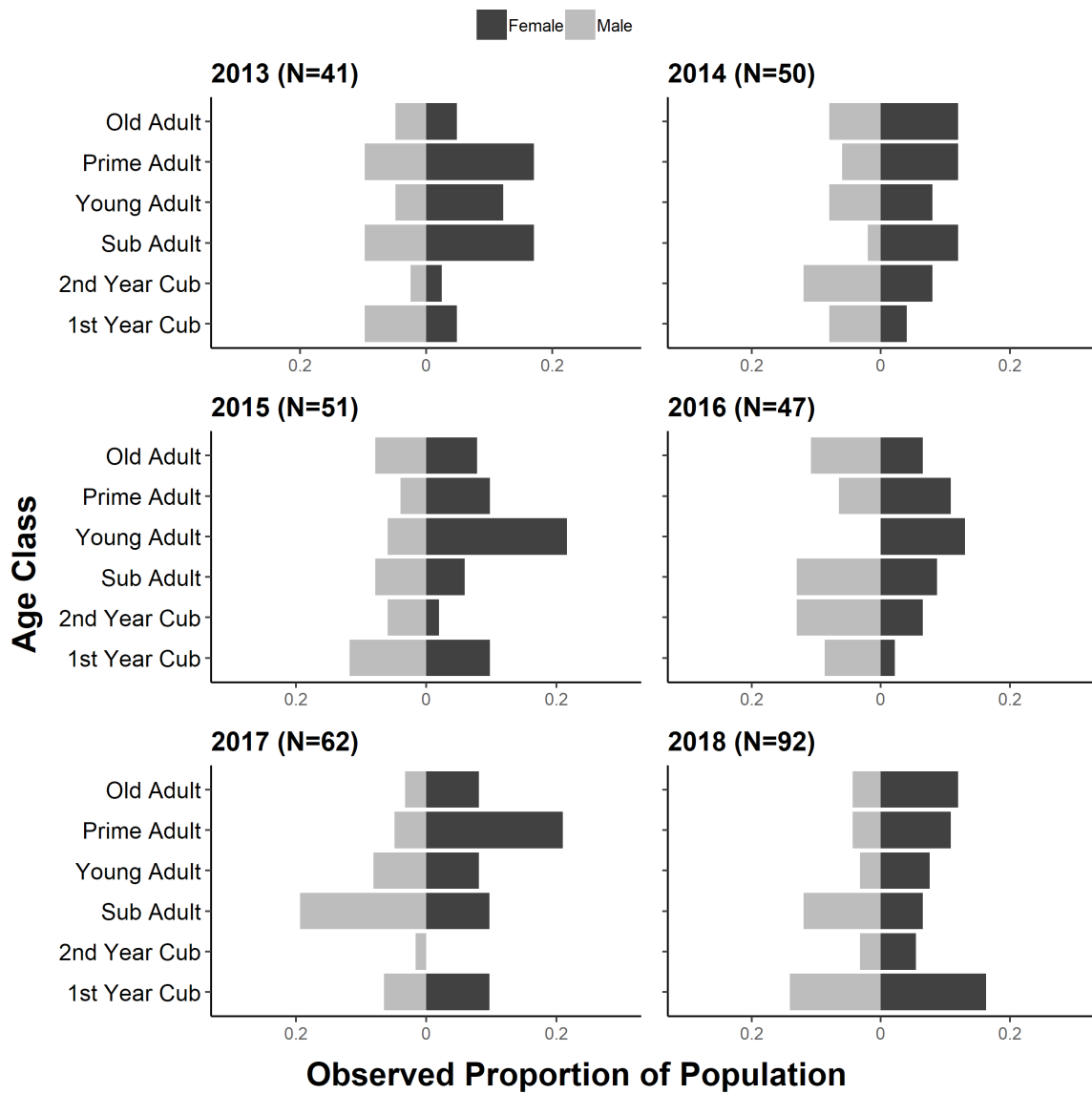


Figure 3.2: Population pyramids depicting observed age and sex distribution for the sample lion population within the detection window (May – November) between 2013 and 2018. This figure highlights low recruitment (except for 2018) and indicates that the majority of females are in the adult age class across years, with the likely propensity to move toward a senescing female population with limited recruitment.

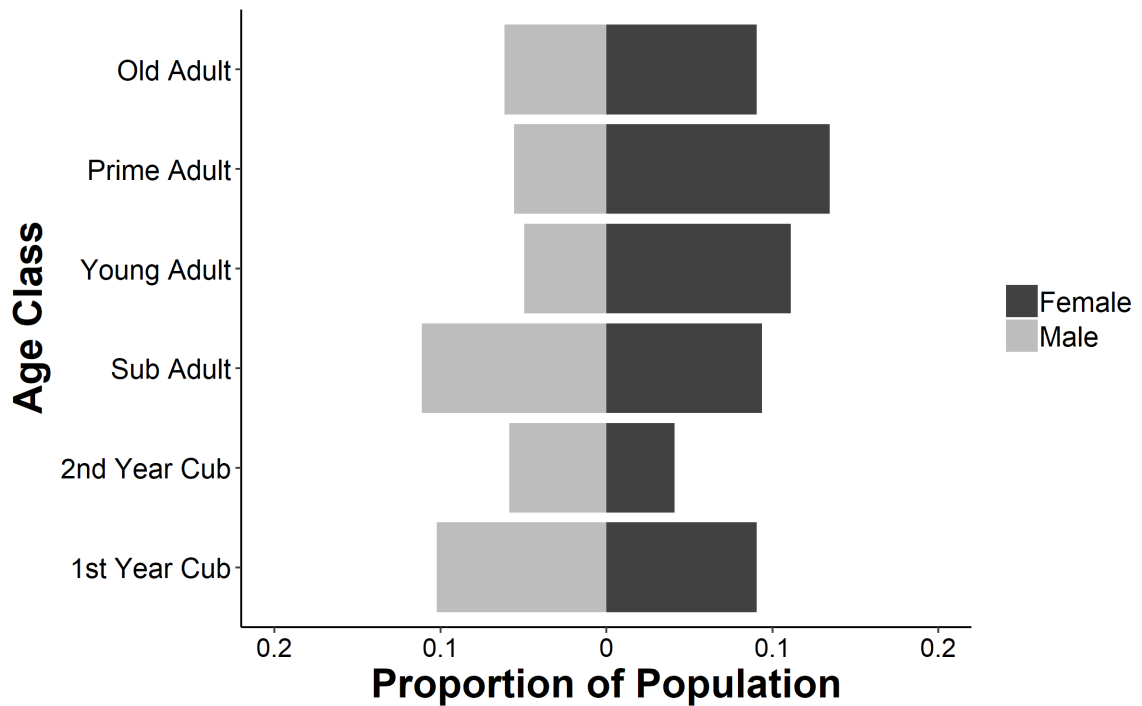


Figure 3.3: Population pyramid depicting combined age and sex distribution across all years of the study (2013-2018) for the sample lion population. This figure highlights a low proportion of second year cubs and indicates that the majority of females are in the adult age classes, with the likely propensity to move toward a senescing female population with limited recruitment.

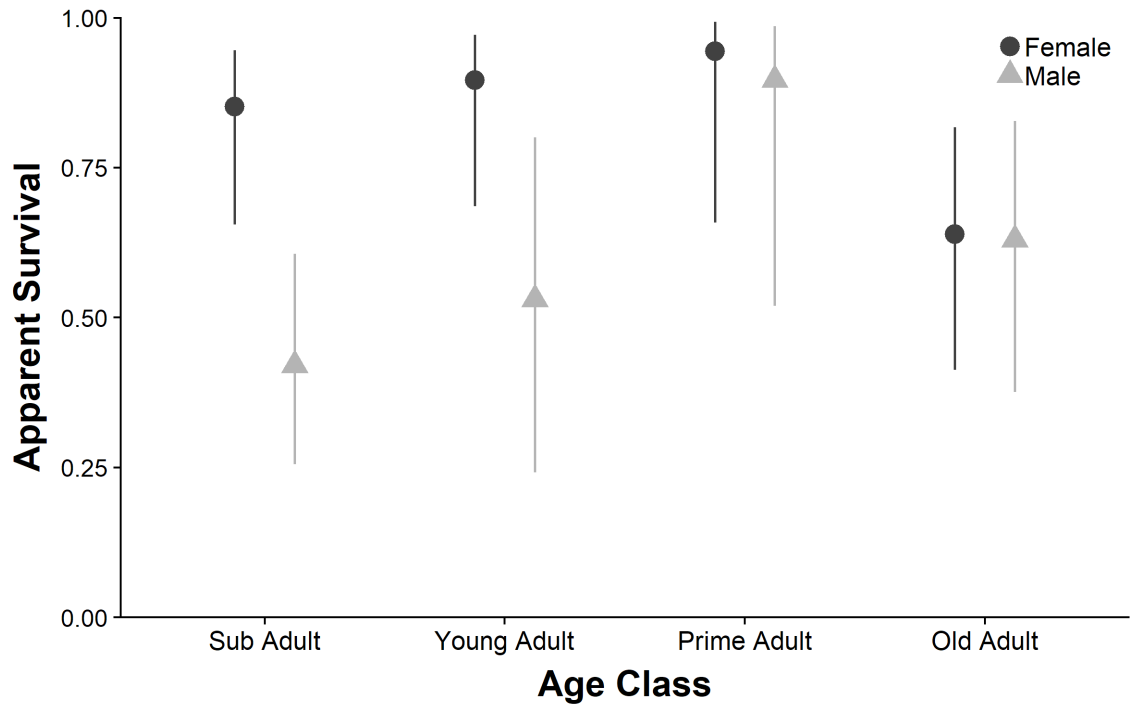


Figure 3.4: Annual apparent survival rates (ϕ) for the KNP lion population, estimated by the single best-supported Cormack-Jolly-Seber model. Error bars indicate 95% confidence intervals.

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CHAPTER FOUR

CONCLUSION TO THESIS

Overall Conclusions

Rapid human population growth across Africa has put tremendous pressure on large herbivore and large carnivore populations, and the success of protected areas (PAs) to which these populations are predominantly limited are hampered by encroachment and illegal offtake (Ripple et al. 2014, 2015, Watson et al. 2014). Insight on large herbivore and large carnivore population dynamics from an ecosystem heavily impacted by human pressure is thus valuable for conservation of these species. This research presents the first rigorous long-term demographic study of the Greater Kafue Ecosystem (GKE) lion population, and builds on long-term efforts to estimate the density and distribution of the GKE large herbivore guild. Here, we provided rigorous estimates of density and distribution of the main apex carnivore and most abundant large herbivore species in this system, using sampling designs and analytic methods that increased precision and reduced bias relative to other studies of large carnivores and their prey. This work will contribute directly to the management and conservation of these critical populations.

In Chapter Two, I presented seven years of ground-based survey data used to measure density and distribution of the ten most abundant large herbivore species in the GKE. These data suggest that population densities of the most abundant large herbivores in the GKE are lower than has been reported historically in miombo woodland ecosystems with less poaching pressure (Rodgers 1979). Low densities were consistent

across species and areas, though there was ecologically important variation among species and size classes. Most notably, larger-bodied herbivores were greatly depressed relative to smaller species. These patterns could have direct and indirect effects on large carnivore populations, with broad implications for the ecotourism and trophy hunting industries. These findings further provide the first empirical support to the suggestion that the GKE is affected by prey depletion.

More broadly, we found that distance sampling with stratified ground-based monitoring is an efficient and effective method to quantify trends in herbivore populations and evaluate the effectiveness of conservation actions. Statistically and methodologically rigorous methods to test the effects of anthropogenic and environmental variables on density and distribution exist, but are rarely applied to large herbivores. Due to the ubiquitous low densities of large herbivores in this system, I suggested that continued increases in resource protection are needed across the GKE to facilitate the recovery of an economically and ecologically important large herbivore guild. Moreover, these findings confirm that anthropogenic effects on large herbivore distribution and abundance can be strong over wide areas for all species (especially the larger members of the guild), even in very large PAs.

In Chapter Three, I presented data from an intensive six-year study of the GKE lion population. These data indicated that age- and sex-specific survival rates for adult females and adult males were generally good, and factors known to correlate with local prey density had small effects on lion survival. In contrast, survival for young males was relatively lower, indicating prey depletion could play a significant role in dispersal

success. Average lion density within our study area was much lower than lion density reported for another miombo ecosystem with similar vegetation structure and rainfall that was less affected by prey depletion (Creel and Creel 1997, Brink et al. 2013). In addition, the proportion of the population comprised of 2nd year cubs was low, indicating that few cubs are recruited into the sub adult age class. We suggested that low lion density, poor survival for young males, and poor cub recruitment is likely linked to prey depletion.

Overall, these findings suggest that low recruitment is a better signal of low prey density than survival. Thus, describing a lion population's age structure may be a simple and effective method of initially evaluating whether a lion population is affected by prey depletion. These dynamics should be evaluated for other lion populations and other large carnivore species in areas with depleted prey populations. Finally, increased resource protection and reducing the underlying drivers of prey depletion are urgent conservation needs for lions and other large carnivores as their conservation is increasingly threatened by range contraction and population declines.

In conclusion, as large herbivore and large carnivore populations continue to face negative human pressures worldwide, unbiased and precise estimates of population density, population trend, and demography will be crucial to detect population declines, identify their causes, and guide conservation and management action. Here, we presented inferences based on a long-term, intensive monitoring program. We acknowledge that such projects are not always feasible for all conservation problems, and suggest that more rapid surveys will be a crucial tool with time. However, if such surveys become more widely implemented we stress that they should maintain statistical and methodological

integrity, while adhering to the IUCN survey criteria (Dröge et al. 2020).

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APPENDIX A

SUPPORTING INFORMATION FOR CHAPTER TWO

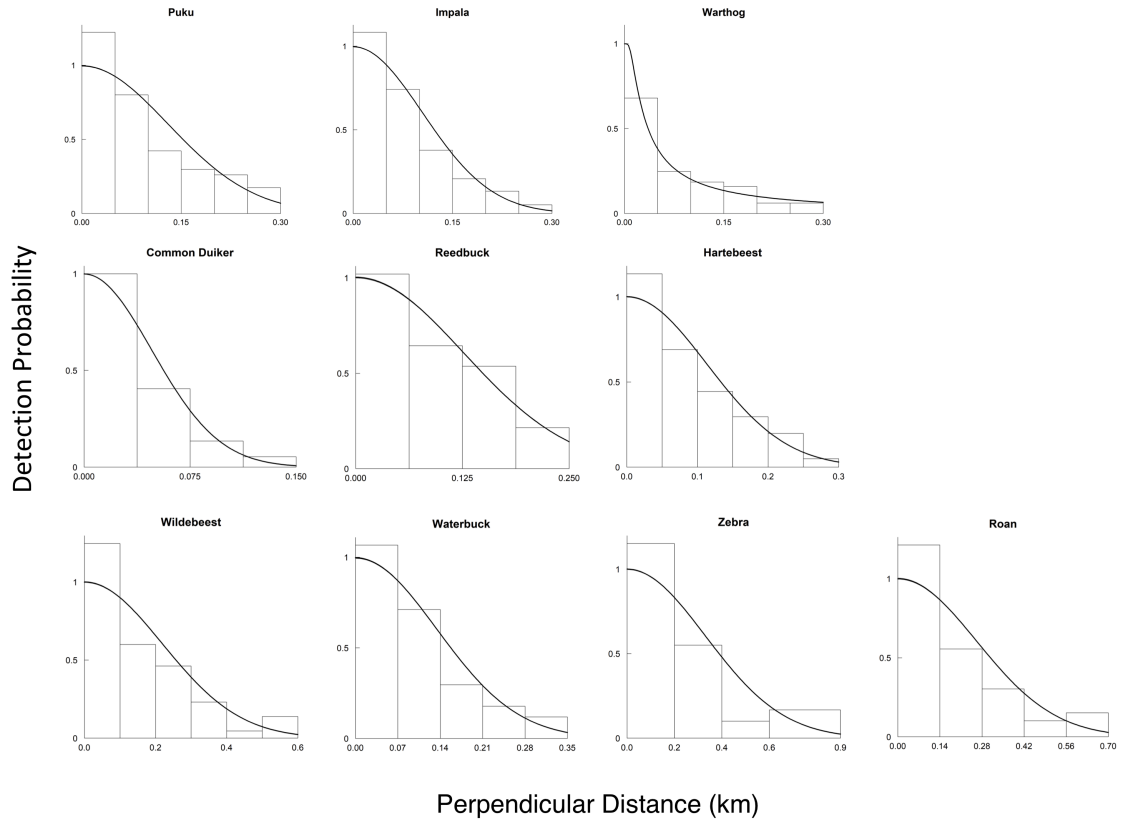


Figure A1: Relationship between fitted detection functions and the observed histogram of herds detected in a set of distance bins for each species' top herd density model.

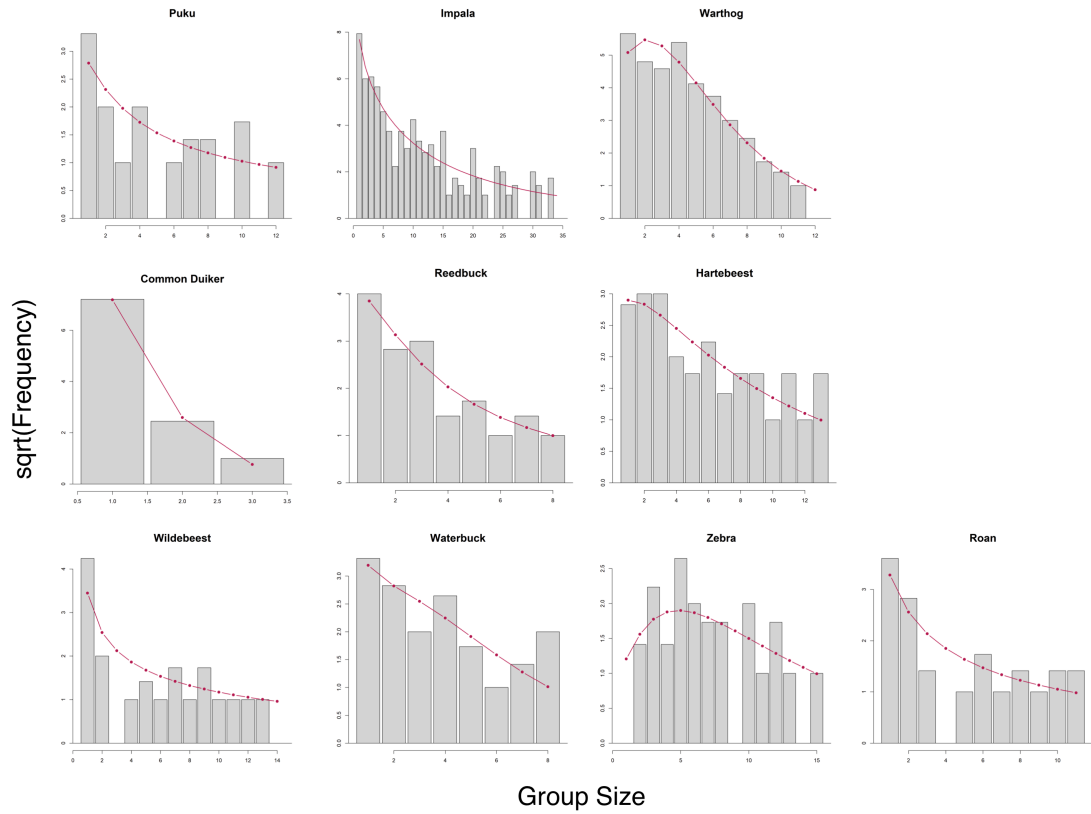


Figure A2: Standing rootograms for each species' top ZTNB/ZTP group size model, depicting observed (grey bars) and expected (red line) group size(s).