Biological Conservation 282 (2023) 110043

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Perspective

Hot or hungry? A tipping point in the effect of prey depletion on African wild dogs

Scott Creel[a,b,c,*], Matthew S. Becker[a,b], Johnathan Reyes de Merkle[a,b], Ben Goodheart[a,b]

[a] *Department of Ecology, Montana State University, Bozeman, MT 59717, USA*
[b] *Zambian Carnivore Programme, PO Box 80, Mfuwe, Eastern Province, Zambia*
[c] *Insitutioned för Vilt, Fisk och Miljö, Sveriges lantbruksuniversitet, Umeå, Sweden*

ARTICLE INFO

Keywords:
Carnivore
Climate change
Interspecific competition
Lycaon pictus
Population density
Prey depletion

ABSTRACT

Interspecific competition has strong effects within carnivore guilds, and African wild dogs are strongly limited by intraguild predation by lions and food loss to spotted hyenas. The densities of these dominant competitors correlate tightly with prey density, and prey depletion due to snaring is contributing to declines of apex carnivores across Africa. As a consequence of snaring, subordinate competitors like the African wild dog and cheetah are simultaneously experiencing a costly reduction in prey and a beneficial reduction of competitors. The net effect is difficult to predict. Here, we describe a previously unrecognized tipping point in the effect of prey density on wild dog density. Above this tipping point, wild dog density increases as prey density decreases, because the benefits of competitive release outweigh the costs of prey depletion. Below this tipping point, wild dog density decreases as prey density decreases, because the costs of prey depletion outweigh the benefits of competitive release. Conservation strategies for wild dogs must recognize this tipping point. As prey depletion due to snaring becomes severe, it limits wild dogs (mesocarnivores), just as it does lions and spotted hyenas (apex carnivores). Recent analyses based on time trends have argued that climate change is likely to cause wild dog populations to collapse. We suggest that prey depletion provides a mechanistically direct explanation of patterns in wild dog dynamics that have been attributed to climate change, and that the effects of prey depletion are likely to go unrecognized in the absence of data on trends in prey density.

1. Limitation of competitively dominant and subordinate large carnivores

Large carnivores are often limited by prey availability, creating a strong, positive correlation between predator and prey densities (Orsdol et al., 1985). For 23 African ecosystems ranging from very low to very high large mammal biomass, Hatton et al. (2015) found that total predator biomass (P) increased with increasing large herbivore biomass (H) following the relationship $P = 0.084H^{0.73}$. This monotonically increasing function explained 92 % of the variation in predator biomass (Hatton et al., 2015). Both lions and spotted hyenas closely mirrored this relationship for the complete large carnivore guild, increasing over two orders of magnitude as large herbivore biomass increased (lions : $P = 0.031H^{0.77}$, $R^2 = 0.77$, hyenas : $P = 0.032H^{0.74}$, $R^2 = 0.69$)) (Hatton et al., 2015). Apex carnivores on other continents (e.g. the wolf [*Canis lupus*] and tiger [*Panthera tigris*]) also followed this pattern, suggesting that most apex carnivores are strongly prey-limited (Hatton et al., 2015) and will decline in response to prey depletion.

The densities of competitively subordinate carnivores are not likely to follow the same pattern. Within carnivore guilds, evolutionary responses to reduce competition result in body size distributions that are spaced more evenly than expected by chance (Dayan et al., 1990; Dayan and Simberloff, 1994; Dayan and Simberloff, 2005). Character displacement with respect to body size leads to asymmetry in competitive relationships, with larger species usually competitively dominant to smaller ones (Palomares and Caro, 1999; Creel et al., 2001; Caro and Stoner, 2003; Karanth et al., 2017; Hunter and Caro, 2008; Creel and Creel, 2002; Mills and Gorman, 1997). These asymmetries are manifest in interference competition, which is strong because the morphological and behavioral adaptations that large carnivores use to kill mammalian prey are effective against mammalian competitors, and because the net energetic value of a fresh carcass is greater than that of the same animal when it is still alive and able to engage in antipredator defense (Gorman et al., 1998; Speakman et al., 2015; Hubel et al., 2016; Creel and Creel, 1995). Thus, interference competition remains strong even if live prey are abundant, particularly in cases where dominant competitors can steal kills with little

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* Corresponding author at: Department of Ecology, Montana State University, Bozeman, MT 59717, USA.
E-mail address: screel@montana.edu (S. Creel).

https://doi.org/10.1016/j.biocon.2023.110043
Received 7 December 2022; Received in revised form 28 March 2023; Accepted 31 March 2023

risk of injury (Palomares and Caro, 1999; Creel, 2001).

For these reasons, African wild dogs are strongly limited by interspecific competition with dominant competitors (Broekhuis et al., 2013; Cozzi et al., 2012; Dröge et al., 2017; Mills and Gorman, 1997; Creel and Creel, 1996; Creel and Creel, 2002). Studies across many years and many sites have found that wild dog density is low where lion and spotted hyena density is high (both within and between ecosystems), and that wild dog populations decline when lion and hyena populations increase (Creel and Creel, 2002; Creel and Creel, 1996; Vucetich and Creel, 1999; Mills and Gorman, 1997). Moreover, the maximum density that wild dog populations attain, even with abundant prey, is far lower than the densities that lions and spotted hyenas commonly attain (Creel and Creel, 2002), and this alone suggests that wild dogs are not limited by prey in the same manner as lions and spotted hyenas.

The limiting effect of lions on wild dogs is partly driven by an obvious direct effect. In most long-term studies of wild dogs, direct killing by lions is a common cause of death, accounting for 9 % to 50 % of deaths with a known cause (Creel et al., 2004, Woodroffe et al., 2007a, Scheepers and Venzke, 1995, Van Heerden et al., 1995, Creel and Creel, 2002 [p. 264]). Lions do not consume the wild dogs that they kill, strongly suggesting that intraguild predation is a manifestation of competition, which also typifies the interactions of lions with cheetahs (*Acinonyx jubatus*) and spotted hyenas (*Crocuta crocuta*) (Swanson et al., 2014; Durant, 2000; Periquet et al., 2015). Wild dog pups are particularly vulnerable to attacks by lions on dens or rendezvous sites where they are guarded by just one or two adults, but adults are also killed in such attacks.

Wild dogs are also affected by the costs of avoiding dominant competitors, just as prey are affected by the costs of avoiding predation. The spatial distribution of lions is only weakly affected by interspecific competition, so variation in the density of lions within ecosystems is positively related to the density of prey (Orsdol et al., 1985; Packer et al., 2005; Vinks et al., 2021), just as it is across ecosystems. Wild dogs avoid lions on both short and long time scales. At long time scales (years), the intensity of space use by wild dogs is inversely related to space use by lions (Creel and Creel, 1996; Mills and Gorman, 1997; Dröge et al., 2017; Swanson et al., 2014; Davies et al., 2021). At short time scales (minutes to hours), wild dogs respond to encounters with lions (or experimental playbacks of their roars) by moving directly away in a rapid and linear fashion (Webster et al., 2012; Creel and Creel, 2002; Goodheart et al., 2022). Both of these responses entail energetic costs. By avoiding areas that are heavily used by lions (in the long-term), wild dogs hunt in areas with low prey density, which reduces their rate of encounter with prey (Creel and Creel, 2002 [p. 247], Gallagher et al., 2017, Goodheart et al., 2022). By fleeing encounters with lions (in the short term), wild dogs must expend energy, and energetic data from other species show that such flights can be costly (Williams et al., 2020; Goodheart et al., 2022). Wild dogs' cursorial hunting behavior causes them to have a tenuously positive energy budget (Creel, 1997; Gorman et al., 1998; Speakman et al., 2015; Hubel et al., 2016; Rasmussen et al., 2008), and the energetic costs of gestation and lactation are exceptionally high for wild dogs (Creel and Creel, 1991), both increasing the likelihood that the energetic costs of avoiding dominant competitors might affect survival or reproduction.

Consistent with these effects of competitive limitation, wild dog density correlates negatively with the densities of dominant competitors (Goodheart et al., 2021; Creel and Creel, 2002). Thus, because lion and hyena densities correlate positively with prey density (Hatton et al., 2015), wild dog density should increase as prey density decreases. However, logic suggests that the benefits of competitive release must eventually be overwhelmed by the costs of resource limitation — as prey density approaches zero, wild dog density must also approach zero. This logic suggests a hypothesis that wild dog density should first increase as prey declines (unlike apex carnivores), but should decrease (in parallel with apex carnivores), once prey density drops below a tipping point (Fig. 1A & B).

2. Testing for a tipping point in the effect of prey density on wild dog density

Using the same methods and data from 23 ecosystems that Hatton et al. (2015) used to describe the positive relationship of lion and hyena densities to total large herbivore biomass, we tested the form of this relationship for wild dogs. We downloaded the raw data from https://www.science.org/doi/full/10.1126/science.aac6284, and extracted rows 123–172 of their table entitled 'African Predators vs Prey > 5 kg Biomass', which provides species-specific densities for 31 herbivore species from 23 ecosystems, some sampled in multiple time periods. Following Hatton et al. (2015), we excluded elephants from total prey biomass because they are very rarely killed by any member of the large carnivore guild. As shown in Fig. S1, we also examined two subsets of these 30 species, one restricted to species that are known to be killed by wild dogs, and one further restricted to species in the size range that is commonly killed by wild dogs (i.e., wildebeest-sized or smaller), and found that the three measures are strongly correlated. Using these data, we tested whether a breakpoint regression model predicted wild dog density better than a linear model (with and without log transformation of both axes).

Unlike their dominant competitors, the density of wild dogs decreased with increasing ungulate density at moderate and high prey densities, and increased with increasing ungulate density only at low ungulate densities (Fig. 1C). Two types of breakpoint regression models each explained 90 % of the variation in wild dog density, while a linear power law (like those of lions and spotted hyenas) explained only 34 %. As discussed previously by Hatton et al. (2015), standard diagnostic plots (quantile-quantile and residuals vs. fitted values) showed that least squares regression models fit these data well. However, the independent variable is measured with error, as in all analyses that relate predator density to prey density. To address the problem, we estimated means for eight quantiles of prey density prior to fitting linear and breakpoint regressions, taking advantage of the central limit theorem to reduce the effect of sampling error in the independent variable (which is to obscure real relationships).

The large herbivore biomass at which the slope of the relationship changed sign was estimated at 419 kg/km^2 (±97 S.E.) by a breakpoint model fit using the *segmented* package in R (Muggio, 2008), which does not allow discontinuity of the regression model at the breakpoint. We also fit a model that allowed discontinuity at the breakpoint with the form

$$lm\,(y \sim x^{*}(x < breaks[i]) + x^{*}(x \geq breaks[i])),$$

tested all possible breakpoints, and selected the model that minimized mean square error. This model identified a tipping point of 837 kg/km^2. The estimated slope at prey densities below the tipping point ($b = 0.38$, $SE_b = 0.09$, $t = 3.34$, $P = 0.021$) was much steeper than the slope above the tipping point ($b = -0.01$, $\Delta b = -0.33$, $t = -3.45$, $P = 0.018$), suggesting that population collapses due to prey depletion could be abrupt (Fig. 1C). This result seems plausible, simply because the density of wild dog populations is invariably low in comparison to other large carnivores. Even large ecosystems hold relatively small wild dog populations that can collapse quickly. To be conservative, the reported slopes are from the model that does not allow discontinuity in the fitted function. The difference in slopes was considerably larger for the breakpoint regression that allowed discontinuity (which also had $R^2 = 0.90$), but logic suggests that the function should be continuous (because the density of a real population must change in a continuous manner). Although only two points fell below the tipping point in Fig. 1C, these points include data from 12 ecosystems, and the breakpoint regression explains almost three times more variation in wild dog density than the best model with a constant slope. More fundamentally, data from many ecosystems establish the negative slope above the tipping point. This negative slope implies that a breakpoint must exist, because wild dogs

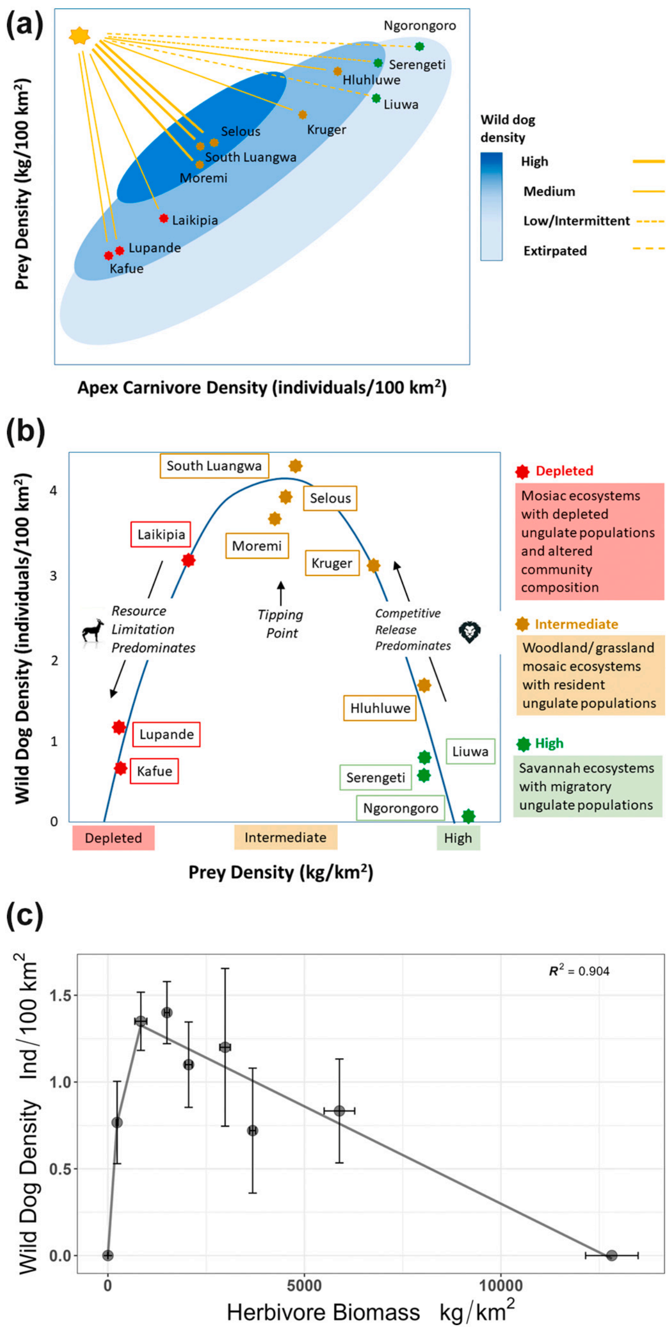

Fig. 1. (A) The population density of African wild dogs is strongly affected by interspecific competition with dominant apex carnivores (lions and spotted hyenas), which are invariably more abundant than wild dogs. In turn, the densities of lions and spotted hyenas are strongly correlated with the density of ungulate prey. In this phase-plane, the star at upper left denotes theoretically ideal conditions for wild dogs, with abundant prey and no apex carnivores: these conditions do not naturally occur. Ellipses show the range of conditions that do occur, with wild dog density increasing as conditions approach the ideal. Points show ecosystems for which wild dog, apex carnivore and ungulate densities broadly support this conceptual model of population regulation. (B) The patterns described in part A suggest a hypothesis that wild dog density should relate to prey density in a different manner than has been reported for apex carnivores (Hatton et al., 2015). At high prey densities, a decrease in prey density should lead to an increase in wild dog density due to competitive release, a pattern that has long been recognized. As prey density further decreases, the costs of prey depletion must eventually outweigh the benefits of competitive release, because wild dog density must approach zero as prey density approaches zero. (C) Published data from 23 ecosystems (data from Hatton et al., 2015) support the hypothesis that wild dog density initially increases as total large herbivore density decreases, until switching sign as total herbivore density drops below a tipping point. Points (with error bars = 1 *S.E.*) are means for eight quantiles of prey density, each including five or six point estimates from 46 observations in 23 ecosystems. We aggregated the data in this manner to reduce the effects of sampling error in the independent variable and methodological variation between studies. The maximum wild dog density in these aggregated means is (necessarily) lower than the maximum density for single populations. The line shows a breakpoint regression with R^2 (adjusted) = 0.904.

(caption on next column)

(like any carnivore) must decline to zero as prey density approaches zero (which is why models relating predator density to prey density typically omit an intercept, e.g., Hatton et al. (2015)).

We tested the relationship of wild dog density to total large herbivore density (excluding elephants), as in Hatton et al.'s (2015) analysis that found a monotonically positive relationship for lions, spotted hyenas and the complete carnivore guild (including wild dogs). In Fig. 1A and B, the predicted increase in wild dog density as prey density (for the complete carnivore guild) decreases from high values is a consequence of a decrease in the densities of dominant competitors (lions and hyenas). Thus, the entire prey set is the variable of primary interest (not just the subset of prey species taken by wild dogs). However, in this dataset there are strong, linear relationships between the densities of all large herbivores (excluding elephants), species that wild dogs are known to hunt, and species small enough to be common prey for wild dogs (Fig. S1).

In this data set, Hatton et al. (2015) partitioned data from some ecosystems into multiple time periods (e.g., Kruger N.P., Serengeti N.P. and Ngorongoro Crater C.A. were each broken into five intervals), to account for pronounced changes through time in the densities of predators and/or prey. Thus, the tipping point revealed by this analysis is consistent with data that include both spatial and temporal variation in the densities of wild dogs and their prey.

Recognition of this tipping point is critical for the conservation and management of wild dogs. In the ecological conditions of the past, the benefits of competitive release protected wild dog populations from the energetic costs of low prey density (Creel, 2001). Now, after a pronounced decline of large herbivore populations over most of the wild dog's range (Lindsey et al., 2013; Lindsey et al., 2011; Ripple et al., 2016; Ripple et al., 2015; Goheen et al., 2018), some ecosystems are being pushed below a threshold at which the costs of prey depletion exceed the benefits of competitive release. Wild dogs do not fare well in prey depleted areas, even though the density of dominant competitors is low (Goodheart et al., 2021). This pattern is illustrated by recent data from wild dogs in two Zambian ecosystems. Bushmeat hunting with snares is intense in Kafue National Park, and prey density is consequently very low (Vinks et al., 2020; Rosenblatt et al., 2019; Watson et al., 2013; Watson et al., 2015). The Nsefu Sector and Main Game areas of South Luangwa National Park are better protected, so that snaring is less common and prey density is higher (Becker et al., 2013a; Becker et al., 2013b; Watson et al., 2013; Rosenblatt et al., 2019). Capture-mark-recapture models fit to data from wild dogs in these parks show that their density in prey-depleted areas is among the lowest on record: Kafue holds 0.8 adults & yearlings/100 km^2, comparable to ecosystems where wild dogs have experienced local extirpation (Goodheart et al., 2021). Their density in areas with more abundant prey (Rosenblatt et al., 2019) is among the highest on record: South Luangwa now holds 2.8–4.0 adults & yearlings/100 km^2. While it has long been recognized that wild dog density is low in ecosystems with high densities of prey that support high densities of lions and spotted hyenas, our results strongly suggest that prey depletion is now limiting some wild dog populations to similarly low densities, despite the low density of dominant competitors in these ecosystems.

Other competitively subordinate carnivores may show a tipping point in the effect of prey depletion, as our analysis reveals for wild dogs. A priori, this pattern seems most likely for species that are competitively subordinate to apex carnivores but depend on heavily overlapping resources (Creel and Creel, 1996; Mills and Gorman, 1997; Swanson et al., 2014; Mills and Biggs, 1993). Considering this suggestion, it is important to recognize that prey depletion can not only reduce resource availability, but also it can change the composition of the prey community and thus increase dietary overlap. The diets of lions and wild dogs in the Kafue ecosystem now overlap more than they did in the 1960s, because the large prey species (particularly buffalo) formerly preferred by lions have been more heavily affected by snaring than the smaller prey (particularly puku and impala) preferred by wild dogs (Creel et al., 2018).

As with other large carnivores (Janeiro-Otero et al., 2020), conflict between wild dogs and humans is likely to be amplified by prey depletion. Conflict between wild dogs and humans is usually low relative to other large carnivores (Creel and Creel, 2002), but conflict increases if native prey are depleted by snaring or displaced by livestock (Romanach et al., 2007; Gusset et al., 2009; Woodroffe et al., 2005).

3. Disentangling direct mortality and prey depletion

Differences in wild dog density due to snaring could be caused by prey depletion or by direct killing of wild dogs. The rate at which wild dogs are snared (and killed by snares) remains poorly known (Becker et al., 2013a; van der Meer et al., 2014), but long term intensive monitoring of known individuals in radio-collared groups showed very similar direct effects of snaring (Fig. 2) on wild dogs in the Luangwa Valley Ecosystem (LVE: where wild dog density is high, 2.8–4.0 adults & yearlings/100 km^2) and the Greater Kafue Ecosystem (GKE: where wild dog density is low, 0.8 adults & yearlings/100 km^2). These density estimates come from identical models (Bayesian closed capture models with logit-normal individual random effects on detection probability), fit to intensive monitoring data from identical field methods (described in detail by Goodheart et al., 2021). Snared wild dogs were detected at similar rates in the two ecosystems (GKE: $\overline{X} = 2.02$ %, 95 % binomial CI $= 1.21$ %–3.36 %, LVE: $\overline{X} = 3.12$ %, 95 % binomial CI $= 2.28$ %–4.28 %), and the observed annual mortality due to snaring was almost identical in LVE ($\overline{X} = 1.10$ %, 95 % binomial CI $= 0.67$ %–1.87 %) and GKE ($\overline{X} = 1.01$ %, 95 % binomial CI $= 0.49$ %–2.07 %). In contrast, the density of large herbivores (including the most common prey of wild dogs) is much lower in GKE than in LVE (Fig. 2), due to heavy illegal offtake (Vinks et al., 2020). Distance sampling using the same protocol in the two ecosystems showed that the combined density of impala and puku (the two most common prey of wild dogs in these ecosystems) was 35.8 individuals/km^2 in LVE and 17.8 in GKE (Vinks et al., 2020; Creel et al., 2018; Rosenblatt et al., 2019). These patterns suggest that snaring has stronger effects on wild dogs through prey depletion than through direct mortality. While patterns for these two ecosystems are striking, data

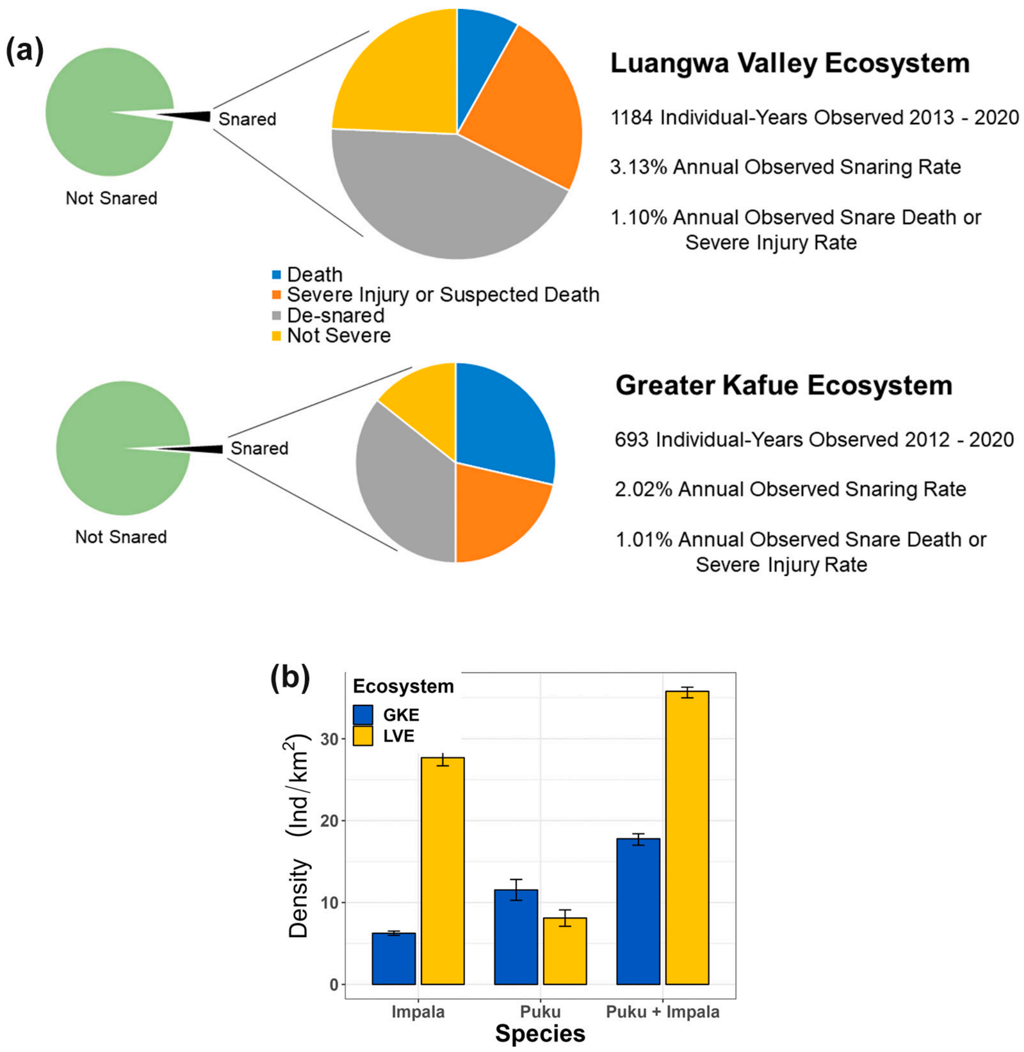

Fig. 2. (A) Intensive monitoring of 1877 known individuals in radio-collared groups shows very similar direct effects of snaring on wild dogs in the Luangwa Valley Ecosystem and the Greater Kafue Ecosystem from 2012 to 2020. Snared wild dogs were detected at similar rates in the two ecosystems, and the observed annual mortality due to snaring was 1.01 % in GKE and 1.10 % in LVE. (B) Ungulate densities are much lower in GKE than LVE, largely as a consequence of excessive illegal harvest. Estimates from distance sampling models show that the density of wild dogs' two most common prey in LVE is double that of GKE ($\overline{X} \pm 95$ % confidence limits).
Data from Rosenblatt et al. (2019) and Vinks et al. (2020).

from more ecosystems should be a priority to assess the generality of this inference.

The true rate of mortality due to snaring is probably higher than the observed rate, particularly if snares are strong enough to restrain a wild dog and kill it at the site of snaring. It has been suggested that wild dogs might escape unharmed from passive snares set with heavy woven wires intended to capture large ungulates (e.g. wildebeest and larger), because the dogs can slip free before the snare fully tightens (Creel et al., 2018). This suggestion was based on the observation that wild dogs were rarely killed or injured by snares in the Selous Game Reserve in the 1990s, even though long snare lines with dozens of snare sets were common. Anecdotally, the snares we now observe in LVE and GKE use lighter wire than those we observed in Selous in the 1990s, but we are not aware of any systematic data on the lethality of snares of different types for wild dogs (or other large carnivores). While recognizing these caveats, the observed rates of snaring and snare mortality are very similar in GKE and LVE, providing no evidence that pronounced differences in wild dog density are due to differences in the rate at which they are killed by snares.

4. Disentangling prey depletion and climate change

Changes through time in wild dog survival and reproduction have recently been attributed to climate change. However, these analyses (*a*) did not yield consistent effects across ecosystems (Rabaiotti et al., 2021) or response variables (Abrahms et al., 2022), (*b*) relied on a tenuous assumption that human killing of wild dogs depends on ambient temperature (Rabaiotti et al., 2021), and (*c*) did not address concurrent changes in prey density or other limiting factors (Rabaiotti et al., 2021; Abrahms et al., 2022). The conclusion that “high ambient temperatures were associated with elevated African wild dog mortality” (Rabaiotti et al., 2021) is questionably aligned with the results of the same study, because the estimated effect of temperature on mortality was positive at one site (0.46 ± 0.27 CI), negative but overlapping zero at another (−0.07 ± 0.18), and positive but overlapping zero at a third (0.07 ± 0.18). In Botswana, changes over time in the date of denning were associated with a decrease in temperature at the time of birth, but an increase in temperature while denning (Abrahms et al., 2022). The lack of consistency in relationships between temperature and demography undermines the suggestion (Rabaiotti et al., 2022) that “climate change is likely to cause population collapse”. This concern is amplified because any environmental variable with a time trend (like decreasing prey density: Fig. 3) will inevitably be correlated with rising temperature (Caro et al., 2022).

Our results, when combined with data showing widespread decline of ungulate populations (Western et al., 2009; Harris et al., 2009; Ripple et al., 2016; Ripple et al., 2015; Lindsey et al., 2013; Vinks et al., 2020; Bolger et al., 2008), suggest that prey depletion might underlie changes through time in wild dog dynamics that have been attributed to climate change. This inference is supported by the biophysical rule that limits on heat dissipation become stronger with increasing body mass (Speakman and Krol, 2010; Schmidt-Nielsen, 1984), so that hot conditions should place stronger constraints on activity for wild dogs' primary prey species than on wild dogs themselves (Creel et al., 2016). Direct observations of hunting confirm that wild dogs make kills more often, and with shorter chases, on hotter days (Creel et al., 2016). Some of the highest wild dog densities on record are from hot ecosystems (e.g. South Luangwa, Selous), and some of the lowest wild dog densities on record are from cold ecosystems (e.g. Kafue, Ngorongoro, Liuwa Plains): such patterns suggest either that high temperature is not a strong limiting factor for wild dogs, or that other factors overwhelm its influence. In the Okavango population where changes in reproduction were recently attributed to climate change (Abrahms et al., 2022), changes in body mass were previously attributed to a 30 % decrease in the density of impala (which comprised 85 % of their diet) from 1990 to 2009 (McNutt and Gusset, 2011). Recent data from Okavango show that “competition between humans and other apex predators for limited prey reduces the ecosystem's carrying capacity for large carnivores”, mainly due to human offtake of impala (Rogan et al., 2017). Large herbivores have also declined substantially in much of Kenya (Western et al., 2009), and the Samburu-Laikipia population where changes in wild dog survival were attributed to climate change occupied areas with “low densities of large prey” including areas in which native herbivores “were greatly outnumbered by livestock” (Woodroffe et al., 2007b). Pastoralist grazing has long been widespread in this area (Letai and Lind, 2013), and effects of livestock on the vegetation are well established (Young et al., 1995). Competition between cattle and wildlife is strong (Young et al., 2005), and reduced grazing resources have recently forced pastoralists to alter the places and times at which they graze their cattle (Letai and Lind, 2013; Pas and Cavanagh, 2022). A review of long term research on plant-herbivore interactions in Laikipia noted that the “loss of wild large mammalian herbivores (LMH) occurs in conjunction with the addition of livestock to the system. Livestock often are kept at higher abundances (higher stocking rate, or more total animal-days per year) than wild LMH, and are often a more continuous presence than more nomadic or migratory wild LMH (even in nomadic pastoral systems)” (Goheen et al., 2018).

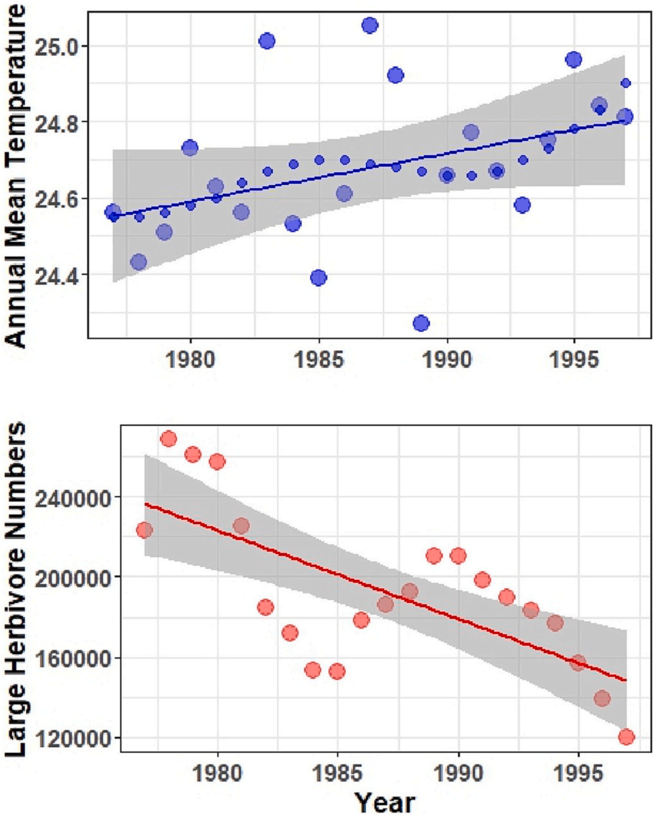

Fig. 3. Changes through time in the survival and reproduction of African wild dogs in Kenya and Botswana have been attributed to changes in environmental temperature, without testing whether they might be driven by other environmental variables. Other variables that are strongly related to wild dogs' fitness, particularly prey availability, have changed over the same period. (A) Changes in mean annual temperature for Kenya (data from the World Bank Climate Knowledge Portal) with (small points) and without (large points) five year moving window smoothing. (B) Changes in large herbivore numbers from six ecosystems broadly distributed across Kenya, for the same time period (data from Western et al. 2014). Prey numbers have declined as a consequence of habitat degradation, competition with livestock and excessive bush meat hunting. For these data from Kenya, the correlation between environmental temperature and large herbivore numbers is strong ($r = -0.896$, $t = -8.77$, $P < 0.0001$), suggesting that fitness effects that have been attributed to climate change might be caused by prey depletion.

Suggestions that wild dog demography or phenology are driven by climate change have all come from models that correlated a change through time in wild dog demography to changes through time in temperature and precipitation, with no other environmental predictors (Abrahms et al., 2022; Rabaiotti et al., 2021; Rabaiotti et al., 2022). The patterns just described strongly suggest that these correlations might be caused (partly or wholly) by prey depletion (Fig. 3).

5. Summary and recommendations for conservation

1. Above a tipping point in prey density, wild dog density increases as prey density decreases, because the benefits of competitive release outweigh the costs of prey depletion.
2. Below this tipping point in prey density, wild dog density decreases as prey density decreases, because the costs of prey depletion outweigh the benefits of competitive release.
3. Breakpoint regression models estimate the tipping point between these regimes at 419–837 kg of ungulate biomass per square kilometer, but a better understanding of this tipping point should be a priority for wild dog conservation. Methods to estimate wild dog density and prey density vary among studies, and this variation could affect the estimated breakpoint.
4. The decline of large herbivore populations through most of the African wild dog's range is beginning to limit wild dogs, for example in Kafue National Park (Goodheart et al., 2021), an important component of the Kavango-Zambezi Transfrontier Conservation Area that is critical for wild dog conservation at the continental scale (KAZA-TFCA-Secretariat, 2014). In prey-depleted ecosystems, efforts to conserve and restore large herbivores (e.g., through increased, targeted patrolling for snare removal) will benefit both wild dogs and their dominant competitors.
5. While data on direct mortality due to snaring remain limited, the available data suggest that snaring has larger effects on wild dogs through prey depletion than through direct killing of wild dogs. We also know little about the lethality of snares of different types for wild dogs, and how this might vary among ecosystems.
6. Prey depletion due to excessive bushmeat hunting (Lindsey et al., 2013; Lindsey et al., 2011; Ripple et al., 2016; van Vliet et al., 2016) and changes in land use (Watson et al., 2015) is an immediate concern for wild dog conservation. Evidence that climate change is harmful to wild dogs is mixed and oblique, particularly when evaluated in parallel with data on prey depletion.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110043.

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

Data will be made available on request.

Acknowledgements

This research was supported by the National Science Foundation (IOS1145749, DEB-2032131 and DEB-2221826); National Geographic Society Big Cats Initiative; 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, Elephant Charge, Musekese Conservation, Flatdogs Camp, Robin Pope Safaris, Mulberry Mongoose, Green Safaris, Mukambi Safaris, Puku Ridge, Ntengu Safaris, 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 Zambian Carnivore Programme and do not necessarily reflect the views of IUCN, or the European Union.

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