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Low apex carnivore density does not release a subordinate competitor when driven by prey depletion

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ABSTRACT

Conservation of competitively subordinate carnivores presents a difficult challenge because they are limited by dominant competitors. Prey depletion is one of the leading causes of large carnivore decline worldwide, but little is known about the net effect of prey depletion on subordinate carnivores when their dominant competitors are also reduced. African wild dogs are often limited by high densities of dominant competitors, particularly lions. We measured African wild dog density and survival, using mark-recapture models fit to 8 years of data from 425 known individuals in the Greater Kafue Ecosystem, Zambia. The GKE is affected by prey depletion, particularly of large herbivores, and thus the density of lions is significantly lower than ecologically comparable ecosystems. Counter to expectations from mesopredator release theory, wild dog density in GKE was far lower than comparable ecosystems with higher lion and prey density, though annual survival rates were comparable to large and stable populations. Average pack size was small and home range size was among the largest recorded. Our results show that low lion density did not competitively release the GKE wild dog population and we infer that the low density of wild dogs was a product of low prey density. Our results suggest that there is an optimal ratio of prey and competitors at which wild dogs achieve their highest densities. This finding has immediate implications for the conservation of the endangered African wild dog, and broad implications for the conservation of subordinate species affected by resource depletion and intraguild competition.

1. Introduction

Large carnivores are experiencing rapid population declines and range reduction, with losses accelerating across the globe (Estes et al., 2011). For most carnivores, these declines are driven by a combination of habitat loss, prey depletion, over-exploitation and direct persecution in response to human conflict (Crooks et al., 2011; Ripple et al., 2014). Many carnivore guilds are strongly influenced by interspecific competition, and the conservation of subordinate competitors is further complicated by the limiting effects of competition with larger, dominant competitors (Creel, 2001; Fedriani et al., 2000; Gorman et al., 1998; Linnell and Strand, 2000; Palomares and Caro, 1999). Understanding how interspecific competition limits subordinate carnivore presence, abundance, ecology and behavior is of importance for management and conservation planning for many species (Dröge et al., 2017; Palomares and Caro, 1999; Steinmetz et al., 2013). Both dominant and subordinate competitors are affected by widespread declines in the densities of their large herbivore prey (Creel et al., 2019), but the demographic responses of subordinate carnivores to decreased densities of both prey and dominant competitors are not well described. A reduction in prey

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density typically leads to a reduction in predator density, but if dominant competitors are strongly affected by the loss of prey, there may be an offsetting benefit for subordinate competitors, and we know little about the net effect.

Large herbivore populations are declining across much of sub-Saharan Africa as a consequence of habitat loss and high levels of illegal offtake (Lindsey et al., 2013; Ripple et al., 2015; Western et al., 2009; Wolf and Ripple, 2016). The densities of dominant competitors such as lions (*Panthera leo*) are strongly correlated to prey density (Van Orsdol et al., 1985), and thus decrease in response to prey depletion (Vinks et al., 2021). The survival rates and population densities of subordinate competitors such as the African wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*) are less tightly correlated with prey density, but are negatively correlated with the density of dominant competitors (Creel and Creel, 1996; Kelly et al., 1998; Mills and Biggs, 1993; Mills and Gorman, 1997; Swanson et al., 2014). The expected effect on subordinate competitor populations from a decline of both prey and competitors is not entirely clear, and has immediate conservation implications (Creel et al., 2018).

African wild dogs provide a good opportunity to study the effects of resource depletion on subordinate competitors that are limited by interference and exploitative competition. Wild dogs are limited by interactions with lions and spotted hyenas (*Crocuta crocuta*) in many ecosystems through the effects of kleptoparasitism and intraguild predation (Broekhuis et al., 2013; Creel and Creel, 1996; Fanshawe and Fitzgibbon, 1993; Gorman et al., 1998; Mills and Gorman, 1997; Speakman et al., 2015; Swanson et al., 2014). As a result, wild dogs consistently select areas with low lion density (Dröge et al., 2017; Estes and Goddard, 1967; Mills and Gorman, 1997; Vanak et al., 2013), and populations respond positively to low densities of lions and hyenas (Creel and Creel, 2002; Pole, 2000). Wild dogs have historically occurred at low density (Selous, 1908) and they never attain population densities comparable to their dominant competitors (Creel and Creel, 1996). They have long been considered endangered by the IUCN, with fewer than 6000 individuals remaining (Fanshawe et al., 1991; Woodroffe and Sillero-Zubiri, 2020), though there is considerable uncertainty about this number and how it may be changing.

Central Zambia's Greater Kafue Ecosystem (GKE), comprised of Kafue National Park (KNP) and surrounding Game Management Areas (GMAs), is thought to hold Zambia's second largest wild dog population. The GKE comprises 13% of the Kavango Zambezi Transfrontier Conservation Area (KAZA TFCA) which might hold the largest remaining wild dog population in Africa, if the protected areas it encompasses function as one population. The GKE has long been considered a potential stronghold for wild dogs in both Zambia and the KAZA TFCA (DNPW, 2019) but no rigorous estimates of population size have previously been available (Fanshawe et al., 1991). Low prey density as a result of bushmeat poaching is well documented in the GKE (Lindsey et al., 2013; Overton et al., 2017; Vinks et al., 2020) and has altered the diets of large carnivores, particularly lions, with an array of potential ecological consequences (Creel et al., 2018). The lion population is now at a lower density than expected for a miombo ecosystem with the rainfall of the GKE (1020 mm/year) (Vinks et al., 2021), and the long-term decline of large prey species in the GKE has led to niche compression, prey-base homogenization, and greatly increased dietary overlap between lions and other large carnivores including wild dogs (Creel et al., 2018). Historically, the GKE has apparently not held high densities of spotted hyenas for poorly-understood reasons (Mitchell et al., 1965), and sightings in the field remain relatively rare.

To test the demographic response of wild dogs to low densities of both prey and dominant competitors, we fit mark-recapture models to data from wild dogs in the GKE that were intensively monitored from 2012 to 2019. We obtained precise estimates of population density and annual survival rates (while avoiding bias by accounting for imperfect detection), and recorded parallel data on reproduction, recruitment, home-range size, and home-range overlap to provide a comprehensive description of wild dog demography under these conditions. Finally, we used these data to estimate annual population growth rates. Similar data have been collected for wild dogs in other populations (Creel and Creel, 2002; Mills and Gorman, 1997; Woodroffe, 2011) and we compared our results to published estimates to comprehensively evaluate the consequences of prey depletion and reduced competitor density on the demography and density of wild dogs. A better understanding of wild dog response to a reduction of both prey and competitors is broadly applicable to conservation planning and policy-making, because most protected networks that hold wild dogs are experiencing (or vulnerable to) prey depletion. More generally, these results will help to better understand the consequence of global declines of large herbivores for the conservation of complete carnivore guilds, which are often strongly structured by interspecific competition (Palomares and Caro, 1999).

2. Materials and methods

2.1. Study area

Our 10,968 km^2 study area was located in the central and northern section of the Kafue National Park and surrounding Mumbwa-West, Kasonso-Busanga, and Lunga-Busanga Game Management Areas, encompassing the eastern and western portions of the Kafue and Lufupa rivers, and areas just to the north and south of the major M9 highway (Fig. 1). Kafue National Park is located in western Zambia (S14.5394, E26.0782) and is the largest protected area in the country (22,319 km^2), surrounded by GMAs managed for multiple use (hunting, wildlife protection, farming and fishing). Hunting safari companies lease management blocks in GMAs for 5–10 years, with harvest quotas set annually by the Department of National Parks and Wildlife for lions, leopards, and most large herbivores. The national park and these surrounding GMA's make up the 66,000 km^2 Greater Kafue Ecosystem, which forms the northernmost portion (and 13%) of the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA), which spans Angola, Botswana, Namibia, Zambia, and Zimbabwe. The ecosystem is dominated by Miombo woodland (*Brachystegia* and *Julbernadia spp.*) and a mosaic of *Acacia* woodland, termitaria woodland, riverine woodland, savannah grassland and seasonally inundated grasslands. The region receives an average of 1020 mm of total rainfall per year (Midlane et al., 2014), which is comparable to other miombo woodland ecosystems (Creel and Creel, 2002; Gillingham and Lee, 2003). There is a pronounced rainy season between December and April with extensive flooding and a dry season between May and November. During the rainy season, most of the park is inaccessible by vehicle.

2.2. Data collection

We recorded 4270 sightings of 425 individually identified wild dogs in 43 unique packs and single-sexed groups between 2012 and 2019, using direct observations supplemented with photographs collected via citizen science. As in prior research on wild dogs, individuals were readily identified by their unique coat patterns (Creel and Creel, 2002). Photos were stored in a digital photo-ID database and unique IDs were assigned to each individual. Radiocollars were used for re-detection, with at least one collar in 15 of the 43 packs, using a combination of Satellite-GPS, store on board-GPS and VHF collars (Telonics Inc., Mesa, Arizona, USA). From 2017 onward, all collared packs had at least 1 Satellite-GPS collar providing locations at 12-hour intervals (morning and evening). We radiocollared wild dogs by intramuscular injection of a combination of Medetomidine and Zoletil (typically 1.2 mg medetomidine and 20 mg Zoletil), reversing the medetomidine by intramuscular injection of Atipamezole after 45 min to 1 h. Anesthetic drugs were delivered by darting with an air-powered DanInject rifle, with all procedures performed by an experienced and Zambian-registered veterinarian, in collaboration with the Zambia Department of National Parks and Wildlife, with a protocol approved by the MSU IACUC (approval

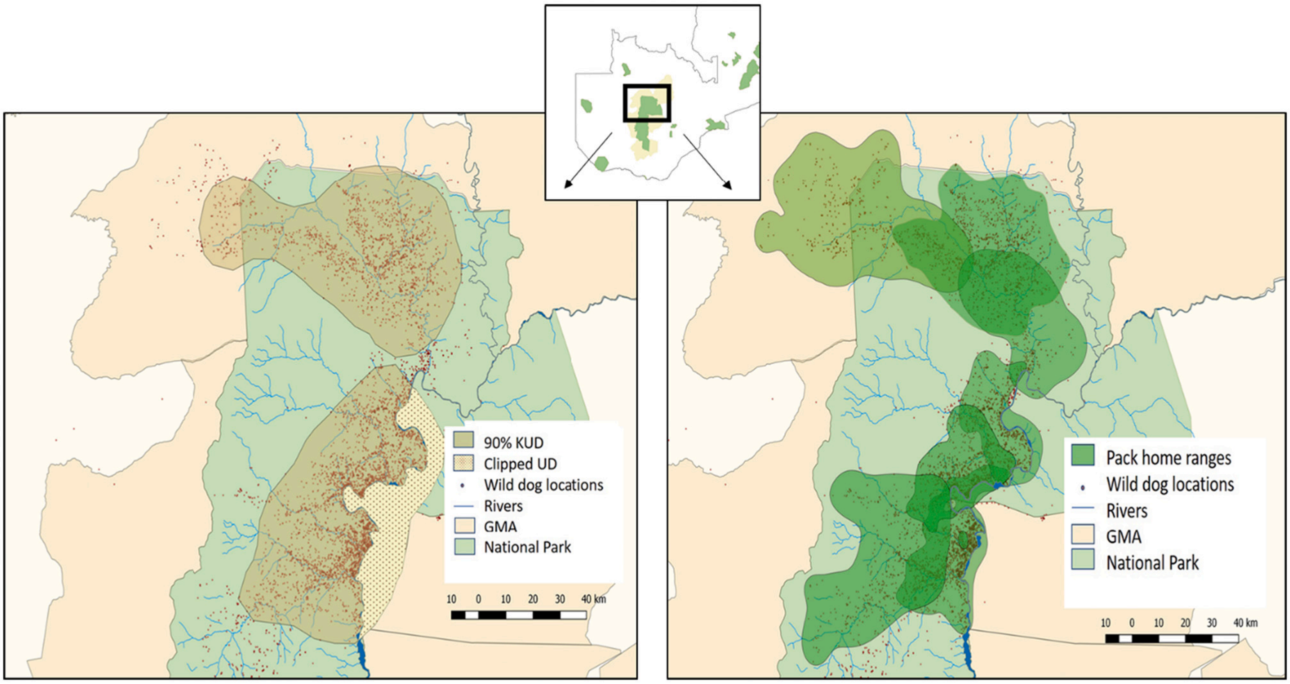

Fig. 1. The study area used by intensively monitored wild dogs in GKE. Left: the area encompassed by the 90% isopleth of a kernel utilization distribution fit to all locations for all monitored wild dogs, cropped to exclude an unmonitored area east of the Kafue River that was little-used by the monitored individuals. Right: The area encompassed by the 95% isopleth of kernel utilization distributions fit to annual locations for each pack. Area was calculated by combining these home-ranges for each year of study.

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Whenever wild dogs were located, we recorded (at minimum) the location, time, and identity of all individuals present, referring to a digital database of ID photos and taking photographs for confirmation of any uncertain identities. All adults were sexed by observation of genitalia, which is unambiguous for wild dogs. Age was known for most individuals by detecting them first as pups or yearlings, and was estimated from tooth wear and pelage for individuals first encountered as adults. Prior research on wild dogs in several populations has shown linear, Type II survivorship curves with little effect of age on survival among adults (Creel et al., 2004), so we pooled adults into a single age class prior to analysis, thus avoiding errors due to uncertainty about age.

Data on recruitment, litter size, and pup survival were gathered by visiting dens approximately 1 month after initial denning date (we did not visit newly established dens to avoid disruption). Initial denning date was determined from satellite-GPS data showing when the pack's resting locations became centralized on one point, or from consistent VHF monitoring that revealed dogs returning to the same area after hunting in successive days, following observations of a pregnant female in that pack. Pups were counted, sexed (genitalia are easily visible even in small pups) and IDs were assigned using digital photos. We investigated recruitment by recording the number of yearlings on June 1st of the following year or as soon as possible thereafter. We calculated average pack size for 25 intensively monitored packs between 2013 and 2019. Pack size was recorded on or near July 1st in order to standardize across all groups and reflect pack numbers in the middle of the denning season, when pack size most directly affects demography.

2.3. Estimating annual survival rates

We used Bayesian methods to fit Cormack-Jolly-Seber (CJS) models to detection records for 425 individuals to estimate age- and sex-specific annual survival rates (φ) and detection probabilities (*p*) that allowed for individual heterogeneity (Pledger et al., 2010). Detections were binned into 3 occasions per year, each of three months duration (April – June, July – September, October –December), for a total of 24 occasions over 8 years (2012–2019) with a total of 4270 unique detections. We did not include detections from January to March in our analysis due to inaccessibility of the study area in the rainy season yielding sparse data.

Wild dogs were categorized into three biologically meaningful age-classes: pups (0–0.99 years old, which depend on older packmates for food and protection), yearlings (1–1.99 years old, partially independent but not yet at full body size, not sexually mature and with limited hunting skill), and adults (2 years or older). All adults and yearlings, and most pups were of known sex, and sex was assigned randomly to a small number of pups (<1% of individuals) to keep the data set constant and thus allow comparison of models using information criteria.

CJS models fit one function to estimate survival (φ) and a second function to estimate detection probability (*p*) in a hierarchical fashion that allows an overlapping set of variables to affect each of these parameters. We used Bayesian methods to fit CJS models to allow flexibility in defining model structure through constraints on the parameters, to provide credible intervals (rather than confidence intervals) for parameter estimates, and to take advantage of tailored posterior predictive checking to assess goodness of fit (Kéry and Royle, 2015; Kéry and Schaub, 2011).

Using the R package R2jags (Yu and Yajima, 2012), we constructed a model in which survival rates varied by age and sex, as these effects were of interest a priori to allow comparison to other wild dog populations. The model allowed for extra-binomial variation between individuals in the probability of detection ('overdispersion') by adding an individual random effect on detection with a Gaussian distribution on logit scale (Kéry, 2010). We used uninformative uniform prior distributions for both φ and *p*, with bounds following recommendations by Kéry and Schaub (2011), and fit the model with three Markov chains, retaining 45,000 iterations after a 5000 step burn in. We assessed the model's goodness of fit by: (*a*) comparing its deviance information criterion (DIC) score with simpler models that did not include the effects of age or sex on survival and did not allow for individual random effects on detection, and (*b*) posterior predictive checking. For posterior predictive checking we simulated individual capture histories with the model and compared the simulated frequency of individuals with few (<5) detections to the real data (Fig. 2). DIC scores unambiguously supported the a priori model, and posterior predictive checking confirmed that the model fit the data well (simulated median p for rarely detected individuals = 0.18, median p for data from the same individuals = 0.19).

2.4. Estimating population density

We used Bayesian methods to fit closed mark-recapture models to estimate wild dog abundance in each year, using the same capture histories as our survival analysis. Two abundance models were compared using DIC scores, one modeling effects of individual heterogeneity in the probability of detection, p (Huggins, 1989), and one without individual heterogeneity. DIC scores unambiguously supported the model including effects of individual heterogeneity in probability of detection (ΔDIC scores >10). As with the CJS model, we modeled variation in p as a random effect of individual identity with a Gaussian distribution on logit scale. To account for variation among years we analyzed each year's detection histories separately using the same time bins as the survival analysis with a 3-occasion encounter history for each individual in each year. To produce accurate estimates of population density, these estimates of population size were limited to well-monitored resident groups whose patterns of space use were well-described. This included all resident packs and single-sexed groups of dispersers that established a resident home-range within the study area. Our criterion for inclusion was that the group was seen for over 1 year within the study area and all individuals were identified. Consistent with prior estimates of wild dog density (Creel and Creel, 2002; Mills and Gorman, 1997; Woodroffe, 2011), we did not include pups in the estimate of density (i.e., we limited the analysis to yearlings and adults to allow comparison to published estimates).

We estimated abundance for four years, 2016 through 2019. We converted the estimate of population size ($\widehat{N}$) for each year to an estimate of density ($\widehat{D}$) by dividing $\widehat{N}$ by the area ($\widehat{A}$) used by the individuals with capture histories. Home-ranges were estimated using the 95th percentile isopleth of a kernel utilization distribution (KUD) (Worton, 1989) based on GPS locations collected at 12-hour intervals, twice daily, for the groups with capture histories that met the criterion for inclusion described above, using the adehabitatHR package in R (Calenge, 2006). To estimate density in a manner that accounts for variation across years in the area that was used by adequately monitored groups, we first fit a separate KUD to locations from each group in each year, and determined the total extent of these KUDs combined, counting areas of overlap only once (Fig. 1). We also provide alternative density estimates using the area of a single 90% KUD fit to locations from all groups combined and clipped to exclude the east side of the Kafue river for which we did not have adequate monitoring data (Fig. 1). These alternative density estimates have the advantage of applying to a constant area of 6374 km^2 but do not directly account for variation across years in the area monitored.

Many recent studies have used spatially explicit capture recapture (SECR) models (Royle et al., 2013; Royle and Young, 2008) to estimate carnivore densities (Broekhuis and Gopalaswamy, 2016; Elliot and Gopalaswamy, 2017). These models are well suited to data sets in which the sightings used to model detection probability also provide the only information about the area used by the detected animals (e.g., data from camera traps). However, most SECR analyses rely on simple models of space use (often by assuming that each individual's probability of use drops in a smooth, bivariate normal fashion from a single point of peak use). Incorporating information from telemetry into SECR models can improve estimates of density, but this approach relies on the same logic as the approach we used to model abundance from detection histories and convert abundance to density using a well-established KUD method to model the area sampled. Our approach aligns well with empirical descriptions of space use by large carnivores, whose movements are shaped by irregular distributions of prey, competitors, vegetation, rivers, and roads. We had extensive locational data from GPS and satellite GPS radio-collars (n = 9624 unique locations, greatly outnumbering the 4270 binned detections) that allowed us to fit flexible KUD models to describe the area used by each group. Apart from providing a good description of the use of space, this approach maximized precision by using all observed locations for all group members (including more than one location for many individuals in many time intervals) when determining the total area occupied.

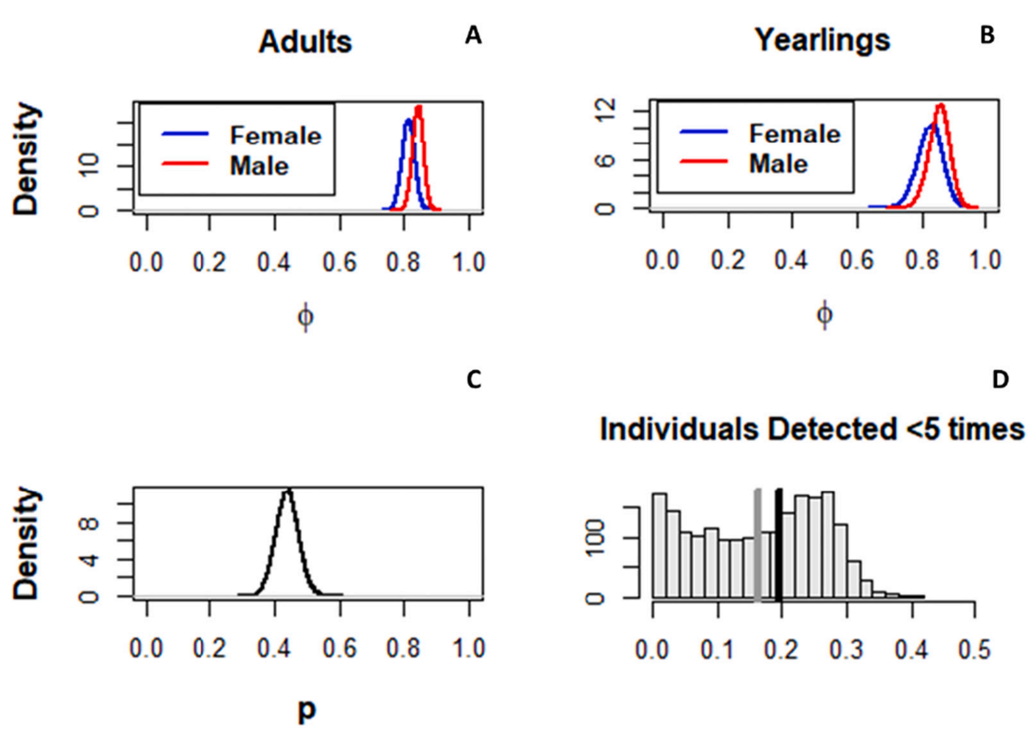

Fig. 2. Posterior distributions of apparent survival rates (φ) of wild dog adults (A) and yearlings (B) from a Cormack-Jolly-Seber model fit to data from 2012 to 2019 using Bayesian methods. (C) Posterior distribution of estimated annual detection probability, p. (D) Posterior predictive checking of the model's fit, comparing a discrepancy statistic for the observed data with data simulated under the fitted model. The plot shows the frequency distribution for p simulated under the model (histogram with median denoted by vertical grey line) vs. the median for the original data (black line) for individuals with fewer than 5 detections.

3. Results

3.1. Population density, and growth rate

In 2019, we estimated that the population held 53.13 individuals (excluding pups <1 years old; 95% CRI: 52–57) in an area of 6752 km^2. This yields an estimated density of 0.79 adult and yearling wild dogs per 100 km^2. Yearly population density estimates for 2016–2019 are compiled in Table 1, and for each year, alternative density estimates are provided, based on a constant area determined from the 90% KUD for all years combined. Both methods reveal that wild dog density in the Greater Kafue is substantially lower than almost all other ecosystems studied to date, including ecosystems with similar vegetation and rainfall (the primary ecological determinants of ungulate densities (East, 1984)) such as the Selous Game Reserve (SGR). The annual population growth rate (λ) ranged from 0.82–1.07 (geometric mean = 0.94) using densities based on yearly pack home-ranges (Table 2). Population growth rates were considerably different when estimated for a constant area, ranging from: 0.73–2.3 (geometric mean = 1.20) (Table 2). We caution that these fluctuations in λ are probably strongly stochastic and suggest that the geometric mean λ of 0.94 that accounts for annual variation in the area monitored is a more accurate representation of the population trend for Kafue wild dogs (see discussion).

3.2. Age and sex-specific annual survival, reproduction, and recruitment

Annual survival rates and patterns of variation between the sexes and age-classes were closely comparable to prior estimates from higher-density wild dog populations. Males had higher survival than females at all age classes (Fig. 3). Estimated annual survival for yearling males and females (1–1.99 years old) was highest of all age-classes at 0.85 (95% CRL 0.79–0.91) and 0.82 (95% CRL 0.75–0.90) respectively (Fig. 2). Estimated annual survival for adult males and females (1.99 years or older) was 0.84 (85% CRL 0.81–0.88) and 0.81 (95% CRL 0.78–0.85) respectively (Fig. 2). Mean detection probability (p) was 0.44 (95% CRL 0.37–0.51).

Our ability to detect very young pups was limited because initial den visits occurred one month after denning began (to avoid disturbance). Consequently, pups who died before our initial den visit would go completely undetected, creating an uncorrectable bias (overestimation) in estimated pup survival rates. Pups that were first detected several months after birth in packs that were less intensively monitored might represent a life stage with higher (or lower) survival than earlier stages of the pup's life. To avoid errors due to these problems, we did not estimate annual survival for pups using the same modeling approach, and instead report pup annual recruitment and average litter size. Litter size at first count averaged 7.53 pups (95% CI: 6.17–8.89, $N = 19$), and the average number of yearlings recruited averaged 4.63 individuals (95% CI: 2.66–6.69, $N = 11$). This yields an estimated survival rate of 61.4% for pups in Kafue National Park (between one month and one year), or 58.7% when annualized.

Table 1
Annual estimates of wild dog population density and growth rate for Kafue National Park, using two methods to estimate area to calculate density. Yearly Pack Range (left) uses an area that changes according to monitoring effort each year. Uniform Area (right) uses a constant area. See Methods for details.

	Yearly pack range			Uniform area (6372 km^2)	
Year	Area (km^2)	Density (adults and yearlings per 100km^2)	Lambda	Density (adults and yearlings per 100 km^2)	Lambda
2016	3185	0.94	–	0.47	–
2017	8101	0.89	0.95	1.1	2.3
2018	5853	0.73	0.82	0.8	0.73
2019	6752	0.78	1.07	0.82	1.03
Average across years		0.84	0.94	0.8	1.20

3.3. Pack size, home range size and overlap

Packs averaged 8.40 yearlings and adults (95% CI: 6.35–10.45, $N = 25$), of which 5.44 were adults (95% CI: 4.44–6.44, N = 25). Eleven annual home ranges for breeding packs between 2013 and 2019 averaged 1375.8 km^2 (95% CI: 970.1–1781.5). Home-range overlap between adjacent breeding packs averaged 21.8% (95% CI: 14% - 28%) of the KUD 95% isopleth for 9 adjacent packs that overlapped each other in the same year.

4. Discussion

Wild dog density in the GKE was 4.8-fold lower than a comparable miombo system with higher densities of both dominant competitors and prey (Creel and Creel, 2002). Kafue holds one of the lowest densities of African wild dogs recorded (Table 2), even though our estimates of density pertain to the core of the GKE, with higher levels of protection than areas outside of our study site that face more anthropogenic pressure (Overton et al., 2017; Watson et al., 2015). Average pack size in GKE was ~25% lower than ecosystems with higher densities of wild dogs, lions, and prey (Table 2). Average home-range in the GKE was nearly twice the size of those in any other ecosystem (Table 2), and over three times the size of home-ranges observed in comparable miombo woodland in Selous (using similar methods).

Low wild dog density was not associated with low survival rates, a pattern also observed for lions in the GKE, and for leopards in prey-depleted Game Management Areas in Zambia's Luangwa Valley (Rosenblatt et al., 2016; Vinks et al., 2021). This result further supports Vinks et al.'s suggestion that survival rates alone may not be a sensitive tool to evaluate the effect of prey depletion on carnivore populations.

We infer that wild dog carrying capacity, and thus density, has slowly declined together with lion carrying capacity in response to prey depletion. Annual population growth rates (λ) fluctuated appreciably but suggested decline (Table 1.). For a population this small, stochastic annual variation in λ is expected (Lande, 1988). Here, such events included the colonization of an unutilized area by a pack of 4 adults, the pack's growth to 11 the next year with the addition of pups, and the pack's demise the following year due to rabies or canine distemper. Such events were common: a pack of 17 wild dogs was killed off by rabies in 2019 just outside of our study area. The alpha male of one study pack was killed by lions and nine of the packs eleven pups died subsequent to his death. The death of the alpha male in another pack led the pack to split, and no offspring were produced the following year. Because such events cause an appreciable change in the growth rate of a population this small, inferences about the current mean growth rate should be made with caution. We recommend targeted analysis that continues to monitor this population's trend as data accumulates.

Despite the low density of lions in the GKE (Vinks et al., 2021), the density of wild dogs is one of the lowest ever recorded. This can be attributed to the depletion of prey in the GKE reported by Vinks et al. (2020). Vegetation structure and rainfall are strong determinants of large herbivore density (East, 1984; Fritz and Duncan, 1994), and both rainfall and vegetation structure are closely comparable between the GKE and Selous, but the higher density of prey in Selous supported a 4.8-fold higher density of wild dogs despite a 3.2-fold higher density of lions (Rodgers, 1979; Creel and Creel, 2002; Vinks et al., 2021, 2020). Thus, low lion density in the GKE does not offset the negative effects of prey depletion and allow 'competitive release' of the wild dog population.

In contrast to their very low density, annual survival rates for wild dogs in the GKE are comparable to those in large, stable populations (Table 2). We therefore cannot attribute the low density of wild dogs to high current levels of direct mortality, despite the local prevalence of wire-snare bycatch, disease, and encroachment. We do not imply that

Table 2
Comparison of wild dog population densities and population parameters for eight protected areas in Africa. Populations are listed from lowest to highest density, together with associated average pack size, litter size, home-range size, annual survival rates, population growth rate, lion density and hyena density. 95% confidence intervals and standard errors are reported where available.

PA	Wild dog density (adults & yearlings/100 km^2)	Lion density (individuals per 100 km^2)	Hyena density (individuals per 100 km^2)	Avg pack size (yearlings & adults)	Avg litter size	Pup survival	Yearling survival	Adult survival	Home-range size (km^2) & Method	Lambda	Source
Serengeti National Park 1985–91	0.67	14	110	7.5 +/− 1.3	9.2 +/− 1.1	0.40 +/− 0.12	No Data	0.73 ± 0.05	665 (MCP)	Not reported	(Burrows et al., 1994; Ginsberg et al., 1995; Hofer and East, 1995)
Kafue Ecosystem, Zambia	0.79	3.43	No Data	8.4 (6.35–10.45)	7.53 (6.17–8.89)	0.61 (0.35–0.89)	0.84 (0.75–0.91)	0.82 (0.78–0.85)	1376 +/− 206, (95% KUD)	0.95	(This study; Vinks et al., 2020)
Save Valley, Zimbabwe	1.4	0.24	0.49	4.9 +/− 0.7	8.0 +/− 0.8	0.84	No Data	No Data	499 +/− 158 (MCP)	No Data	(Pole, 2000)
Hluhuwe-iMfolozi Game Reserve, SA	1.6	4.3	32.4	8.1 +/− 1.1	7.9 +/− 0.8	0.75	0.8	0.88	No Data	1.01 +/− 1.19	(Somers et al., 2008)
Samburu - Laikipia, Kenya	3.3	5.5	No Data	9.1 +/− 0.90	7.3 +/− 0.53	0.71 (0.61–0.80)	0.69 (0.29–0.90)	0.75 (0.62–0.86)	423 (95% KUD)	1.21	(Woodroffe, 2011)
Kruger National Park, SA	1.9–3.9	9.55	8–12	9.7 ± 1.0	9.4 +/− 0.70	0.35 (0.29–0.52)	0.45 (0.34–0.57)	0.72	537 (MCP)	1.00	(Creel et al., 2004; Ferreira and Funston, 2010; Mills et al., 2001; Mills and Gorman, 1997)
Moremi Game Reserve, Botswana	3.5	8.4	14.4	10.4 +/− 0.95	10.1 +/− 0.32	0.48 (0.42–0.54)	0.74 (0.72–0.79)	0.40–0.67	739 +/− 81, (95% KUD)	1.00	(Cozzi et al., 2013; Creel et al., 2004; Mcnutt and Silk, 2008)
Selous Game Reserve, Tanzania	3.8	11	32	14.1	7.5 +/− 0.56	0.75 (0.66–0.84)	0.84 (0.73–0.91)	0.71	433 +/− 64, (95% KUD)	1.04	(Creel and Creel, 1995; Creel and Creel, 1996; Creel and Creel, 2002)

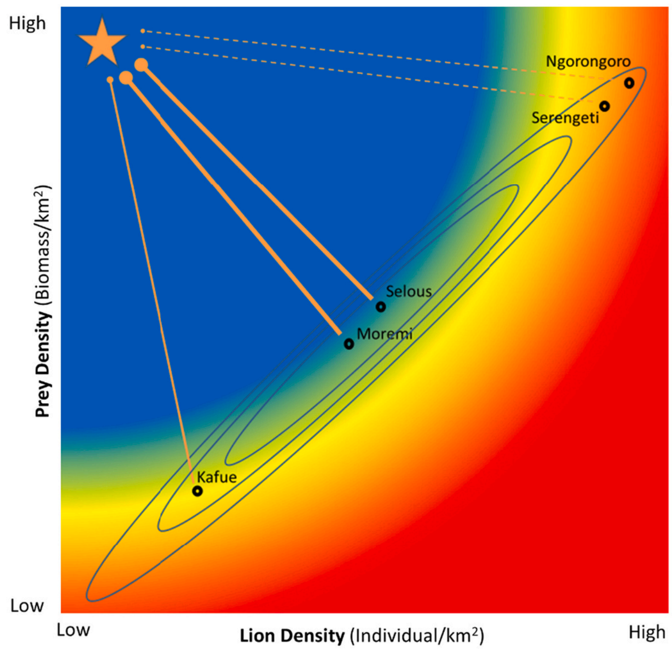

Fig. 3. A graphical model of wild dog density in relation to lion density and prey density. Variation in wild dog density is shown by heat mapping, where blue is associated with conditions that allow for high wild dog density and red is associated with conditions that lead to intermittent populations characterized by extirpation/recolonization cycles. The star represents the ideal state of these limiting factors for wild dogs: an ecosystem with high prey density and no lions. Concentric ellipses enclose the observed set of conditions in real ecosystems, where lion density is positively correlated with prey biomass. Within the set of real-world conditions defined by the ellipses, wild dog density is highest at points that fall in the central ellipse that are closest to the ideal conditions at top left: these populations are identified by shorter and thicker lines. Five populations are plotted as examples consistent with published data. Wild dog populations have been locally extirpated or only intermittently present in areas with high prey density and very high lion density (Ngorongoro and Serengeti, long dashed lines). Populations with low prey and lion density persist at low densities (Kafue, long solid line). Ecosystems with intermediate densities of prey and lions support the highest wild dog densities (Selous and Moremi, short solid lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

these anthropogenic factors are not important, but they are clearly not driving low population density in the core of KNP by reducing adult or yearling survival rates relative to high-density wild dog populations. GKE wild dogs live in small packs with exceptionally large home ranges, but within those packs their survival is comparable to that of dense, stable populations. These results suggest that there may be an optimal ratio of prey and supported dominant competitors, both at intermediate densities, which allows wild dogs to achieve their highest population densities (Fig. 3). Systems with the highest density of competitors (e.g., Serengeti National Park and Ngorongoro Crater Conservation Area) exclude wild dogs, particularly in open habitats that promote interference competition (Carbone et al., 1997). Systems with very low prey density also do not support high densities of wild dogs, despite low competitor density, as seen in Kafue.

Unsustainable bushmeat poaching has been linked to prey depletion in the GKE (Overton et al., 2017; Schuette et al., 2018), with larger-bodied herbivores showing greater reductions in density than smaller-bodied herbivores (Vinks et al., 2020). This uneven prey reduction has important ecological consequences for large carnivores and the competition among them (Creel et al., 2018; Vinks et al., 2021). Lions now prey heavily on smaller bodied ungulates, and therefore dietary niche overlap between large carnivore competitors has increased (Creel et al., 2018). This increase in niche overlap may be one reason that wild dogs do not benefit from meso-predator release in the GKE.

For a group-living species like the wild dog, low population density must be associated with mean pack size that is small, mean home range size that is large, or both. Average pack size in the GKE was roughly 25% lower than other populations, and 39% lower than packs in the ecologically similar miombo woodland of Selous (mean adult pack size = 8.9). While it has previously been suggested that small pack size may be related to low population density, evidence for this relationship has been elusive (Courchamp and Macdonald, 2001). With the addition of this study, we have shown a correlation between pack size and population density (Fig. 4), even after accounting for sampling error in mean pack size (Fig. S1, supplemental material). This relationship does not establish that small pack size drives low density through Allee effects as suggested by Courchamp and Macdonald (2001). It is possible that Allee effects occur, but it is also likely that low wild dog density and small pack size are both consequences of low prey density. Past studies have consistently found a positive relationship between pack size and reproductive success in wild dogs, suggesting that small pack size could have negative effects on population growth. Adults, and to a lesser extent yearlings, cooperate to kill prey and defend dens, babysit, and feed pups (Malcolm and Marten, 1982). Pup survival and litter size are positively correlated with increased pack size (Courchamp et al., 2002; Creel et al., 2004), though adult and yearling annual survival decrease as pack size increases (Creel and Creel, 2015). Increases in lion populations have also resulted in decreases in both pack size and pup survival (Groom et al., 2016). Small wild dog packs focus on small prey (Creel and Creel, 2002) so the decrease in mean prey size and density in Kafue (Creel et al., 2018) could cause the optimal pack size for hunting to decrease in parallel (Creel et al., 2018; Creel and Creel, 2015; Vucetich and Creel, 1999). However, there is no reason to assume that optimal pack size for pup rearing and defense should decrease in the same manner. Fewer individuals in the pack mean fewer to babysit and defend pups, and fewer to bring food back to the den to feed pups. Pup survival has a strong effect on population growth (Creel et al., 2004), and our estimates of pup survival were low (Table 2), even though adult and yearling survival rates were comparable. Studies have shown that small prey can support large packs, but only if that prey is abundant and dominant competitors are suppressed (Woodroffe, 2011; Woodroffe et al., 2007).

Home ranges in the GKE were among the largest reported in a study system (Table 2), yet home range overlap was comparable to other

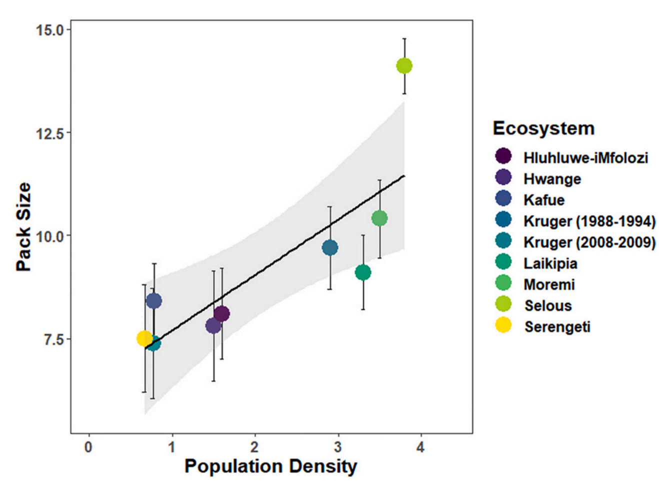

Fig. 4. Average pack size in relation to population density for African wild dogs across multiple studies. Error bars show +/− one standard error. Pack size is positively correlated with population density ($b = 1.35$, $r^2 = 0.61$, $t = 3.70$, $P < 0.01$). (Burrows et al., 1994; Creel et al., 2004; Creel and Creel, 2002; Fuller et al., 1992; Ginsberg et al., 1995; Marnewick et al., 2014; Somers et al., 2008; Woodroffe, 2011).

systems (Creel and Creel, 2002; Pole, 2000; Reich, 1981), Average yearly home-range in Kafue was nearly double the next largest home-range calculations in a similar system, which come from Moremi Game Reserve in Botswana (739 $km^2 \pm 81$), a relatively well-protected area (Pomilia et al., 2015). We also calculated utilization distributions using dynamic Brownian Bridge movement models (Kranstauber et al., 2012) and still found very large ranges, even though this method tends to exclude 'donut holes' that are included in the KUDs we reported (873 km^2, $\pm$ 127). Low density is thus related to both small pack size and large ranges. These exceptionally large home ranges might increase the exposure of wild dogs to threats known to be present in the GKE, such as viral disease transmission from domestic dogs and wire snares.

The effects of prey depletion are likely affecting protected areas and their carnivore inhabitants throughout the world, especially in developing countries (Wolf and Ripple, 2016). Our results show that wild dog density appears to decrease in parallel with prey depletion, and that the costs of low prey density on the wild dog population in the GKE far outweighed the benefits of meso-carnivore release due to low lion density. Because wild dog densities are invariably lower than lion densities (even in undisturbed ecosystems), their populations are likely to reach critically low numbers prior to their dominant competitors as an ecosystem becomes prey depleted. The combined effects of prey depletion and meso-carnivore release are not well understood, and this pattern may hold true for other competitively subordinate carnivores. This finding has important implications for conservation strategy, because it calls into question the recommendation to target wild dog conservation and reintroductions in areas of low competitor density. If dominant competitor densities are low as a consequence of low prey density (as is common), our data suggest this strategy will not work well. Conservation efforts should instead focus on areas with intact prey communities and effective protection. In ecosystems like the GKE, increasing protection and addressing the drivers of prey depletion is likely to be the most effective strategy to conserve wild dogs, their competitors, and their prey.

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CRediT authorship contribution statement

Ben Goodheart: Conceptualization, Formal analysis, Investigation, Data curation, Writing – Original Draft, Visualization.: **Scott Creel**: Conceptualization, Formal analysis, Methodology, Validation, Writing – Review and Editing, Supervision, Funding acquisition.: **Matt Becker**: Conceptualization, Writing – Review and Editing, Supervision, Project administration, Funding acquisition.: **Milan Vinks**: Software, Investigation.: **Kambwiri Banda**: Investigation.: **Carolyn Sanguinetti**: Investigation.: **Paul Schuette**: Investigation.: **Elias Rosenblatt**: Investigation.: **Chase Dart**: Investigation, Data Curation.: **Anna Kusler**: Investigation.: **Kim Young-Overton**: Investigation,: **Xia Stevens**: Investigation.: **Alstone Mwanza**: Investigation.: **Chuma Simukonda**: Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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