Received: 8 June 2023 | Accepted: 4 January 2024

DOI: 10.1111/1365-2656.14052

Journal of Animal Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

An integrated population model reveals source-sink dynamics for competitively subordinate African wild dogs linked to anthropogenic prey depletion

Scott Creel[1,2] | Johnathan Reyes de Merkle[1,2] | Ben Goodheart[1,2] | Thandiwe Mweetwa[2] | Henry Mwape[2] | Twakundine Simpamba[3] | Matthew S. Becker[1,2]

[1]Department of Ecology, Montana State University, Bozeman, Montana, USA

[2]Zambian Carnivore Programme, Mfuwe, Eastern Province, Zambia

[3]Department of National Parks and Wildlife, South Luangwa Area Management Unit, Mfuwe, Eastern Province, Zambia

Correspondence
Scott Creel
Email: screel@montana.edu

Funding information
World Wildlife Fund; National Geographic Society; International Union for the Conservation of Nature; NSF Division of Environmental Biology, Grant/Award Number: DEB-2032131 and DEB-2221826; The Bennink Foundation; NSF Division of Integrative & Organismal Systems, Grant/Award Number: IOS-1145749

Handling Editor: Laura Prugh

Abstract

1. Many African large carnivore populations are declining due to decline of the herbivore populations on which they depend. The densities of apex carnivores like the lion and spotted hyena correlate strongly with prey density, but competitively subordinate carnivores like the African wild dog benefit from competitive release when the density of apex carnivores is low, so the expected effect of a simultaneous decrease in resources and dominant competitors is not obvious.
2. Wild dogs in Zambia's South Luangwa Valley Ecosystem occupy four ecologically similar areas with well-described differences in the densities of prey and dominant competitors due to spatial variation in illegal offtake.
3. We used long-term monitoring data to fit a Bayesian integrated population model (IPM) of the demography and dynamics of wild dogs in these four regions. The IPM used Leslie projection to link a Cormack–Jolly–Seber model of area-specific survival (allowing for individual heterogeneity in detection), a zero-inflated Poisson model of area-specific fecundity and a state-space model of population size that used estimates from a closed mark–capture model as the counts from which (latent) population size was estimated.
4. The IPM showed that both survival and reproduction were lowest in the region with the lowest density of preferred prey (puku, *Kobus vardonii* and impala, *Aepyceros melampus*), despite little use of this area by lions. Survival and reproduction were highest in the region with the highest prey density and intermediate in the two regions with intermediate prey density. The population growth rate (λ) was positive for the population as a whole, strongly positive in the region with the highest prey density and strongly negative in the region with the lowest prey density.
5. It has long been thought that the benefits of competitive release protect African wild dogs from the costs of low prey density. Our results show that the costs of

Scott Creel and Johnathan Reyes de Merkle—Joint first authors.

prey depletion overwhelm the benefits of competitive release and cause local population decline where anthropogenic prey depletion is strong. Because competition is important in many guilds and humans are affecting resources of many types, it is likely that similarly fundamental shifts in population limitation are arising in many systems.

KEYWORDS
fecundity, interspecific competition, population dynamics, prey depletion, snaring, survival

1 | INTRODUCTION

True apex carnivores like the lion (*Panthera leo*) are limited mainly by access to prey, which creates a consistently strong and positive correlation between prey and apex carnivore densities (Hatton et al., 2015; Orsdol et al., 1985; Packer et al., 2005). Because apex carnivores are competitively dominant and exploit areas with high prey density, competitively subordinate species like the African wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*) must optimize a trade-off between avoiding dominant competitors and maintaining access to prey (Bhandari et al., 2021; Broekhuis et al., 2013; Creel et al., 2023; Creel & Creel, 1996; Dröge et al., 2017; Durant, 2000; Groom et al., 2017; Mills & Gorman, 1997; Swanson et al., 2014). Field studies have consistently shown that African wild dog density correlates negatively with the densities of lions and spotted hyenas (*Crocuta crocuta*), both within and between ecosystems (Creel & Creel, 2002; Goodheart et al., 2021). Because lion and hyena densities correlate positively with prey density (Hatton et al., 2015), wild dog density should increase as prey density decreases, as long as the benefits of competitive release outweigh the costs of low prey availability (Goodheart et al., 2021).

However, large herbivore populations are declining substantially across sub-Saharan Africa due to illegal hunting, competition with livestock and land conversion (Bolger et al., 2008; Goheen et al., 2018; Morrison & Bolger, 2014; Ripple et al., 2015, 2016; Venter et al., 2016; Watson et al., 2013, 2015; Western et al., 2009), and the benefits of competitive release must eventually be overwhelmed by the costs of prey depletion; as prey density approaches zero, wild dog density must also approach zero. This suggests that a tipping point should be expected in the relationship of wild dog density to prey density (Creel et al., 2023; Goodheart et al., 2021). Above the tipping point, wild dog density should increase as prey density decreases, because the benefits of competitive release outweigh the costs of prey depletion. Below the tipping point, wild dog density should decrease as prey density decreases, because the costs of prey depletion must eventually outweigh the benefits of competitive release. A recent meta-analysis supports this tipping-point hypothesis (Creel et al., 2023), and recent field studies suggest that prey density has dropped below the tipping point in some ecosystems, for example in the Greater Kafue Ecosystem, where wild dog density is very low ($<1/100\,\text{km}^2$) even though the density of dominant competitors is also low, as a consequence of prey depletion (Creel et al., 2018; Goodheart et al., 2021, 2022; Vinks et al., 2020). Because few studies have directly tested the relationships of wild dog demography and dynamics to prey density, the generality of this problem remains poorly understood. The broad decline of African large herbivore populations makes a better understanding of the effect of prey depletion on wild dogs a high priority for their conservation and management.

Subordinate competitors in many large carnivore guilds are limited by interspecific competition and intraguild predation (Creel et al., 2001; Johnson et al., 1996; Palomares & Caro, 1999; Polis et al., 1989; Sivy et al., 2018), and large herbivore population declines are not restricted to sub-Saharan Africa (Ripple et al., 2015; Wolf & Ripple, 2016). Thus, it is reasonable to hypothesize that fundamental changes in the relationship between predator and prey densities might now be emerging in other guilds. It is logical to hypothesize that a similar tipping point might emerge for subordinate competitors in any guild that is structured by interspecific competition and is affected by habitat degradation or resource depletion.

Integrated population models (IPMs) have emerged as a method to accurately describe demography and dynamics by pooling data on population size, survival and reproduction into a single model (Arnold et al., 2018; Schaub & Abadi, 2011; Schaub et al., 2007; Schaub & Kery, 2022; Zipkin & Saunders, 2018). IPMs are particularly useful to detect cryptic source-sink dynamics driven by local differences in population growth rates (Weegman et al., 2016). Here, we fit a Bayesian IPM to long-term data from intensive monitoring of African wild dogs in the Luangwa Valley Ecosystem (LVE), where they occupy four regions with substantial, well-described variation in prey density (Rosenblatt et al., 2019) that is largely due to differences in the intensity of poaching, particularly wire-snare poaching (Watson et al., 2013). This provides an opportunity to test whether differences in prey density are associated with differences in survival and reproduction, and whether differences in demography lead to cryptic source-sink dynamics by holding the local population growth rate (λ) below one in prey-depleted areas. A Bayesian IPM is well suited to this analysis, because it allows data on reproduction, survival and population size to be integrated into one joint likelihood (thus aligning inferences and increasing precision). An IPM can also reveal cryptic source-sink dynamics by testing whether region-specific population growth rates (λ) fall above or below one on the basis of growth-in-place.

2 | METHODS

2.1 | Study area

The Luangwa Valley Ecosystem lies in Zambia's Eastern Province, and includes four National Parks (South Luangwa, North Luangwa, Luambe and Lukusuzi) that are contiguously linked by Game Management Areas (GMAs). Human settlement and extractive use (including professional hunting of lions) are allowed in the GMAs, but not in the National Parks, which are also better protected through photo-tourism and anti-poaching patrols by the Department of National Parks and Wildlife and law enforcement partners. The Luangwa River flows from north to south through the LVE, and wildlife concentrates on both sides of the river year-round, but especially in the dry season. Areas to the east and west of the river are ecologically similar but differ greatly in the densities of prey (Rosenblatt et al., 2019) and lions (Creel et al., 2016; Mweetwa et al., 2018; Rosenblatt et al., 2014) due to differences in protection (Watson et al., 2013, 2015). Our long-term study site of 6938 km^2 is comprised of four areas that span this gradient (Figure 1). *Nsefu (NS)* is a 1318 km^2 region that includes parts of SLNP east of the Luangwa River, Upper Lupande GMA and Lumimba GMA, with intermediate protection, intermediate use by lions and the highest densities of wild dogs' primary prey, which is primarily puku (*Kobus vardonii*) and impala (*Aepycyros melampus*). *Main Game (MG)* is a 2209 km^2 region of South Luangwa NP (SLNP) west of the Luangwa River that includes the primary photo-tourism area, with high protection, high use by lions and intermediate densities of wild dogs' prey, (Rosenblatt et al., 2019).

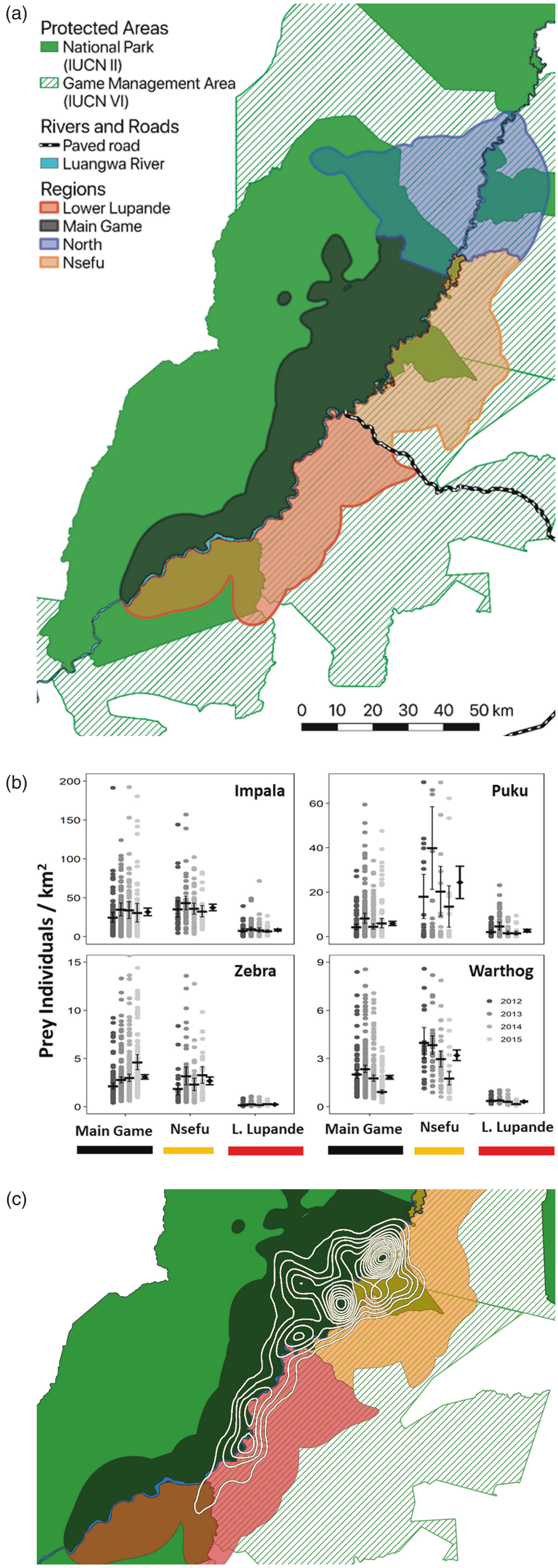

FIGURE 1 (a) The Luangwa Valley Ecosystem (LVE) includes ecologically similar areas that are highly protected within National Parks (green) and less protected within Game Management Areas (cross-hatched). This creates a gradient in the density of large herbivore prey across four areas in which we monitored wild dog demography. The boundaries of these four areas are shown here by colour and were determined by merging the 90% isopleths of utilization distributions from dynamic Brownian bridge movement models fit to fixes from GPS collars carried by at least one member of all resident packs in each region. (b) Distance sampling models fit to line transect data have previously shown (Rosenblatt et al., 2019) that large herbivore densities are consistently higher in the Nsefu (*NS*) and Main Game (*MG*) regions than in the Lower Lupande (*LL*) region. Puku and impala are wild dogs' primary prey in the LVE and attain a considerably higher combined density in NS than other areas, particularly LL, where their density is very low. Individual points show densities for each transect, with the mean and 95% CI for each year shown by a bar and whisker. The mean and CI for all years combined are shown by a diamond and whisker just to the right. Comparable data are not available for the North (ML) region, but conditions are most comparable to the Main Game region. (c) A kernel utilization distribution fit to 196,471 lion locations in the MG, MS and LL regions from the same period as the wild dog study, showing that lion use was highest in MG, intermediate in NS and lowest in LL (and locally concentrated along the Luangwa River in all regions).

North (ML) is a 1801 km^2 region including the northeastern part of SLNP along the Muphamadzi river, the western part of Luambe NP and parts of the Lumimba and Munyamadzi GMAs that link the two parks, with intermediate protection, prey density and lion use. *Lower Lupande (LL)* is a 1610 km^2 region in the Lower Lupande GMA and the Lusangazi sector of SLNP east of the Luangwa River, with the lowest protection, prey density and lion use. Spatial variation in prey density is shown in Figure 1b, and spatial variation in the intensity of use by lions is shown in Figure 1c. For the study area as a whole, lion density was 8.8–11.7 individuals/100 km^2 (Rosenblatt et al., 2014). Spotted hyenas are present but had relatively low rates of interaction with wild dogs. Their density has not been formally estimated, but the spatial distribution of 1157 sightings showed that they are rarely observed in LL and more often observed in MG and NS. Leopards rarely interact with African wild dogs, but their density in the study area ranged from 4.2 to 10.2 individuals/100 km^2, and (as with lions) was highest in MG, intermediate in NS and lowest in LL (Rosenblatt et al., 2016). Cheetahs have long been absent from the ecosystem.

2.2 | Field monitoring

We monitored all resident wild dog packs within the study area by radiocollaring 1–2 adults in each pack, using a combination of VHF and satellite-GPS collars (MOD-335-3 and TGW-4277-4, Telonics, Mesa, Arizona) to allow frequent direct observation. We radiocollared wild dogs after intramuscular injection of ~1.2 mg medetomidine and ~20 mg tiletamine–zolazepam, reversing the medetomidine by intramuscular injection of atipamezole after 45 min to 1 h. Anaesthetics were injected by darting with an air-powered DanInject rifle, and all procedures were performed by an experienced and Zambian-registered veterinarian, in collaboration with the Zambia Department of National Parks and Wildlife (MSU IACUC 2020-123). We confirmed that radiocollaring did not detectably affect survival rates using a Bayesian Cormack–Jolly–Seber model that controlled for individual variation in the probability of detection. As in prior studies (Creel et al., 1997), the annual survival rate of radiocollared adults (0.75, 95% credible interval 0.62–0.85) tended to be higher than the survival of uncollared adults (0.66, 95% credible interval 0.61–0.70), probably because we avoided injured and very old individuals when collaring.

Wild dog packs are highly cohesive, so that locating a collared individual allows good monitoring of its packmates, and individuals are easily identified by variation in their coats using a photographic database of digital ID cards. For this analysis, we recorded 9685 sightings of 463 individually identified wild dogs in 40 breeding packs or single-sex groups from 2014 to 2020. Sex was determined by observation of external genitalia for all age classes. Age was known for most individuals, and when it was not known, we assigned one of three age classes (pup, yearling and adult) on the basis of body size. For adult wild dogs, survival in several well-studied populations is relatively constant across ages (Creel et al., 2004).

2.3 | Integrated population model

To test for differences in local population growth rates, we fit a Bayesian integrated population model of the demography and dynamics of wild dogs in these four regions. The IPM used Leslie projection to link a Cormack–Jolly–Seber model of area-specific rates of survival, a zero-inflated Poisson model of area-specific fecundity and a state-space model of variation in population size that used estimates from a closed capture–mark–recapture model as the counts from which the latent population size was estimated (Schaub & Kery, 2022). Figure 2 shows the model's structure as a directed acyclic graph, and Supplement S2 shows the JAGS code. The model was fit in R and JAGS using the jagsUI package (Kellner, 2021) with three MCMC chains of 4000 steps, a burn-in of 1000 steps and an adaptive phase of 300 steps.

Area-specific estimates of survival rates came from a Cormack–Jolly–Seber model (Kery & Schaub, 2011; Royle, 2008) fit to capture histories with nine monthly time bins (April–December) in each year, for a total of 63 occasions. The area an individual lived in was tracked through time, and individuals who dispersed between areas were re-assigned. For dispersers whose area was unknown for a period of floating (i.e. after known emigration), we assigned the area in which they were next detected to the floating period. We excluded January–March because the peak of the wet season caused rates of detection to be low. We modelled area-specific annual apparent survival rates (φ) for all age classes combined and modelled variation in detection probability (p) with an individual random effect that was normally distributed on the logit scale, using uninformative flat priors with bounds suggested by Schaub and Kery (2022). Allowing for variation in detection at the individual level captures any variation between regions, packs or age–sex classes and DIC scores were worse for alternative detection models. Our data were not sufficient to yield precise estimates of φ for multiple age classes in each area, so (separately from the IPM), we examined the population age structure for each area to rule out the possibility that differences in survival between areas could be due to differences in age structure (i.e. to rule out that there were more pups with relatively poor survival rates in areas with lower annual survival).

Area-specific estimates of fecundity came from a zero-inflated Poisson GLM fit to data on the number of offspring raised to 1 year of age. Because most adult wild dogs are social subordinates who do not breed (Creel et al., 1997), the distribution of fecundity is bimodal, with one mode at zero (Figure S2). To account for this pattern, the GLM combined a Bernoulli distribution of zero inflation and a Poisson model, with uninformative wide priors for both parameters using bounds suggested by Schaub and Kery (2022).

We used Leslie projection to estimate the local population growth rate for each area by determining the number of yearlings and adults expected in each area in each year in the absence of immigration or emigration (i.e. 'growth-in-place'). We used uninformative flat priors for the number of individuals of each age in each area, using guidance for bounds from Schaub and Kery (2022). The joint likelihood of the IPM forced these estimates to align with

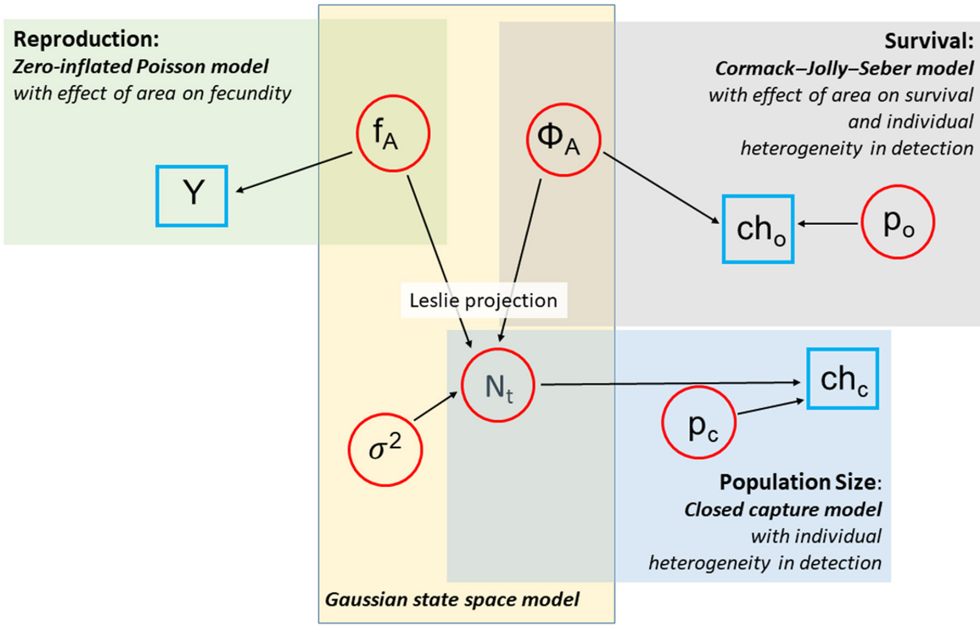

FIGURE 2 The integrated population model's structure is shown as a directed acyclic graph. The four component models are identified by shaded boxes. Data are identified by blue squares, and estimated parameters are identified by red circles. *Data*: Y = yearlings produced/adult/year, ch_O = capture history for multi-year CJS model, ch_c = capture histories for closed capture model fit separately for each year. *Parameters*: p_o = detection probability for CJS model, p_c = detection probability for closed capture model, f_A = area-specific annual fecundity, φ_A = area-specific annual apparent survival, $N_{A,t}$ = area-specific population size, summed to obtain total population size, σ_t^2 = Gaussian sampling error in total population size. All parameters were estimated from a single joint likelihood using Bayesian methods.

independent estimates of total population size across the four areas. These estimates of total population size came from a state-space model that used point estimates of population size from a closed capture–mark–recapture model as the counts. This closed capture–mark–recapture model estimated total population size in each year using the same nine monthly time bins as the CJS model of survival, and (like the CJS model) used a logit-normal individual random effect to account for variation in the probability of detection (p). Because the exact area under study varied from year to year as packs formed and failed, we obtained annual estimates of population size for a constant area by multiplying the estimated population density for each year from 2014 to 2020 by the mean area for which population size was estimated (which was 3357 km^2). Treating these estimates as counts that were subject to error, we then fit a state-space model of population size with normally distributed sampling variance using an uninformative flat prior with bounds suggested by Schaub and Kery (2022). This approach allowed for the possibility that population density could be overestimated or underestimated due to an imperfect estimation of the probability of detection in the closed capture–mark–recapture model or an imperfect estimation of the area that was used by the population.

We used the IPM to test for differences among areas in annual survival, fecundity and population growth by comparing credible intervals from posterior probability distributions. These values of λ are measures of the growth rate that would be expected in each region in the absence of immigration or emigration that is growth based only on local rates of birth and death. We estimated apparent survival (φ) for each region using a Cormack–Jolly–Seber model, which cannot distinguish death from permanent emigration out of the study population. Individuals who dispersed from one region to another were recorded as surviving (and re-assigned to their new region in subsequent time periods), but individuals who left the study area entirely would cause φ to underestimate true survival. Because wild dogs disperse most frequently from packs that are large as a consequence of good survival and reproduction (Behr et al., 2020; Creel & Creel, 2002), we expected emigration rates to be higher in regions with high local survival and reproduction. If this expectation is correct, permanent emigration would cause differences between regions in local growth rates to be underestimated by our modelling approach; this approach would not create false differences between regions. To confirm that there was net emigration from areas with high local growth and net immigration into areas with low local growth, we determined rates of dispersal between regions.

Goodness-of-fit tests are not well established for IPMs, particularly those that incorporate a state-space model of population dynamics (Schaub & Kery, 2022). Therefore, we confirmed the model's fit in several ways. First, we confirmed that the trace plots were well mixed for all parameters. Second, we confirmed that $\hat{R}$ values were near one (≤1.02) for all parameters. Third, we used diagnostic plots to confirm that the variation in the probability of detection in the survival model was well described by an individual random effect that was normally distributed on the logit scale (Figure S1 in supplement S1). Fourth, we used posterior predictive checks to confirm that the observed distribution of fecundity closely matched the simulated distribution from the fecundity model for each of the four regions (Figure S2 in supplement S1). Finally, we confirmed that estimates from the IPM for survival and fecundity were similar to results from the same models run in isolation (Schaub & Kery, 2022).

3 | RESULTS

The IPM showed that the LVE wild dog population as a whole was stable with a slight tendency for growth over the 7-year interval (Figure 3). Rates of survival (Figure 4a), fecundity (Figure 4b) and population growth (Figure 4c) were all highest in the area where prey density was highest (*NS*), lowest in the area (*LL*) where snaring is most common and prey density was lowest (Rosenblatt et al., 2019; Watson et al., 2013, 2015) and intermediate in the areas with intermediate prey density (*ML* and *MG*).

The 90% credible intervals for annual survival (φ) did not overlap for LL (median = 0.54, CI: 0.48–0.62) and NS (median = 0.69, CI: 0.64–0.73), and were intermediate in the areas with intermediate prey density (*MG* and *ML*) (*MG* median = 0.63, CI: 0.58–0.67; ML median = 0.64, CI: 0.58–0.71). These differences between areas in survival rates cannot be explained by differences in age structure, because pups (which have lower survival than yearlings or adults (Creel & Creel, 2002; Goodheart et al., 2021)) were a large component (14.2% pups, 16.8% yearlings and 69.0% adults) of packs in *NS*, where survival was best, and a small component (6.6% pups, 9.6% yearlings and 83.8% adults) of packs in *LL*, where survival was worst.

As expected from the differences in age structure just described, differences among areas in mean fecundity (Figure 4b) followed the same pattern as differences in survival. Annual fecundity (in units of yearlings raised) was lowest in *LL* (median = 0.55, CI: 0.34–0.81) and highest in *NS* (median = 1.28, CI: 1.03–1.56). Fecundity was intermediate in *MG* (median = 0.93, CI: 0.75–1.14) and *ML* (median = 1.23, CI: 0.80–1.79). The 90% credible intervals for fecundity in the areas of lowest (*LL*) and highest (*NS*) prey density were non-overlapping, and median fecundity in *LL* was only 43% of median fecundity in *NS*.

As expected given the parallel patterns just described for survival and fecundity, the local annual population growth rate (λ) (Figure 4c) was lowest in *LL* (median = 0.88, CI: 0.67–1.07), highest in *NS* (median = 1.34, CI: 1.04–1.59) and intermediate in *MG* (median = 1.13, CI: 0.84–1.36) and *ML* (median = 1.26, CI: 0.95–1.57). In the *NS* area with high prey density, the local population was expected to grow in 96% of years, and in the *LL* area with low prey density, the population was expected to decline in 87% of years. The MG and ML areas were expected to grow in 89% and 93% of years, respectively.

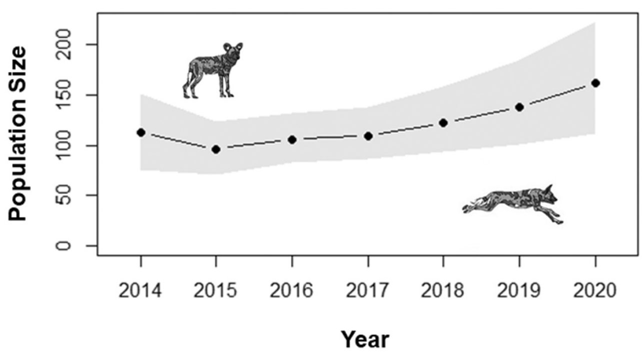

FIGURE 3 The Luangwa Valley Ecosystem wild dog population was stable or growing from 2014 to 2020, based on estimates of population size from the integrated population model. Points show the median population size from the posterior probability distribution, and shading shows the 80% credible interval from the posterior probability distribution.

Observed dispersal between areas confirmed that net migration was from areas with high local growth to areas with low local growth. For the NS area (where local growth was strongly positive), there were 33 emigrants and 7 immigrants, or 4.71 emigrants per immigrant. For the MG area (where estimated local growth tended to be positive), there were 25 emigrants and 17 immigrants, or 1.47 emigrants per immigrant. For the LL area (where local growth was negative), there were 9 emigrants and 14 immigrants, or 0.64 emigrants per immigrant. This pattern of net migration did not hold for the ML area, with 10 emigrants and 39 immigrants (0.26 emigrants per immigrant), even though local growth tended to be positive. For the ML area, this pattern was strongly affected by the movement of several large dispersing groups.

4 | DISCUSSION

Many field studies of African wild dogs and other competitively subordinate species like the cheetah (*Acinonyx jubatus*) have shown that their distributions and abundance are limited by competition with dominant competitors (Broekhuis et al., 2013; Creel & Creel, 1996; Davies et al., 2021; Dröge et al., 2017; Durant, 2000; Gorman et al., 1998; Mills & Gorman, 1997; Speakman et al., 2015; Swanson et al., 2014). Because the densities of dominant competitors like the lion and spotted hyena are strongly correlated with prey density (Hatton et al., 2015) and wild dogs benefit from competitive release when lion and hyena density is low, there has been relatively little concern or direct research about the consequences of prey depletion for African wild dogs (Creel, 2001; Woodroffe & Sillero-Zubiri, 2020). However, ecological conditions are changing rapidly in sub-Saharan Africa, and large herbivore populations have declined substantially across most of the wild dog's range (Bolger et al., 2008; Goheen et al., 2018; Ripple et al., 2015, 2016; Rogan et al., 2017; Western et al., 2009). Recent meta-analysis shows that there is a tipping point in the effect of prey density on wild dog density, below which wild dog density decreases as prey density decreases (Creel et al., 2023). Recent field research suggests that the effects of excessive illegal poaching in general, and snaring in particular, are now reducing prey density below this tipping point in some ecosystems. For example, the Greater Kafue Ecosystem was long thought to hold Zambia's largest wild dog population because it is a huge protected area (KAZA-TFCA-Secretariat, 2014) comprised largely of miombo woodland, in which wild dog density can be very high (Creel & Creel, 2002). Due to intense poaching pressure, large herbivore density is much lower in the GKE than would be expected, and the densities of wild dogs' primary prey in the GKE

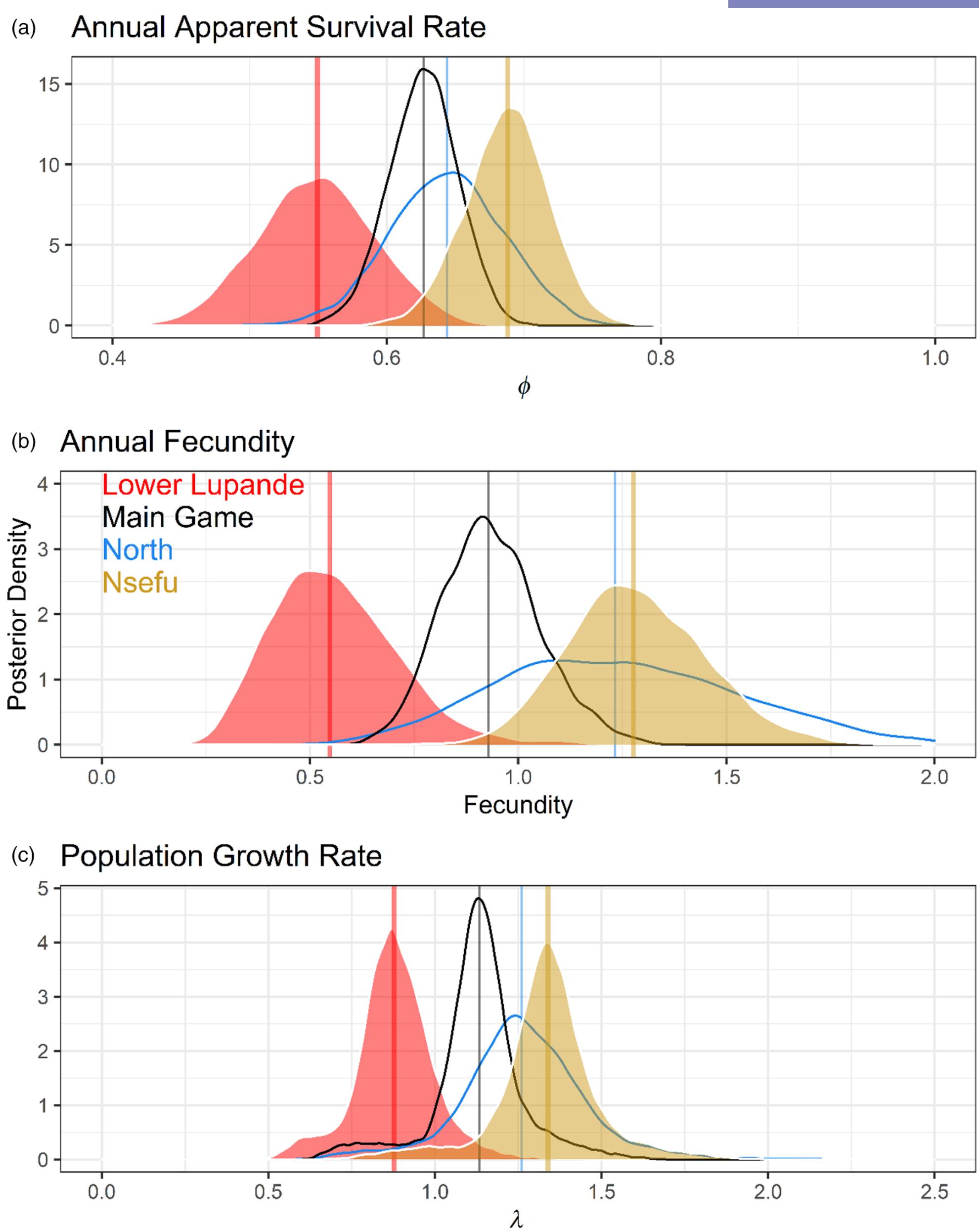

FIGURE 4 Posterior probability distributions showing differences among the four areas in demography and dynamics: (a) annual apparent survival, (b) annual mean fecundity and (c) the local population growth rate (λ). Regions are denoted by colours that are consistent with Figure 1, with vertical lines showing the median for each region. Fill is used to show the difference between the regions with the highest (*NS*) and lowest (*LL*) prey density.

are now 6-fold to 20-fold lower than those reported for miombo woodland ecosystems with similar rainfall in other studies (Schuette et al., 2018; Vinks et al., 2020). As expected given the depletion of prey in GKE, lion and hyena densities are also low (Creel et al., 2018; Vinks et al., 2021), but this does not allow wild dogs to attain a high density (Goodheart et al., 2021). Capture–mark–recapture models fit to long-term monitoring data reveal a very low density of only 0.8 wild dogs/100 km^2 (Goodheart et al., 2021). Given the well-described decline of large herbivore populations across sub-Saharan Africa (Bolger et al., 2008; Goheen et al., 2018; Lindsey et al., 2013; Western et al., 2009), it is reasonable to hypothesize that wild dogs are becoming prey-limited in other ecosystems (Creel et al., 2023).

We found that survival, reproduction and population growth were all related to prey density in the LVE. Differences between areas in survival rates could also potentially be driven by direct snaring of wild dogs (rather than by prey depletion), but prior research suggests this is not the case (Creel et al., 2023). The observed annual mortality due to snaring was too low ($\overline{X}$ = 1.10%, 95% binomial CI = 0.67%–1.87%) to drive the differences between areas that we observed. Direct mortality due to snaring was also very similar in the LVE and the Greater Kafue Ecosystem ($\overline{X}$ = 1.01%, 95% binomial CI = 0.49%–2.07%), where wild dog density is much lower (Creel et al., 2023). Finally, direct mortality due to snaring cannot explain differences between areas in fecundity, which were mainly due to differences in litter size at first count. The energetic costs of gestation are exceptionally high for wild dogs (Creel & Creel, 2002), and their cursorial hunting is energetically costly (Creel & Creel, 1995; Gorman et al., 1998; Speakman et al., 2015), lending support to the inference that prey depletion is likely to affect reproduction. Studies in other ecosystems testing the relationship of wild dog demography and dynamics to changes in prey density are needed to test the generality of these inferences.

To our knowledge, this study provides the first comparison of a large carnivore's demography and dynamics in several ecologically similar areas that differ in the intensity of snaring (Watson et al., 2013) and the density of prey and competitors (Rosenblatt et al., 2019). A Bayesian IPM is well suited to this analysis, because it allows data on reproduction, survival and population size to be integrated into one joint likelihood, and can reveal cryptic source-sink dynamics by testing whether area-specific population growth rates (λ) fall above or below one. In particular, the structure of this IPM allowed us to test for differences between regions in 'growth in place' (i.e. the growth expected from local rates of birth and death without migration), while aligning the estimated effects with estimated changes in total population size. By estimating population size as a latent variable in a state-space model, the IPM's structure also considered sampling variance in population estimates more completely than is typical for large carnivores. Like all models, the IPM is not a perfect description of the demography and dynamics of this population, but the coherent pattern of results increases our confidence that the inferences are correct.

The IPM revealed parallel differences in fecundity, survival and population growth, all suggesting strong effects of prey depletion on wild dog dynamics in some parts of the LVE. Differences in estimated population growth rates in the best (*NS*) and worst (*LL*) areas show that, while the less-protected portions of the LVE hold an appreciable number of wild dogs, they are nonetheless a population sink. Patterns of net migration between areas were consistent with the source-sink dynamics revealed by the IPM, with strong net migration out of the area with the highest prey density and local population growth. The observation that survival and fecundity change in parallel shows that differences between areas in population growth are not solely due to direct mortality (Creel et al., 2023). Observed direct mortality due to snaring was low (partly because we removed snares when they were detected); we observed no deaths due to disease and only two deaths due to vehicles. These observations leave prey depletion as the most plausible explanation for the observed patterns. It is notable that local source-sink dynamics existed even though the population as a whole was stable or growing, and even though the density of wild dogs on the LVE site is one of the highest on record (Creel et al., 2023). Even under these highly favourable circumstances, local prey depletion was associated with local population decline.

5 | CONCLUSIONS

Under the ecological conditions of the past, the benefits of low competitor density protected African wild dog populations from the costs of low prey density. After a prolonged and pronounced decline of large herbivore populations over most of the wild dog's range, some populations are being pushed below a tipping point at which the costs of prey depletion exceed the benefits of competitive release. Long-term data from the Luangwa Valley ecosystem show that the fecundity, survival and population growth of wild dogs are all lower in areas where prey density has been reduced by bushmeat hunting than in adjacent, ecologically similar areas where prey density remains high. Wild dog density is low in prey-depleted areas, even though these areas are less used by dominant competitors. Threatened and endangered species in many large carnivore guilds are limited by interspecific competition and intraguild predation (Creel et al., 2001; Johnson et al., 1996; Palomares & Caro, 1999; Polis et al., 1989; Ritchie & Johnson, 2009), and anthropogenic depletion of large herbivore prey is widespread (Estes et al., 2011; Fa & Brown, 2009; Ripple et al., 2015, 2016; Rogan et al., 2017; Vinks et al., 2020; Western et al., 2009). Consequently, it is reasonable to hypothesize that fundamental changes in the relationship between subordinate competitor densities and prey (or other limiting resources) might now be common; testing the generality of this pattern should be a priority for the conservation of subordinate competitors. It seems likely that patterns will differ considerably between regions where apex carnivores have decreased in recent decades (as in most of Africa and Asia: Ripple et al., 2015) and regions where apex carnivores have increased in recent decades (as in parts of Europe and North America: Chapron et al., 2014). We hypothesize that the mechanisms limiting competitive subordinates are likely to shift to bottom-up control by prey availability in the former scenario but are likely to remain top-down control by dominant competitor density in the latter scenario.

AUTHOR CONTRIBUTIONS

Scott Creel and Matthew S. Becker conceived the ideas and designed the methodology; Matthew S. Becker, Thandiwe Mweetwa, Henry Mwape, Johnathan Reyes de Merkle and Ben Goodheart collected the data; Johnathan Reyes de Merkle processed the data; Scott Creel, Ben Goodheart and Johnathan Reyes de Merkle analysed the data; and Scott Creel led the writing of the manuscript. Twakundine Simpamba provided research integration with the Zambia Department of National Parks and Wildlife. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

This research was supported by the National Science Foundation (IOS-1145749, DEB-2032131 and DEB-2221826); National Geographic Society Big Cats Initiative and Predator Research Grant; Dazzle Africa, World Wildlife Fund—Netherlands & Zambia; The Bennink Foundation, Mfuwe Lodge/Bushcamp Company, Tusk Trust, Painted Dog Conservation Inc., Gemfields Inc., Rob and Kayte Simpson, Prabha Sarangi and Connor Clairmont, Milkywire, Flatdogs Camp, Robin Pope Safaris, Mulberry Mongoose, Green Safaris, Puku Ridge, Sungani, Africa Hope Fund, Companies 4 Conservation, Remembering Wild Dogs, Vulcan, Johann van Zyl, African Bushcamps, Vreugdenhill Bulbs & Plants, ZoosSA, Explorers Against Extinction, Tribal Textiles, Wild in Africa, African Wild Dog Survival Fund and IUCN Save Our Species/European Union. This publication was produced with the financial support of the European Union through IUCN Save Our Species. Its contents are the sole responsibility of the authors and the Zambian Carnivore Programme and do not necessarily reflect the views of the IUCN or the European Union.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.tdz08kq61 (Creel et al., 2024).

ORCID

Scott Creel https://orcid.org/0000-0003-3170-6113

REFERENCES

Arnold, T. W., Clark, R. G., Koons, D. N., & Schaub, M. (2018). Integrated population models facilitate ecological understanding and improved management decisions. *The Journal of Wildlife Management*, *82*, 266–274.

Behr, D. M., Mcnutt, J. W., Ozgul, A., & Cozzi, G. (2020). When to stay and when to leave? Proximate causes of dispersal in an endangered social carnivore. *Journal of Animal Ecology*, *89*(10), 2356–2366.

Bhandari, A., Ghaskadbi, P., Nigam, P., & Habib, B. (2021). Dhole pack size variation: Assessing the effect of prey availability and apex predators. *Ecology and Evolution*, *11*, 4774–4785.

Bolger, D. T., Newmark, W. D., Morrison, T. A., & Doak, D. F. (2008). The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, *11*, 63–77.

Broekhuis, F., Cozzi, G., Valeix, M., Mcnutt, J. W., & Macdonald, D. W. (2013). Risk avoidance in sympatric large carnivores: Reactive or predictive? *Journal of Animal Ecology*, *82*, 1098–1105.

Chapron, G., Kaczensky, P., Linnell, J. D. C., Von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J. C., Breitenmoser, U., Bröseth, H., Bufka, L., Bunikyte, R., … Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, *346*, 1517–1519.

Creel, S. (2001). Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology*, *15*, 271–274.

Creel, S., Becker, M., Reyes De Merkle, J., & Goodheart, B. (2023). Hot or hungry? A tipping point in the effect of prey depletion on African wild dogs. *Biological Conservation*, *282*, 110043.

Creel, S., & Creel, N. M. (1995). Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, *50*(5), 1325–1339.

Creel, S., & Creel, N. M. (1996). Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, *10*, 526–538.

Creel, S., & Creel, N. M. (2002). *The African wild dog: Behavior, ecology and conservation*. Princeton.

Creel, S., Creel, N. M., & Monfort, S. L. (1997). Radiocollaring and stress hormones in African wild dogs. *Conservation Biology*, *11*, 544–548.

Creel, S., Matandiko, W., Schuette, P., Rosenblatt, E., Sanguinetti, C., Banda, K., Vinks, M., & Becker, M. S. (2018). Changes in Zambian large carnivore diets over the past half century reveal the loss of large prey. *Journal of Applied Ecology*, *55*, 2908–2916.

Creel, S., Merkle, J., Goodheart, B., Mweetwa, T., Mwape, H., Simpamba, T., & Becker, M. (2024). Data from: An integrated population model reveals source-sink dynamics for competitively subordinate African wild dogs linked to anthropogenic prey depletion [dataset]. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.tdz08kq61

Creel, S., Mills, M. G. L., & McNutt, J. W. (2004). Demography and population dynamics of African wild dogs in three critical populations. In D. W. MacDonald & C. Sillero-Zubiri (Eds.), *Biology and conservation of wild canids* (pp. 337–350). Oxford University Press.

Creel, S., M'soka, J., Droge, E., Rosenblatt, E., Becker, M., Matandiko, W., & Simpamba, T. (2016). Assessing the sustainability of African lion trophy hunting, with recommendations for policy. *Ecological Applications*, *6*, 2347–2357.

Creel, S., Spong, G., & Creel, N. M. (2001). Interspecific competition and the population biology of extinction-prone carnivores. In J. L. Gittleman, S. Funk, D. W. Macdonald, & R. Wayne (Eds.), *Carnivore conservation* (pp. 36–60). Cambridge University Press.

Davies, A. B., Tambling, C. J., Marneweck, D. G., Ranc, N., Druce, D. J., Cromsigt, J. P. G. M., Le Roux, E., & Asner, G. P. (2021). Spatial heterogeneity facilitates carnivore coexistence. *Ecology*, *102*, e03319.

Dröge, E., Creel, S., Becker, M. S., & M'soka, J. (2017). Spatial and temporal avoidance of risk within a large carnivore guild. *Ecology and Evolution*, *7*, 189–199.

Durant, S. M. (2000). Living with the enemy: Avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, *11*, 624–632.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. R., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoerner, T. W., … Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, *333*, 301–306.

Fa, J. E., & Brown, D. (2009). Impacts of hunting on mammals in African tropical moist forests: A review and synthesis. *Mammal Review*, *39*, 231–264.

Goheen, J. R., Augustine, D. J., Veblen, K. E., Kimuyu, D. M., Palmer, T. M., Porensky, L. M., Pringle, R. M., Ratnam, J., Riginos, C., Sankaran, M., Ford, A. T., Hassan, A. A., Jakopak, R., Kartzinel, T. R., Kurukura, S., Louthan, A. M., Odadi, W. O., Otieno, T. O., Wambua, A. M., … Young, T. P. (2018). Conservation lessons from large-mammal manipulations in east African savannas: The Klee, Uhuru, and GLADE experiments. *Annals of the New York Academy of Sciences*, *1429*, 31–49.

Goodheart, B., Creel, S., Becker, M. S., Vinks, M., Schuette, P., Banda, K., Sanguinetti, C., Rosenblatt, E., Dart, C., & Kusler, A. (2021). Low apex carnivore density does not release a subordinate competitor when driven by prey depletion. *Biological Conservation*, *261*, 109273.

Goodheart, B., Creel, S., Vinks, M. A., Banda, K., Reyes De Merkle, J., Kusler, A., Dart, C., Banda, K., Becker, M. S., Indala, P., & Simukonda, C. (2022). African wild dog movements show contrasting responses to long and short term risk of encountering lions: Analysis using dynamic Brownian bridge movement models. *Movement Ecology*, *10*, 1–14.

Gorman, M. L., Mills, M. G., Raath, J. P., & Speakman, J. R. (1998). High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature*, *391*, 479–481.

Groom, R. J., Lannas, K., & Jackson, C. R. (2017). The impact of lions on the demography and ecology of endangered African wild dogs. *Animal Conservation*, *20*, 382–390.

Hatton, I. A., Mccann, K. S., Fryxell, J. M., Davies, T. J., Smerlak, M., Sinclair, A. R. E., & Loreau, M. (2015). The predator–prey power law: Biomass scaling across terrestrial and aquatic biomes. *Science*, *349*, aac6284.

Johnson, W. E., Fuller, T. K., & Franklin, W. L. (1996). Sympary in canids: A review and assessment. In J. L. Gittleman (Ed.), *Carnivore behavior, ecology and evolution* (Vol. *2*, pp. 189–218). Cornell University Press.

KAZA-TFCA-Secretariat. (2014). *Conservation strategy and action plan for the African wild dog (Lycaon pictus) in the Kavango—Zambezi transfrontier conservation area*. KAZA Secretariat.

Kellner, K. (2021). *jagsUI: A wrapper around 'rjags' to streamline 'JAGS' analyses* (1.5.2 ed.). CRAN.

Kery, M., & Schaub, M. (2011). *Bayesian population analysis using WinBUGS: A hierarchical perspective*. Academic Press.

Lindsey, P. A., Balme, G., Becker, M., Begg, C., Bento, C., Bocchino, C., Dickman, A., Diggle, R. W., Eves, H., & Henschel, P. (2013). The bushmeat trade in African savannas: Impacts, drivers, and possible solutions. *Biological Conservation*, *160*, 80–96.

Mills, M. G., & Gorman, M. L. (1997). Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology*, *11*, 1397–1406.

Morrison, T. A., & Bolger, D. T. (2014). Connectivity and bottlenecks in a migratory wildebeest Connochaetes taurinus population. *Oryx*, *48*, 613–621.

Mweetwa, T., Christianson, D., Becker, M., Creel, S., Rosenblatt, E., Merkle, J., Droge, E., Mwape, H., M'soka, J., Simpamba, T., & Masonde, J. (2018). Quantifying demographic recovery in lions during a three-year moratorium on trophy hunting. *PLoS ONE*, *13*(5), e0197030.

Orsdol, K. G. V., Hanby, J. P., & Bygott, J. D. (1985). Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology*, *206*, 97–112.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., & Sinclair, A. R. (2005). Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science*, *307*, 390–393.

Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *The American Naturalist*, *153*, 492–508.

Polis, G. A., Myers, C. A., & Holt, R. D. (1989). The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annual Review of Ecology and Systematics*, *20*, 297–330.

Ripple, W. J., Abernethy, K., Betts, M. G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P. A., Macdonald, D. W., & Machovina, B. (2016). Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science*, *3*, 160498.

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W., Kerley, G. I., Levi, T., & Lindsey, P. A. (2015). Collapse of the world's largest herbivores. *Science Advances*, *1*, e1400103.

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, *12*, 982–998.

Rogan, M., Lindsey, P. A., Tambling, C., Golabek, K., Chase, M., Collins, K., & Mcnutt, J. (2017). Illegal bushmeat hunters compete with predators and threaten wild herbivore populations in a global tourism hotspot. *Biological Conservation*, *210*, 233–242.

Rosenblatt, E., Becker, M. S., Creel, S., Droge, E., Mweetwa, T., Schuette, P. A., Watson, F., Merkle, J., & Mwape, H. (2014). Detecting declines of apex carnivores and evaluating their causes: An example with Zambian lions. *Biological Conservation*, *180*, 176–186.

Rosenblatt, E., Creel, S., Becker, M. S., Merkle, J., Mwape, H., Schuette, P., & Simpamba, T. (2016). Effects of a protection gradient on carnivore density and survival: An example with leopards in the Luangwa valley, Zambia. *Ecology and Evolution*, *6*, 3772–3785.

Rosenblatt, E., Creel, S., Schuette, P., Becker, M. S., Christianson, D., Dröge, E., Mweetwa, T., Mwape, H., Merkle, J., M'soka, J., Masonde, J., & Simpamba, T. (2019). Do protection gradients explain patterns in herbivore densities? An example with ungulates in Zambia's Luangwa Valley. *PLoS ONE*, *14*, e0224438.

Royle, J. A. (2008). Modeling individual effects in the Cormack–jolly–Seber model: A state–space formulation. *Biometrics*, *64*, 364–370.

Schaub, M., & Abadi, F. (2011). Integrated population models: A novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology*, *152*, 227–237.

Schaub, M., Giminez, O., Sierro, A., & Arlettaz, R. (2007). Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. *Conservation Biology*, *21*, 945–955.

Schaub, M., & Kery, M. (2022). *Integrated population models: Theory and ecological applications with R and JAGS*. Academic Press, Elsevier.

Schuette, P., Namukonde, M., Becker, M., Watson, F., Creel, S., Chifunte, C., Matandiko, W., Millhouse, P., Rosenblatt, E., & Sanguinetti, C. (2018). Boots on the ground: In defense of low-tech, inexpensive, and robust survey methods for Africa's under-funded protected areas. *Biological Conservation*, *27*, 2173–2191.

Sivy, K. J., Pozzanghera, C. B., Colson, K. E., Mumma, M. A., & Prugh, L. R. (2018). Apex predators and the facilitation of resource partitioning among mesopredators. *Oikos*, *127*, 607–621.

Speakman, J. R., Gorman, M. L., Mills, M. G., & Raath, J. P. (2015). Wild dogs and kleptoparasitism: Some misunderstandings. *African Journal of Ecology*, *54*, 125–127.

Swanson, A., Caro, T., Davies-Mostert, H., Mills, M. G., Macdonald, D. W., Borner, M., Masenga, E., & Packer, C. (2014). Cheetahs and wild dogs show contrasting patterns of suppression by lions. *Journal of Animal Ecology*, *83*, 1418–1427.

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., Possingham, H. P., Laurance, W. F., Wood, P., Fekete, B. Í. M., Levy, M. A., & Watson, J. E. M. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, *7*, 12558.

Vinks, M. A., Creel, S., Schuette, P., Becker, M. S., Rosenblatt, E., Sanguinetti, C., Banda, K., Goodheart, B., Young-Overton, K., & Stevens, X. (2021). Response of lion demography and dynamics to the loss of preferred larger prey. *Ecological Applications*, *31*, e02298.

Vinks, M. A., Creel, S., Schuette, P., Rosenblatt, E., Matandiko, W., Sanguinetti, C., Banda, K., Goodheart, B., Becker, M., & Chifunte, C. (2020). Testing the effects of anthropogenic pressures on a diverse African herbivore community. *Ecosphere*, *11*, e03067.

Watson, F., Becker, M. S., Mcrobb, R., & Kanyembo, B. (2013). Spatial patterns of wire-snare poaching: Implications for community conservation in buffer zones around National Parks. *Biological Conservation*, *168*, 1–9.

Watson, F. G., Becker, M. S., Milanzi, J., & Nyirenda, M. (2015). Human encroachment into protected area networks in Zambia: Implications for large carnivore conservation. *Regional Environmental Change*, *15*, 415–429.

Weegman, M. D., Bearhop, S., Fox, A. D., Hilton, G. M., Walsh, A. J., Mcdonald, J. L., & Hodgson, D. J. (2016). Integrated population modelling reveals a perceived source to be a cryptic sink. *Journal of Animal Ecology*, *85*, 467–475.

Western, D., Russell, S., & Cuthill, I. (2009). The status of wildlife in protected areas compared to non-protected areas of Kenya. *PLoS ONE*, *4*, e6140.

Wolf, C., & Ripple, W. J. (2016). Prey depletion as a threat to the world's large carnivores. *Royal Society Open Science*, *3*, 160252.

Woodroffe, R., & Sillero-Zubiri, C. (2020). *Lycaon pictus* (amended version of 2012 assessment). *The IUCN Red List of Threatened Species* 2020: e.T12436A166502262.

Zipkin, E. F., & Saunders, S. P. (2018). Synthesizing multiple data types for biological conservation using integrated population models. *Biological Conservation*, *217*, 240–250.

Journal of Animal Ecology BRITISH ECOLOGICAL SOCIETY

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supplement S1: Goodness-of-fit diagnostic plots for the fecundity sub-model and the detection sub-model for estimates of survival.

Supplement S2: JAGS code for integrated population model.

How to cite this article: Creel, S., Reyes de Merkle, J., Goodheart, B., Mweetwa, T., Mwape, H., Simpamba, T., & Becker, M. S. (2024). An integrated population model reveals source-sink dynamics for competitively subordinate African wild dogs linked to anthropogenic prey depletion. *Journal of Animal Ecology*, *93*, 417–427. https://doi.org/10.1111/1365-2656.14052