



# Testing the effects of anthropogenic pressures on a diverse African herbivore community

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**Abstract.** Large herbivore communities around the world have declined steeply in recent decades. Although excessive bushmeat harvesting 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.

**Key words:** anthropogenic; bushmeat; distance sampling; Kafue; large herbivore; poaching; prey depletion; protected areas.

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## 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 PAs (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 bushmeat consumption (Bra-shares 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 bushmeat trade and its effects received little attention in the savannas of eastern and southern Africa (Lindsey et al. 2013), though prey depletion due to bushmeat poaching 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, bushmeat poaching 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 effects on 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 fifth largest PA in Africa. The park encompasses 22,319 km<sup>2</sup> dominated by miombo woodland (*Brachystegia* and *Julbernardia* sp.) and includes a mixture of savanna grassland, riverine woodland, mixed acacia woodland, termitaria woodland, and seasonally inundated grasslands. The surrounding GMAs encompass another 44,000 km<sup>2</sup>, so that the GKE exceeds 66,000 km<sup>2</sup>. 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 1020 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/km<sup>2</sup>), herd size (individuals/herd), and individual density (individuals/km<sup>2</sup>) for 10 herbivore species across northern KNP. We surveyed eighteen approximately linear transects, ranging in length from 2 to 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 d 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 the observation level as required by our analysis, described below.

Transects were sampled on 15 occasions between 2012 and 2018. Surveys were conducted during daylight hours (09:00–17:00) 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 (December–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](http://www.qgis.org), Pebesma 2018) with data layers from the Zambia Department of National Parks and Wildlife (DNPW).

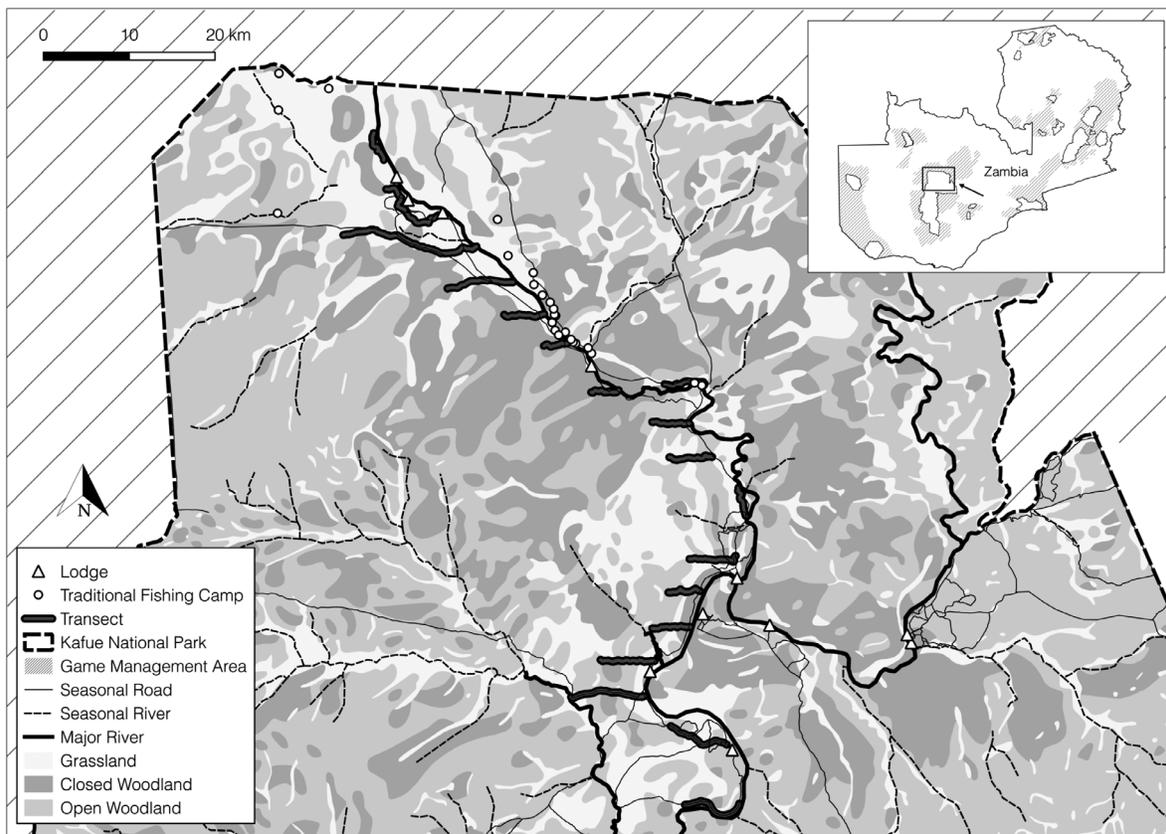


Fig. 1. Our intensive study area in northern Kafue National Park, Zambia. Our 18 transects were stratified across bottom-up, abiotic, and anthropogenic covariates. Each transect was comprised of multiple segments ( $n = 77$ ; not shown), for which we, respectively, predicted herd density and herd size for ten herbivore species.

### 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 semipermanent 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](http://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 < 10 cm, intermediate 10–100 cm, and tall >100 cm). 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](http://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](http://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  $\geq 0.6$  discarded.

#### *Herd density estimation*

We used a multinomial generalized distance sampling model to estimate superpopulation size ( $\lambda$ ) for each of the 10 species within each segment across all transects, while accounting for variation in availability for detection ( $\phi$ ) 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 the 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 ( $\phi$ ) by testing effects of all combinations of year and season. (3) We then used the models of detection ( $p$ ) and availability ( $\phi$ ) identified in steps 1 and 2, and used AIC scores to identify the best-supported combination of variables within each of the three classes of effects on the superpopulation ( $\lambda$ ) of herds: bottom-up, abiotic, and anthropogenic. Continuous variables were allowed to appear as linear, logarithmic, or second-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 superpopulation ( $\lambda$ ) of herds identified in step 3. This multistage 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 (Fig. S1; Schuette et al. 2016, Rosenblatt et al. 2019).

We used our final best-supported model to estimate herd superpopulation size ( $\lambda$ ) and availability ( $\phi$ ) 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 (Fig. S3; 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

Table 1. Model selection results for distance sampling models estimating herd density for the 10 herbivore species of interest.

Model $\lambda$	Model $\varphi$	Model $P$	$k$	$\Delta AIC$	AIC weight
<b>Puku</b>					
~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
<b>Impala</b>					
~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
<b>Warthog</b>					
~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
<b>Common Duiker</b>					
~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
<b>Reedbuck</b>					
~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
<b>Hartebeest</b>					
~poly(Dist to FC) + log(Dist to Rd) + %CW	~Yr + Sea	~1	15	0	0.46
~poly(Dist to FC) + log(Dist to Rd) + %CW + Edge D	~Yr + Sea	~1	16	1.83	0.18
~poly(Dist to FC) + log(Dist to Rd) + %CW + Dist to Riv	~Yr + Sea	~1	16	1.98	0.17
<b>Wilbebeest</b>					
~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
<b>Roan</b>					
~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
<b>Zebra</b>					
~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
<b>Waterbuck</b>					
~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:* AIC, Akaike's information criteria; Dist to Bound, distance to park boundary; Dist to FC, distance to nearest traditional fishing camp; Dist to Lodge, distance to nearest safari lodge; Dist to Rd, distance to nearest road; Dist to Riv, distance to nearest permanent river; Edge D, density of edges between dominant vegetation types; Sea, season of survey; Veg, dominant vegetation types; Yr, study year of survey. 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 second-order polynomial (poly) association with the parameter.

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  $< 0.15$ , we used observed herd size on

Table 2. Coefficient estimates and standard errors (in parentheses) from each species' top herd density model.

Covariate	Puku	Impala	Warthog	Duiker	Reedbuck	Hartebeest	Wildebeest	Roan	Zebra	Waterbuck
$\lambda$										
Intercept	1.52 (0.31)*	2.93 (0.46)*	2.17 (0.43)*	0.44 (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 <sup>2</sup>	...	...	...	...	...	...	...	...	3.37 (2.26)	...
% CW	-0.01 (0.003)*	...	...	...	...	0.01 (0.004)*	...	...	-2.35 (4.45)	...
% CW <sup>2</sup>	...	...	...	...	...	...	...	...	-6.27 (2.30)*	...
% OG	...	...	...	...	...	...	...	...	...	...
% OG <sup>2</sup>	...	...	...	...	...	...	...	...	...	...
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 (1.02)*	...	-6.76 (1.17)*	-5.50 (1.68)*	5.53 (3.04)	-5.73 (1.53)*	3.54 (2.88)	-1.34 (2.18)	20.85 (10.28)*	-0.97 (2.10)
Distance to fishing camp <sup>2</sup>	10.53 (1.33)*	...	4.45 (1.27)*	14.52 (2.83)*	23.93 (4.64)*	14.51 (2.58)*	23.43 (4.27)*	19.30 (2.96)*	42.33 (12.55)*	15.67 (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 <sup>2</sup>	0.88 (0.73)	...	1.76 (0.83)*	2.78 (1.33)*	...	...	...	...	...	...
$\phi$										
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 (0.38)	...	...	...	2.03 (1.04)	...	...	...	...
SeasonLate	0.60 (0.14)*	0.31 (0.17)	0.47 (0.22)*	...	0.66 (0.35)	-0.45 (0.31)	...	...	...	...
SeasonMid	0.33 (0.20)	0.37 (0.27)	0.7 (0.31)*	...	0.41 (0.50)	0.86 (0.51)	...	...	...	...
Estimate	...	...	...	-2.40 (0.53)*	...	...	-2.21 (0.52)*	-4.63 (0.54)	-3.77 (0.34)	-4.67 (3.19)
$P$										
Intercept	-1.77 (0.10)*	...	...	...	...	...	...	...	...	...
Flooded grassland	-0.39 (0.12)*	...	...	...	...	...	...	...	...	...
Open bushland	-0.41 (0.16)*	...	...	...	...	...	...	...	...	...

(Table 2. Continued.)

Covariate	Puku	Impala	Warthog	Duiker	Reedbuck	Hartebeest	Wildebeest	Roan	Zebra	Waterbuck
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)	...	...	...	...	...	...	...

Notes: 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 (+). Ellipses indicate that those covariates were not incorporated in the species' top herd density model.

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 stepwise 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 (Fig. S2; 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, and reedbuck) and five large-bodied herbivores (Lichtenstein's hartebeest, blue wildebeest, roan antelope, zebra, and 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 ( $\lambda$ ), phi ( $\phi$ ), and detection probability ( $p$ ) varied across species (Tables 1, 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, 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/km<sup>2</sup> (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/km<sup>2</sup> (95% CI 5.99–6.51) and 2.51 animals/km<sup>2</sup> (95% CI 2.36–2.67), respectively (Table 4). Hartebeest, reedbuck, common duiker, roan, waterbuck, and zebra were all found at densities  $< 1$  animal/km<sup>2</sup> (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.

Table 3. Coefficient estimates and standard errors (in parentheses) from final ZTNB and ZTP group size models.

Covariate	Puku	Impala	Warthog	Duiker	Reedbuck	Hartebeest	Wildebeest	Roan	Zebra	Waterbuck
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)*	...	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 (0.39)*	0.31 (0.29)	0.69 (0.32)*	+	-	+	-	+	1.41 (0.33)*	-
Burn:Present	+	-	+	+	+	+	-	+	+	+

Notes: ZTNB, zero-truncated negative binomial; ZTP, zero-truncated Poisson. 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 (\*).

Table 4. Estimates and range across segments of herd density and individual density.

Species	Herd density ( $n/\text{km}^2$ )			Individual density ( $n/\text{km}^2$ )		
	Mean	95% CI	Range across segments	Mean	95% CI	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

Notes: Mean herd density estimates are mean values for 1155 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 1155 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.

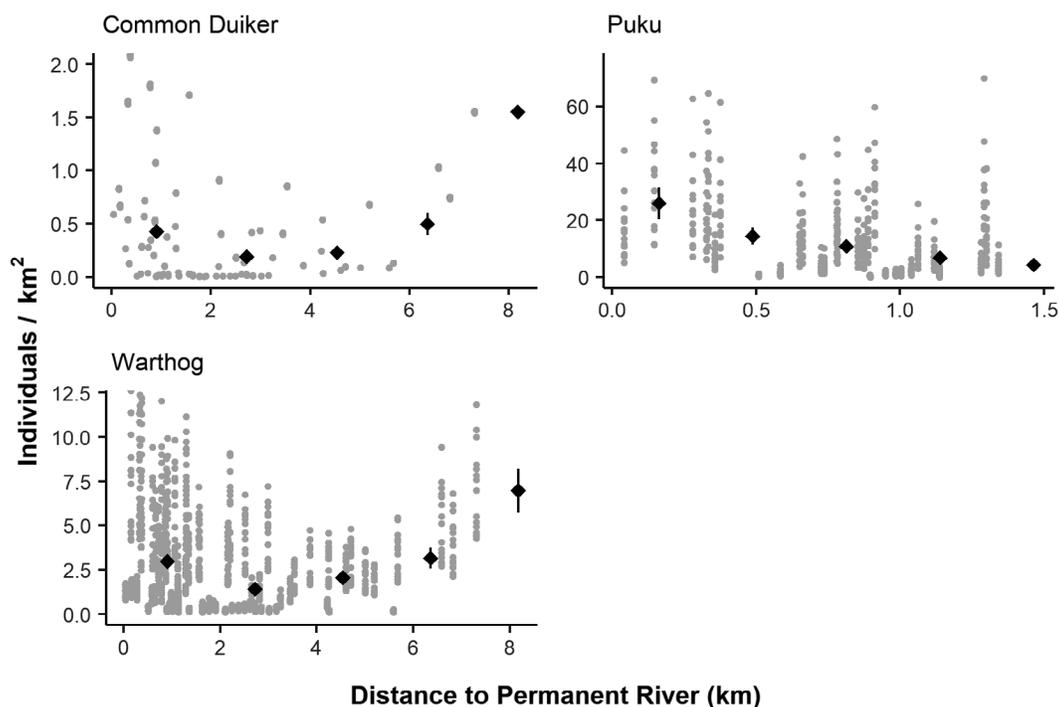


Fig. 2. Effect of distance to permanent rivers on population densities for three herbivore species in Kafue National Park. Gray points are segment-specific density estimates across the seven-year study. Black diamonds depict mean density estimates across binned distances, along with 95% CIs. Y-axes were truncated to clearly display variation in the effect across species.

#### 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

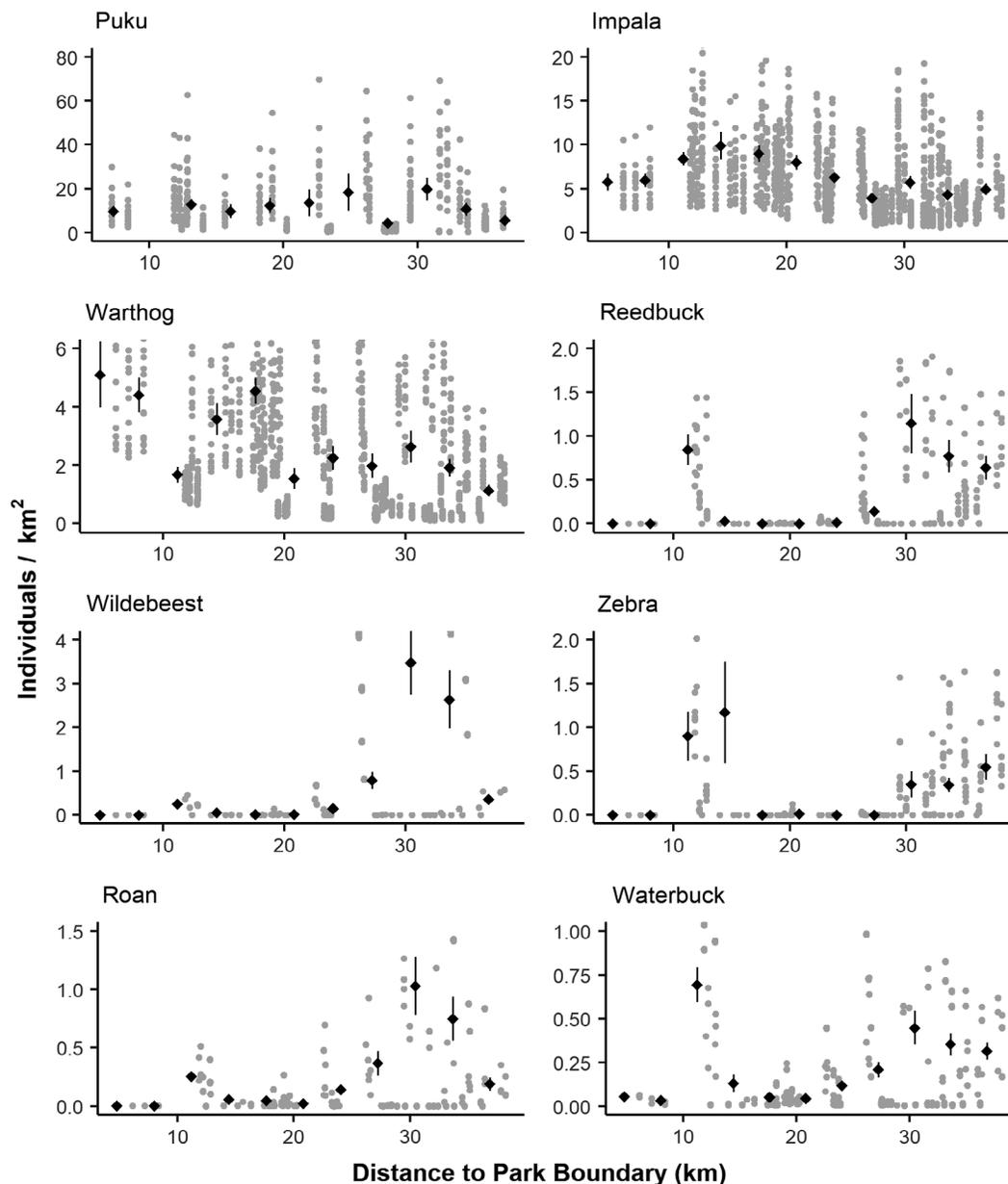


Fig. 3. Effect of distance to park boundary on population densities for eight herbivore species in Kafue National Park. Gray points are segment-specific density estimates across the seven-year study. Black diamonds depict average density estimates across binned distances, along with 95% CIs. Y-axes were truncated to clearly display variation in the effect across species.

(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

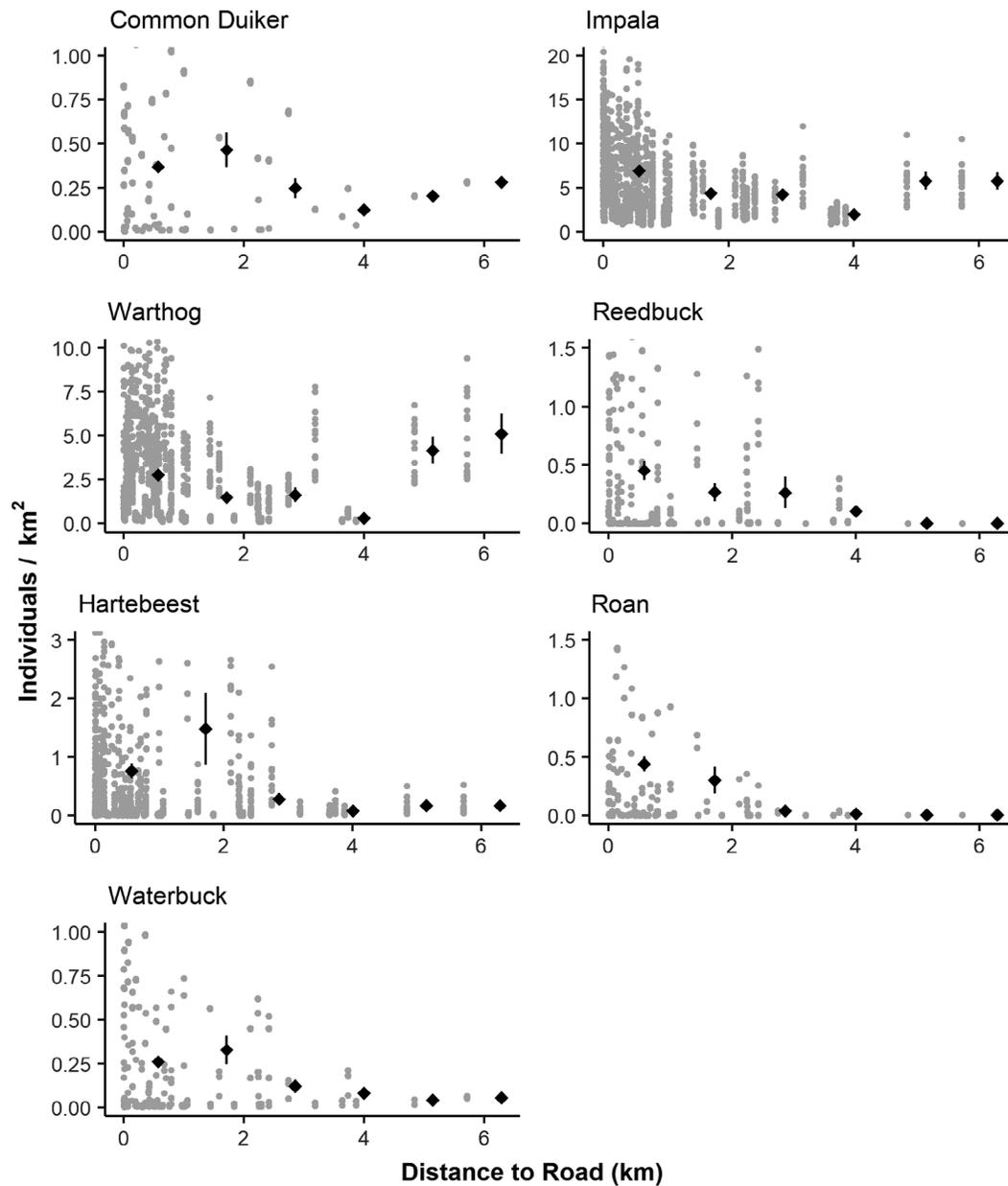


Fig. 4. Effect of distance to road on population densities for seven herbivore species in Kafue National Park. Gray points are segment-specific density estimates across the seven-year study. Black diamonds depict average density estimates across binned distances, along with 95% CIs. Y-axes were truncated to clearly display variation in the effect across species.

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

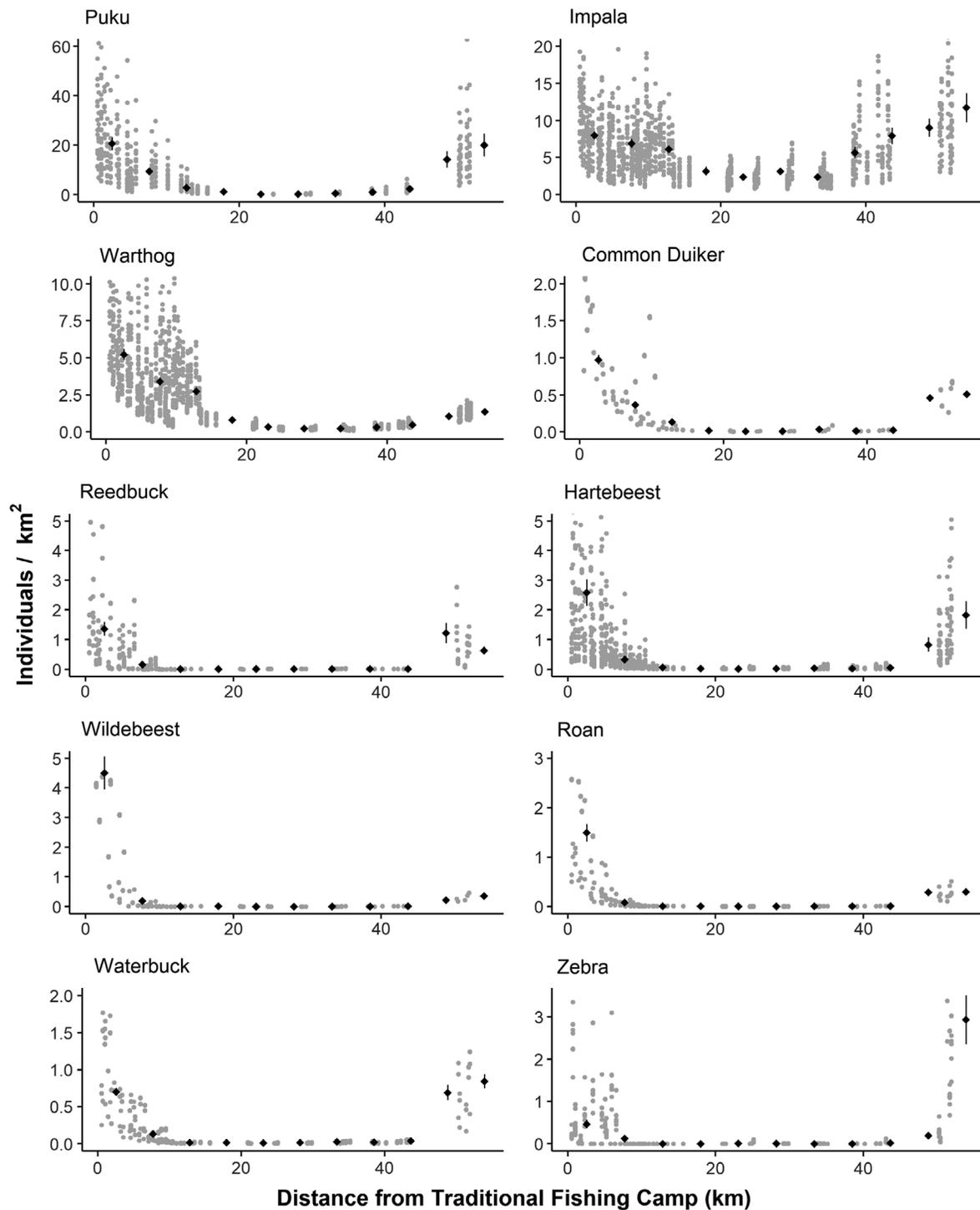


Fig. 5. Effect of distance to traditional fishing camp on population densities for all ten herbivore species in Kafue National Park. Gray points are segment-specific density estimates across the seven-year study. Black diamonds depict average density estimates across binned distances, along with 95% CIs. Y-axes were truncated to clearly display variation in the effect across species.

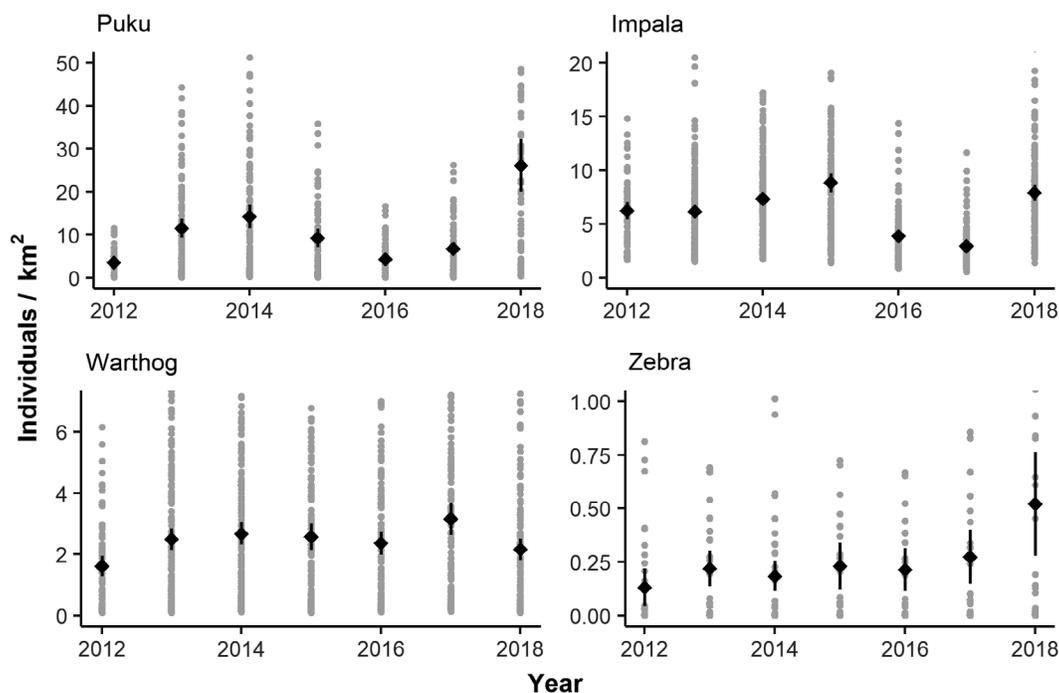


Fig. 6. Temporal effects on population density for four herbivore species in Kafue National Park. Gray points are segment-specific density estimates across the seven-year study, overlaid with average annual densities (black diamonds) and 95% CIs. Y-axes were truncated to clearly display variation between annual averages.

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, and 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 vs. smaller prey distribution because herd density has been suggested as a measure of hunting opportunities for large carnivores (Fryxell et al. 2007,

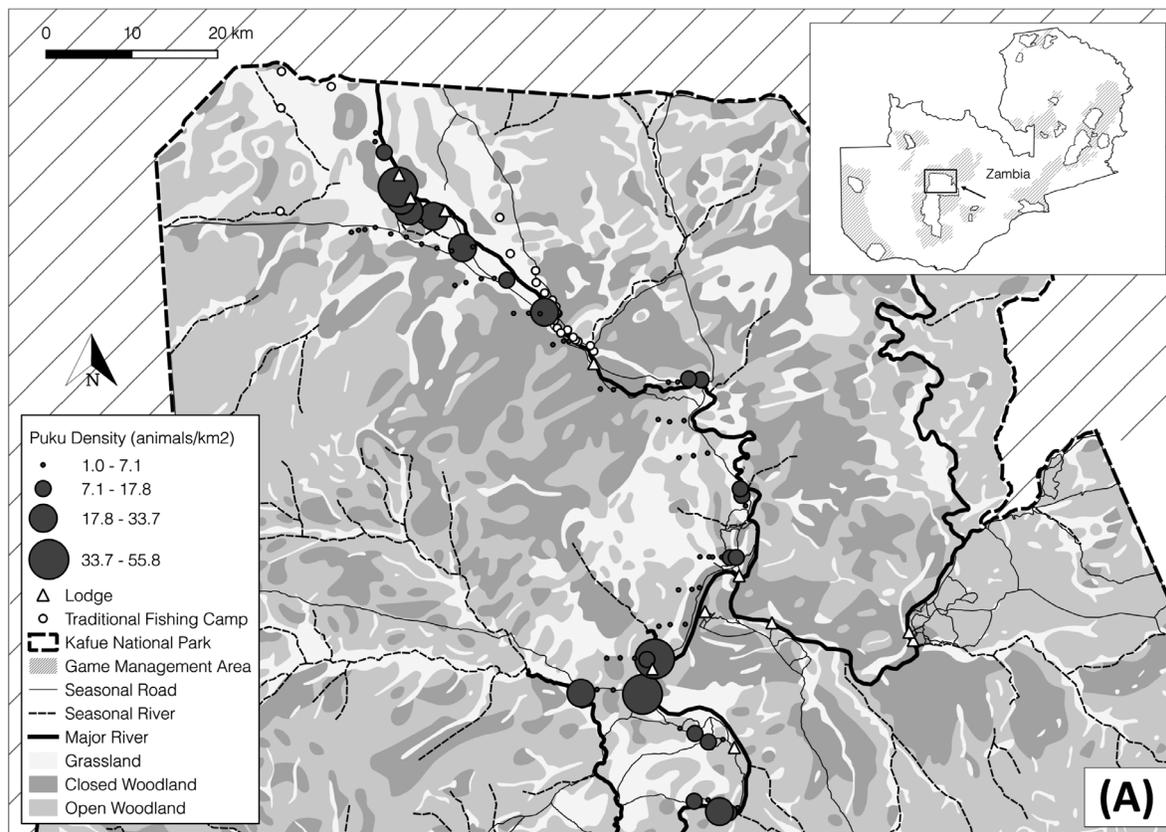


Fig. 7. Predicted distribution of population density (animals/km<sup>2</sup>) for puku (A), impala (B), and warthog (C) across each surveyed transect segment using ground-based distance sampling methods in northern Kafue National Park, Zambia. Estimates are based on the top herd density and herd size models.

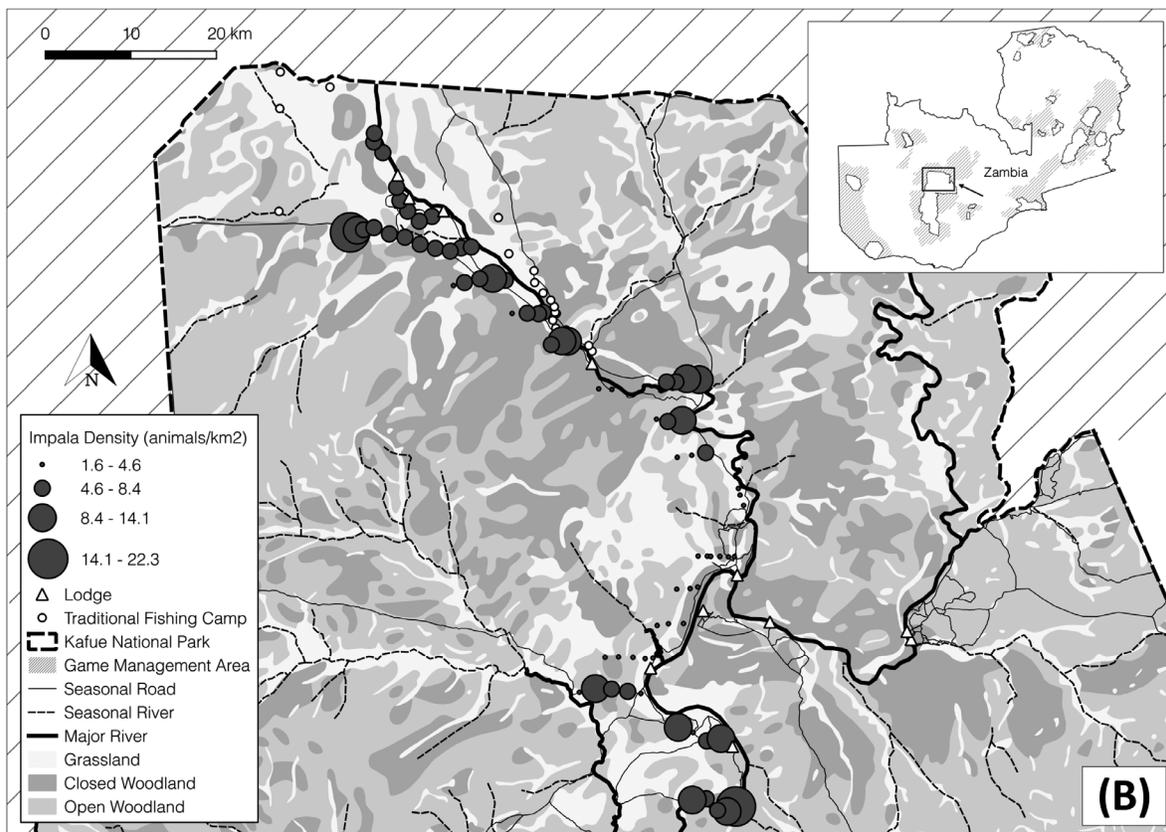
Mosser et al. 2009). These figures reveal relatively high densities in the north-central portion of the study area, with important variation between the concentrations of different size classes (Figs. 7, 8); in particular, puku densities were highest in proximity to major rivers (Fig. 7A).

## 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 yr), 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, Tanzania, where anti-poaching efforts were strong in the early 1960s (Rodgers 1979). Like Kafue, the Selous is a miombo-dominated ecosystem that is similar in vegetation type and rainfall,

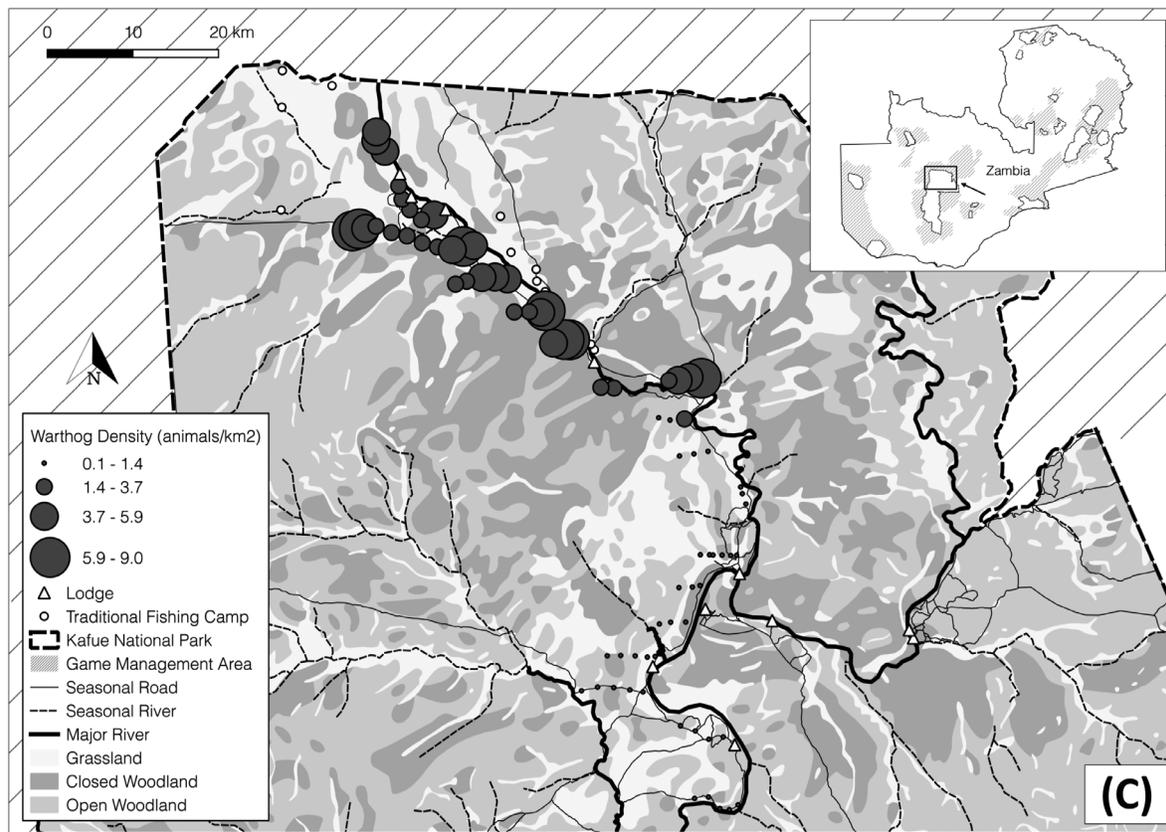
(Fig. 7. *Continued*)

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, 8). Importantly, we observed considerable variation between the densities of larger-bodied vs. smaller-bodied 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 with 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



(Fig. 7. Continued)

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. 2013, 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 bushmeat poaching 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 bushmeat poaching is consistent throughout the GKE (Overton et al. 2017). Bushmeat poaching 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

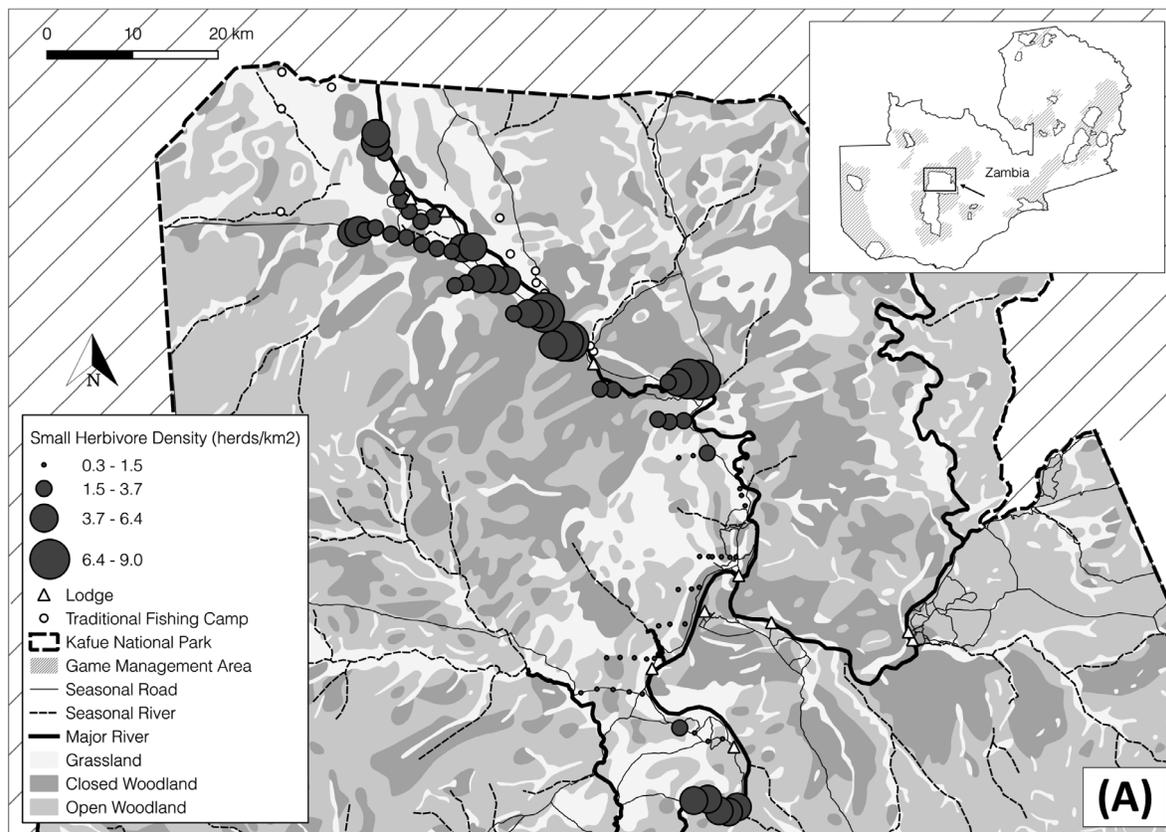


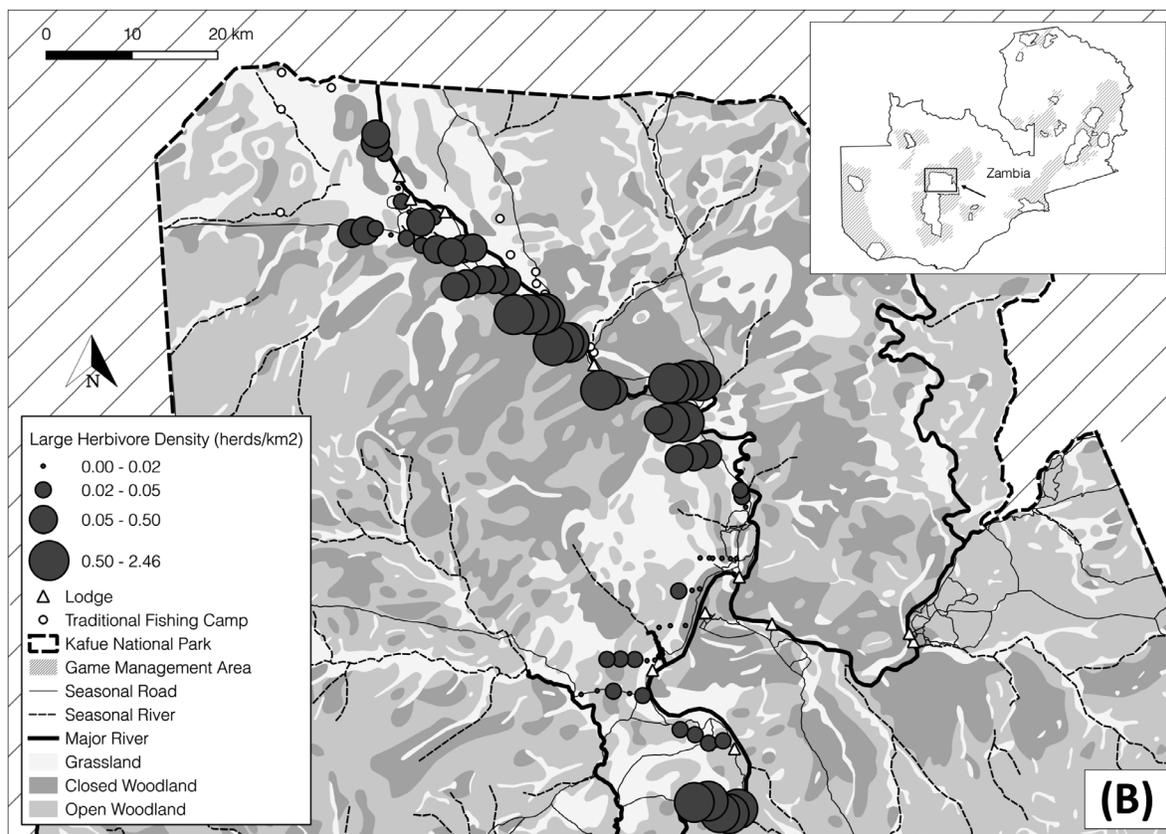
Fig. 8. Predicted distribution of combined small-bodied (A) and large-bodied (B) herbivore density (herds/km<sup>2</sup>) across each surveyed transect segment using ground-based distance sampling methods in northern Kafue National Park, Zambia. Estimates are based on the top herd density and herd size models.

fishing camps simply reflect the fact that these camps are predominantly located within the Busanga floodplain, 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 data*). Given the increase in fishing pressure beyond current regulations, increased resources for enforcement are recommended to protect both important wildlife areas and 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

(Fig. 8. *Continued*)

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 bushmeat 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, 2015, Rosenblatt et al. 2016). In KNP, a comparison of carnivore diets now and 50 yr ago showed that the

importance of relatively abundant smaller-bodied herbivores has increased, whereas the importance of larger-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 bushmeat poaching (Midlane 2013, Overton et al. 2017,

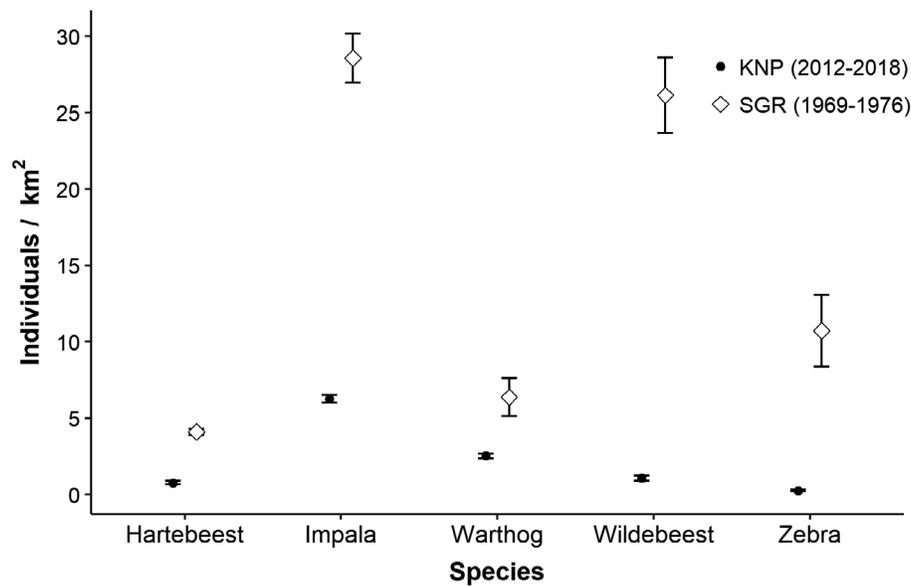


Fig. 9. Comparison of herbivore densities between two ecologically similar miombo ecosystems. White diamonds depict mean densities in Selous Game Reserve (SGR) from 1969 to 1976. Black circles depict mean densities in Kafue National Park (KNP) from 2012 to 2018. Error bars depict 95% confidence intervals. Both sets of estimates were generated using ground-based distance sampling methods.

Creel et al. 2018). The effect of bushmeat 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 bushmeat poaching and evaluate their effectiveness, we emphasize that stratified ground-based monitoring continues 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.

#### ACKNOWLEDGMENTS

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