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Letter to the editor

The evidence for and urgency of threats to African wild dogs from prey depletion and climate change

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Many African large carnivore populations are declining due to decline of the herbivore populations on which they depend. We recently noted that the densities of true 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 density of apex carnivores is low, so the expected effect of a simultaneous decrease in resources and dominant competitors is not obvious. We found that when prey density drops below a tipping point, the relationship of wild dog density to prey density changes sign, and wild dog density declines. We also noted that 'prey depletion provides a mechanistically direct explanation of patterns in wild dog dynamics that have been attributed to climate change' (Creel et al., 2023).

Woodroffe et al. concur that prey depletion is an important threat, but suggest that we fail to understand the logic of their assertion that "climate change is likely to cause population collapse" (Rabaiotti et al., 2022), because the "identification of climate change as a threat is not based upon observed temporal trends in wild dog demography". This statement misses our fundamental point. The data that Woodroffe et al. analyzed were collected over a period with rising temperatures and declining prey populations, so whether or not one tests for a time trend in demography, the data themselves are affected by two patterns:

(1) Rising temperature over time (Fig. 1 in Abrahms et al., Fig. S5 in Woodroffe et al., 2017, Fig. 3 in Creel et al., 2023).
(2) Declining prey density over time (Fig. 3 in Creel et al., 2023, also see the supporting information in Woodroffe et al., 2017).

In these data, declining prey density and rising temperature are collinear. Our intention was not to exhaustively review the climate change hypothesis, but to point out that prey density "was not measured consistently within or between sites" (Woodroffe et al., 2017) in these studies, so it could not be included in tests of the correlation between wild dog demography and temperature. Consequently, prey depletion might underlie demographic effects that have been attributed to temperature. To further illustrate this point with a study highlighted by their letter, Woodroffe et al. (2017) found negative correlations between temperature and pup survival for Okavango and Laikipia (their Table 3: note that these coefficients differ more than 8-fold) where prey density was decreasing (supporting information lines 63 & 98 in Woodroffe et al., 2017). They did not detect this correlation in Save, where prey density was not decreasing (supporting information line 133). Here again, "evidence that climate change is harmful to wild dogs is mixed and oblique, particularly when evaluated in parallel with data on prey depletion". We chose these words carefully to avoid dismissing the possibility that climate change might affect wild dogs, although the signs and magnitudes of causal effects are not well-resolved.

Temperature, precipitation and the availability of vulnerable juvenile prey are all seasonal in most subtropical ecosystems. It remains plausible to hypothesize that seasonal reproduction by wild dogs aligns the period of maximal pup growth with the best hunting conditions (with a correlation between denning and cold, dry weather as a by-product). We do not claim to know that the correlation with hunting conditions is causal, but we have reservations about the assertion that correlations between wild dog demography and temperature are causal. High temperatures affect both wild dogs and their prey, and the only study to date with direct observation of wild dogs hunting at known temperatures revealed higher hunting success with shorter chases on hotter days (Creel et al., 2016). This result aligns well with biophysical constraints that cause larger endotherms to accumulate heat more rapidly when running (Speakman and Krol, 2010).

Critically, the hypothesis that wild dogs are directly limited by high temperatures does not explain differences among ecosystems. Both now and in the past, many of the highest wild dog densities are from very hot ecosystems such as Selous (Creel and Creel, 2002, Fig. 2.2), Okavango (Woodroffe et al., 2017, Fig. S3B) and South Luangwa, and many of the lowest densities are from colder ecosystems such as Liuwa, Kafue, Serengeti and Ngorongoro. As we noted, "such patterns suggest either that high temperature is not a strong limiting factor for wild dogs, or that other factors overwhelm its influence."

Woodroffe et al. state that our paper includes two 'anomalies'. Incorrectly, they state that "supplementary material and data cited in the text are in fact not provided". The supplementary material was

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provided and published. Second, they state that "it is not clear whether [Fig. 1A and 1B] are graphs or infographics." As stated in its caption, Fig. 1A presented our 'conceptual model of population regulation of wild dogs'. As stated in its caption, Fig. 1B then presented our hypothesis: "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". Finally, Fig. 1C presented a formal test of the hypothesis that wild dog density declines when prey density drops below a tipping point.

Woodroffe et al. note that we have previously used elasticities from matrix models to infer that "population dynamics are most affected by juvenile survival… thus, juvenile survival should be a focal point for any direct conservation actions" (Creel et al., 2004). This point remains important, but is perhaps not fully resolved. The sentence immediately following the quoted passage cites Woodroffe et al.'s (1997) contrary conclusion that "in all but the smallest populations, varying juvenile mortality in the region 50 – 70% has little effect on population persistence".

Importantly, there is emerging consensus that prey depletion is a threat for wild dogs. Woodroffe et al. suggest that "this threat has been repeatedly recognised in wild dog conservation strategies", but we cannot agree. The current IUCN Red List assessment for African wild dogs (Woodroffe and Sillero Zubiri, 2020) identifies fragmentation, livestock conflict, snaring, road accidents and infectious disease as causes of decline, but does not mention prey depletion. We are aware of no prior research concluding that wild dogs are prey limited, but many studies (including our own) have concluded the opposite. For example, Creel and Creel (1998) stated that "wild dogs are rarely limited by prey availability…. the simple observation that spotted hyenas attain much higher densities, while relying on similar prey, makes this explanation unlikely… ecosystems with high prey densities do not maintain higher wild dog densities". The 2020 IUCN Red List assessment reiterates that lions and spotted hyenas "keep African Wild Dog numbers below the level that their prey base could support" (Woodroffe and Sillero Zubiri, 2020). Under the ecological conditions of the past, this inference had strong support from many ecosystems (Creel and Creel, 1996, 2002), but the decline of large herbivores across sub-Saharan Africa is changing the processes that limit wild dogs: below a tipping point, prey depletion is a binding constraint on population growth (Goodheart et al., 2021). The intent of our paper was to bring attention to this fundamental change, the problem that it creates, and the action that is needed. If prey depletion is beginning to limit African wild dogs, then efforts to protect and restore depleted prey populations are a priority across much of their range.

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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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] *Insitutionen för Vilt, Fisk och Miljö, Sveriges lantbruksuniversitet, Umeå, Sweden*

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