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## Population limitation of a non-ruminant in a nutrient-poor ecosystem - predation rather than food.

**Short title:** Processes driving a plains zebra population

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### Abstract

Current theory predicts that plains zebra (*Equus quagga*) populations should be resource-limited. Long-term, detailed work in the Hwange ecosystem (Zimbabwe) on zebras and all their major predators provides empirical data to test this on a population that has been at a low density for at least two decades and is largely naturally regulated. Information on body condition is used as an indicator of resource use, and offtakes by the three major predators are estimated from a synthesis of data on densities and diets. This information leads to rejection of the expectations for resource-limitation. Zebras provide a significant part of the diets of all the main predators, and are important (11%) for the most abundant of these, spotted hyaenas (*Crocuta crocuta*). Using conservative values, we calculate that the three main predators, hyaenas, lions (*Panthera leo*), and leopards (*Panthera pardus*) kill some 17.5% of the zebra population. Given that this estimated offtake is of the same order of magnitude as maximum population growth (22.3% per year), we conclude that this population is likely to be limited by predation. Further work is needed to better understand the mechanisms by which the greater susceptibility of juveniles to predation in ungulates contributes to population limitation.

**Key words:** *Equus quagga*, Zimbabwe, resources, body condition, spotted hyaena, lion, leopard

### Introduction

The processes limiting the abundance of animal populations are of central importance in understanding the functioning of ecological systems, and the 2 basic types of limiting processes are known as 'top-down' (predator-based) and 'bottom-up' (resource-based). Early attempts to understand the relative importance of these two types of processes include the

'green world' hypothesis of Hairston, Smith & Slobodkin (1960), who noted that plants dominate many ecosystems in biomass and concluded that herbivores must generally be 'top-down' limited; the abundance of plants was thought to be determined largely by the availability of abiotic resources, 'bottom-up' processes. The importance of top-down processes in structuring animal populations has been revealed when apex predators have been reduced or reintroduced to ecosystems (Estes et al. 2011; Ripple et al. 2014). It is now realised that these processes can interact, so variations in resource abundance can change the impact of predation (see Sinclair & Krebs 2002; Andersen, Linnell & Solberg 2006).

It is particularly important to understand the processes limiting populations of herbivores since these animals are often 'ecosystem engineers' and valuable resources for people (Danell & al. 2006). In this paper, we document the potential importance of 'bottom-up' and 'top-down' limitation processes simultaneously in an African savannah system. In these systems, all the trophic levels appear to be limited by their resources (Sinclair 1975) and Fritz & Duncan (1994) confirm this for the community of mammalian herbivores. However, the processes limiting the populations of different species in these communities vary, and recent theory has clarified that the relative importance of resources and predation limiting such populations depends on body size of the herbivore species in interaction with the nutrient status of the ecosystem (Hopcraft, Olf & Sinclair 2010).

This theoretical framework leads to the expectation that large herbivores like plains zebras (*Equus quagga*, the average adult weight is  $\approx 300$ kg in Southern Africa), should be resource-limited in systems with low nutrients and medium grass abundance (Hopcraft, Olf & Sinclair 2010). However, the processes limiting zebra populations appear to be different from those limiting grazing bovids (Grange & Duncan 2006). Further, from birth to 9 months they weigh 34-150kg (Smuts 1975), hence juveniles are in the body size range expected to be limited by predation (Sinclair, Mduma & Brashares 2003). The balance of bottom-up and top-down processes driving plains zebra populations is not well understood.

In this paper, we examine the processes limiting plains zebra (*Equus quagga chapmani*) in the Hwange socio-ecological system, Zimbabwe, a low-nutrient system with medium grass abundance. This population has been stable at low density for at least 2 decades ( $\approx 0.5$  zebras/km<sup>2</sup>, see **Results**) which is very low compared with zebra populations in large savannah conservation areas like Serengeti or Amboseli (3.3 – 15.8 individuals/km<sup>2</sup>), and lower than Kruger (2.7 individuals/km<sup>2</sup>) and most other large savannah systems where soil nutrient levels are medium or low (see Grange & Duncan 2006). A demographic model for zebras in Hwange, based on long-term individual-based data, shows that the demographic

process limiting this population is mortality in first and second-year animals, 56% of foals die in their first year and another 44% in their second (Grange & al. 2015). This demographic study did not discover the ecological processes limiting the population but provides a useful start for understanding them.

Zebras in this system have very poor foraging resources: 4-8% crude protein in the wet season (Barnier & al. 2014) and about 3% crude protein in the dry season (unpublished data; F. Barnier). Maintenance requirements for zebras are not known, but their patterns of food intake and digestion are similar to those of horses (see data in Foose 1982); horses require 5% crude protein for maintenance and >10% for growth and lactation (National Research Council 2007) so horses would be limited by resource quality in Hwange.

Abundant large carnivores, including African lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), and leopards (*Panthera pardus*) coexist here with the zebras, which are relatively sedentary (though some migrate seasonally for a few tens of kilometres, unpublished GPS data; S. Chamaillé-Jammes), making the population susceptible to limitation by predation (see Sinclair, Mduma & Brashares 2003). Hence resources and/or predation could limit the Hwange zebra population.

If they are resource-limited, we expect their body condition to be variable, declining to critical levels particularly in sensitive age/sex classes with high nutrient requirements (i.e. lactating females, juveniles), and in the period of poor resources, the dry seasons, as happens in many herbivores of savannah systems (e.g. impalas *Aepyceros melampus*, Marshal & al. 2012). If the zebra population is predator-limited, offtake by the predators should be high enough to limit the population.

## **Material and Methods**

### *Study site*

The large Hwange socio-ecosystem in western Zimbabwe includes the National Park (14 651 km<sup>2</sup>) and surrounding hunting, forestry and multiple use areas, all of which are part of the five-nation [Kavango - Zambezi Transfrontier Conservation Area](#). The Park has been modified since its creation in 1928 by roads and artificial waterholes (≈60), mainly in the eastern and northern parts. Artificial waterholes allow water-dependent large mammals to use the area year-round. Zebras are widely distributed in the largely unfenced park, and most adjoining areas, but are rarely seen in multiple use areas. Shooting and snaring outside the Park kill a few zebras and some have been exported by management; such anthropogenic offtake would have an additive effect but the numbers are very small. A moratorium on hunting lions

was in place between 2005 and 2008 (Davidson et al. 2011), followed by low offtake ( $\approx 6$  male lions per year outside the Park, Loveridge & al. 2016). The populations of zebras and their predators studied here can, therefore, be considered as largely naturally regulated.

This study was conducted in the Main Camp unit, in 1261 km<sup>2</sup> of the northern part of the Park. The vegetation is typical of southern African dystrophic wooded savannahs with patches of grasslands (Rogers 1993). The long-term average annual rainfall is about 600 mm (Chamaillé-Jammes & al. 2006), and almost all the rain falls in the wet season (November–April). Rainfall in the years 1999-2019 included several dry years, with 393mm in 2001-2, 475 mm in 2002-3 and 331 mm in 2004-5 at Main Camp station; also dry were the years 2006-7, 2011-12, 2015-2016 and 2018-19 with 427mm, 409mm, 439 mm and 364mm respectively at Makalolo station.

### *The zebra population*

The density of zebras was estimated from road counts (line transect method) using Distance Sampling at the end of the wet and dry seasons between 1999 and 2019 (for detailed methodology see Chamaillé-Jammes & al. 2009). This density is likely to be overestimated as the roads visit many of the artificial waterholes where zebras occur at higher densities. The size of the zebra population was also estimated using aerial strip samples during the dry season of 2014 (for the methodology see Dunham & al. 2015). This provides an underestimate since zebras are undercounted in aerial strip samples. For this study, we therefore use the average of the 2 estimates from the road and aerial censuses.

Research on the zebras involved regular sessions of field observations from July 2004 until 2019, twice a year in July–August in the dry season and in November–March in the wet season. The individuals were identified from variations in their stripe patterns (Klingel 1967); for details of the methodology please see Grange & al. (2015).

Fifty individuals in 9 family groups were identified in July 2004, and the database updated during biannual sessions each subsequent year. In the wet seasons  $\approx 100$  animals were detected in known groups; in the dry seasons fewer known groups were resighted. The database includes nearly 500 individuals and >11 000 sightings between 2004 and 2019.

Zebras respond to variations in food and other environmental factors by mobilising quantities of subcutaneous body fat (Smuts 1975, page 95). Owing to the lack of fresh zebra carcasses from which to estimate body fat reserves from bone marrow (Smuts 1975, Mduma, Sinclair & Hilborn, 1999), we used an indirect body condition score (BCS) as a proxy for zebra health

as in horses, where visual assessment of body condition has been shown to be a reliable indicator as the body condition scores correlate well with body fat reserves ( $r = 0.81$  Henneke & al. 1983). BCS are widely used for the management of domestic horses and cattle.

Long-term information on the zebras' use of resources in Hwange was obtained by assessing their BCS scores (developed for horses Pollock 1980 from Lowman & al. 1976); there are 9 levels from 'Extremely fat' (Condition 5) descending by half-levels to 'Poor' (Condition 1) (see Appendix 1). 'Moderate' condition (here Condition 3) is considered ideal for breeding domestic mares (American Quarter Horse Association <https://www.aqha.com/-/body-condition-score>, note that the 9 classes of condition in horses are in the same order as ours, but are numbered 1-9 with Condition 1 the fattest). Our data were collected by P. Duncan and colleagues trained by him to minimise observer biases, between 2008-2017, during both dry and wet seasons, including two dry years with 409 mm and 439 mm of rain. We analysed BCS variations according to season, sex and age using ordinal regression with a cumulative link model.

Finally, to assess whether resources were ever insufficient for the zebras' nutritional requirements for a subset of females we compared their BCS during lactation (from a birth for one year) and non-lactation (i.e. high vs. low nutrient needs, Pond 1977).

### *Predation*

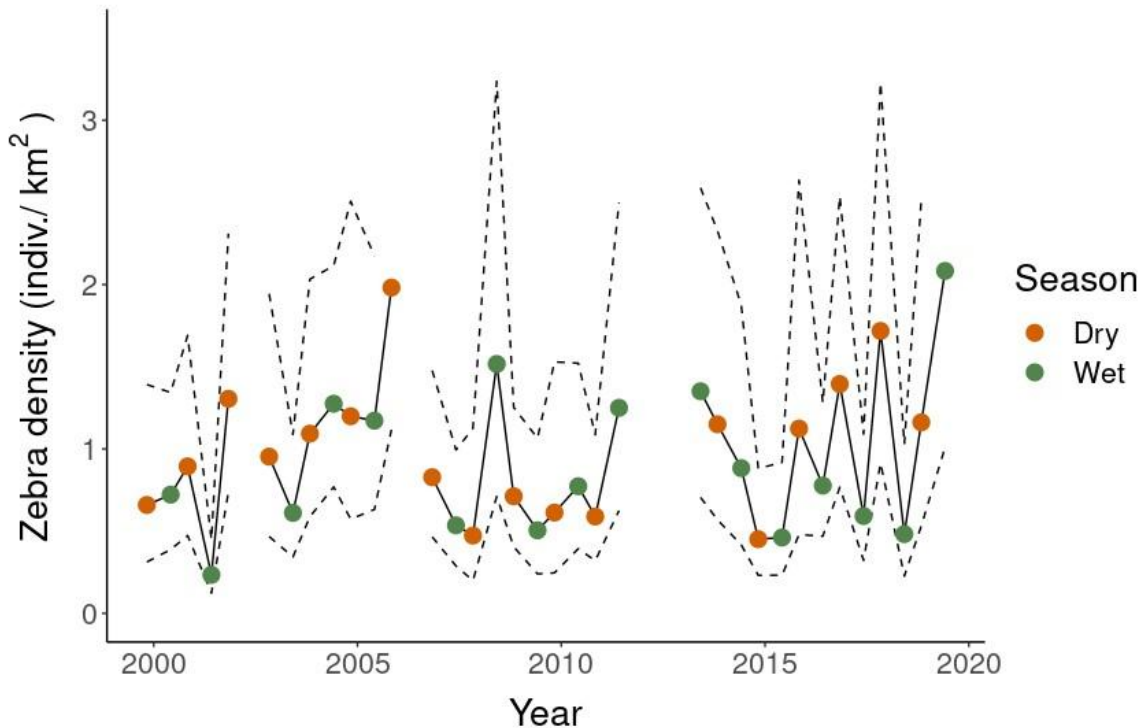
Hwange contains abundant predators of large herbivores. Wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*) are uncommon, and zebras represent little of their diet (0.58% for wild dogs: Hayward & al. 2006a, and 2% for cheetah: Hayward & al. 2006b, see also Hayward & Kerley 2008). Consequently, we focus on the three other large predators in Hwange: lions, spotted hyaenas and leopards. Assessment of the impact of predation requires data on predator numbers, their diets and daily food requirements which we synthesize to calculate the impact of predation on the zebra population. Numbers of predators were estimated from camera-trap surveys (Loveridge & al. 2022); for lion, we also used individually based monitoring of this population, these data allowed the use of capture-mark-recapture (CMR) to estimate the number of individuals in the lion study area between 1999 and 2012 (Loveridge & al. 2016). Kill sites may underestimate the contribution to the diets of small prey like zebra foals, we therefore used data from scats only to assess the contribution of zebras to the diet of the predators (Davidson & al. 2013 for lions; Périquet & al. 2015 for hyaenas, unpublished results for leopards, using the same methodology as for lions). Daily food requirements for the predators were extracted from Carbone & al. (2007).

We estimated the biomass of zebras consumed by each predator from the product of predator population density, study area size, the proportion of zebras in their diets, and the food intake of individual predators. To calculate the numbers of zebras from the biomass eaten, we needed to estimate body mass at death. The average weight of adult zebras is 322 kg for females and 319 kg for males; newborns average 34 kg (Smuts 1975). However, no information is available on the proportions of the different age classes killed. Hyaenas in Hwange hunt mostly alone or in small groups of 2-4 (Périquet & al. 2015) and hyaenas in small groups are unlikely to kill adult zebras (Kruuk 1972). This is also the case for leopards, for which the range of prey is 1-100kg (Sinclair & al. 2003) and preferred prey is 15-45 kg (Clements & al. 2014). Here we use 45 kg as a conservative average value for leopards. Lions predate zebra foals proportionally more than older zebras in Etosha and Kruger (Stander, 1992; Mills & Shenk, 1992), this appears to be so in Hwange too (Davidson & al. 2013). For hyaenas and lions we therefore use 200kg, as in Fritz & al. (2011), which is close to the body mass of yearlings (205kg, Smuts 1975), and a conservative average for body mass at death for zebras killed by these two predators.

## **Results**

### *Zebra density*

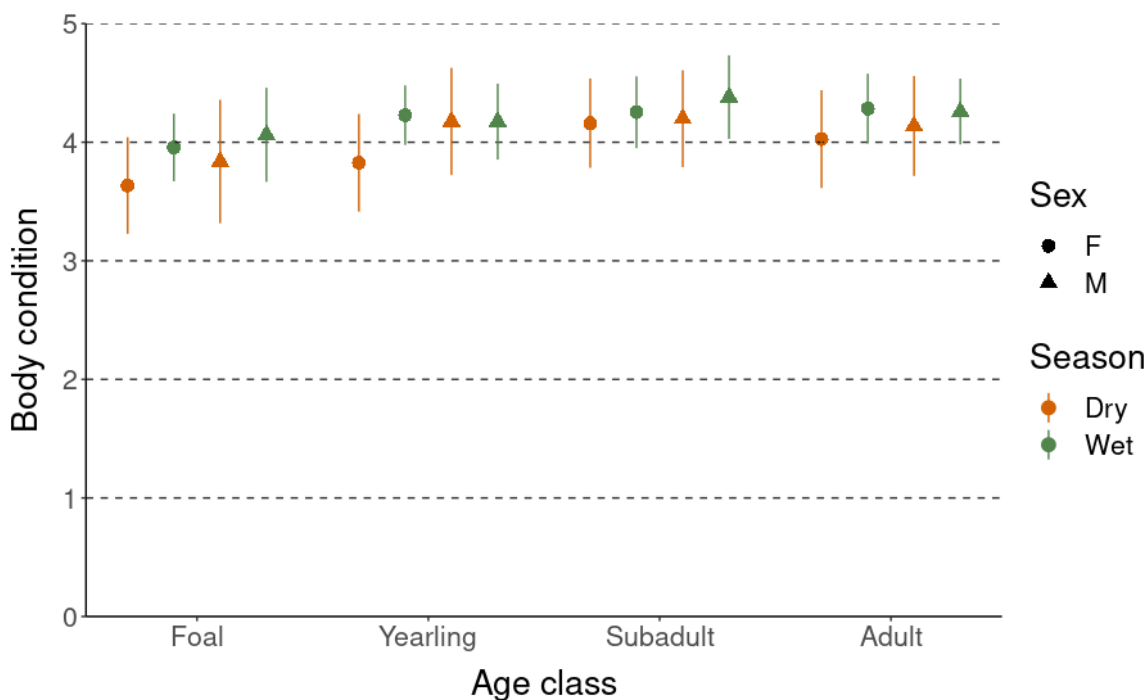
For the whole period 1999-2019, the mean zebra density estimated from road counts was 0.958 ( $\pm$  0.446 SD) zebras/km<sup>2</sup> in 1261 km<sup>2</sup> of the Main Camp area. No trend has been detected for the study period (Fig. 1), or indeed since 1973 (Valeix & al. 2008), and there was no difference between the seasons ( $F_{2,32}=0.84$ ;  $p = 0.44$ ). The 2014 dry season aerial zebra count for this Main Camp area was 241 ( $\pm$  393; 95% confidence limits, Dunham & al. 2015) which gives a density of 0.19 ( $\pm$  0.31; 95% confidence limits) zebras/km<sup>2</sup>, close to the long-term average for the whole Hwange system. The average of these densities is 0.574 zebras/km<sup>2</sup>, which gives an estimated study population of 724 zebras (1261 km<sup>2</sup> x 0.574 zebras/km<sup>2</sup>).



**Fig. 1.** The density of zebras ( $\pm$  95% CL) in the study area (1261 km<sup>2</sup>) estimated from road counts in the wet season (green dots) and the dry season (orange dots).

#### *Resource-limitation*

The body condition of the zebras (Fig. 2) was generally Moderate (BCS 3) to Fat (BCS 4 ½). BCS fell below 3 ½ (Moderately Fleishy) for only a few animals, most of which had been injured in a fight or were limping from an old wound, probably caused by predators. Sample sizes per category of sex-age-season averaged 60, ranging from n=20 to n=216; the data are available, see **Data Availability Statement** below. For the 'AgeClass' effect, the BCS of foals was generally lower than adults (Fig. 2; Table 1). For most animals, their BCS were slightly lower in the dry seasons than wet seasons (Fig. 2; Table 1); particularly for the foals, yearlings ('AgeClass:Season', Fig. 2; Table 1) and females ('AgeClass:Sex:Season', Fig. 2; Table 1).



**Fig; 2.** Body condition in plains zebras in Hwange National Park, using a 9-point body condition score (BCS), scaling from 5 ('Extremely fat') to 1 ('Poor'), with intermediate values for animals whose condition falls between these (see Appendix 1). Mean values +/- 1 SD. **Age classes** are 'Foal' (1<sup>st</sup> year), 'Yearling' (2<sup>nd</sup> year), 'Subadult' (3<sup>rd</sup> and 4<sup>th</sup> years) and 'Adult' (5<sup>th</sup> year and older). The **seasons** are wet and dry seasons for the years 2008-17.

### Table 1

Between 2006 –10, including the dry year 2006-7 with 427mm of rain, median BCS for 20 lactating adult females was 'Fat' (4 ½), and similar for non-lactating females (4 ½, Appendix 2a). For 10 additional females with less complete data, the median scores were also 4 ½ in both the high and the low states (Appendix 2b). Variation in the requirements of all these females (n=32) therefore had no detectable effect on their body condition, and they always maintained condition which was 'Fleshy' (4) or better.

### Predation

The density of lions from individual based monitoring and CMR was 0.022 lions/km<sup>2</sup> (range = 0.015-0.030 lions/km<sup>2</sup>, excluding cubs) for a large study area which included both the Main Camp zebra study area (1261 km<sup>2</sup>) and the Ngamo/Wilderness area. We used camera-trap surveys to evaluate lion abundance between these two areas. The Main Camp density was 0.009 ± 0.009 indiv./km<sup>2</sup> in 2015, and 0.013 ± 0.009 indiv./km<sup>2</sup> in 2018, (excluding cubs), which was lower than in the Ngamo area at 0.026 ± 0.009 indiv./km<sup>2</sup> in 2015 and 0.023 ± 0.009 indiv./km<sup>2</sup> in 2018 (Loveridge & al. 2022). We estimate lion density in the zebra study

area was 0.015 lions/km<sup>2</sup> (excluding cubs) because density in Ngamo was approximately twice that in the Main Camp area and the average density based on the more accurate demographic data for the two areas was 0.022. Zebras comprised 5% of the prey (Davidson & al. 2013) for the period 2005-2007. The daily food consumption per lion is estimated at 8.5 kg (Carbone & al. 2007). The annual consumption of zebra by the lion population was estimated from the product of their density, the area (1261km<sup>2</sup>), the proportion of zebras in their diets, and the annual food consumption of an individual lion, giving 2934 kg of zebra eaten per year (Table 2).

The abundance of hyaenas estimated from camera-trap surveys was 0.113 ± 0.009 indiv./km<sup>2</sup> in 2015 and 0.145 ± 0.014 indiv./km<sup>2</sup> in 2018 (excluding cubs, Loveridge & al. 2022). We used conservative estimates from the 2015 camera-trap survey, as it is closer to the middle of this study of zebras. Hyaenas are the most abundant predator in Hwange, seven times the density of lions. DNA analysis of a small number of hyaena scats found 9/10 scats positive for zebras. Zebras represented 16.3% of the prey found in scats for 1999-2005 and 11.4% for 2008-2013 (Périquet & al. 2015). We use the conservative proportion of 11.4% zebra in hyaena diet from 2008-2013, in the middle of the zebra study. The daily food consumption required by an hyaena is estimated as 3.51 kg (Carbone & al. 2007), giving 20 811 kg of zebra eaten by the hyaena population annually (Table 2).

Camera-trap surveys provided leopard density estimates of 0.020 ± 0.009 indiv/km<sup>2</sup> in 2015 and 0.026 ± 0.009 indiv/km<sup>2</sup> in 2018 for the study area (Loveridge & al. 2022). Leopards and lions are thus of similar abundance in this area. We conservatively used the density of 0.020 leopard/km<sup>2</sup> (excluding cubs) from the estimate closer to the middle of the zebra study. Leopard diet was estimated from the analysis of 162 scats using the same method as for lions, from the North West and Southern sectors of the National Park. These sectors do not overlap with the zebra study area but are the best diet data available. Zebras represented 1% of the prey found in these scats (Sandoval-Seres & al. submitted). The daily food consumption required by a leopard is estimated as 3.78 kg (Carbone & al. 2007), giving 348 kg of zebra eaten per year by the leopard population (Table 2).

The numbers of zebras eaten by these predators were calculated as in Table 2. The offtake by lions is 14.7, by leopards 7.7 zebras. The offtake by hyaenas, 104, was the greatest; the three species together are estimated to have taken ≈126 zebras a year. Since the number of zebras in the study area is estimated at 724 individuals this estimated offtake represents 17.5% of the population.

## Table 2

### Discussion

This zebra population has remained at a low density for at least 2 decades. The aim of this analysis was to test the theoretical expectation that it is resource-limited and, if not, whether it could be predator-limited.

#### *Resource-limitation*

For limitation by resources, we expected that body condition scores would be variable, declining to levels which affect reproduction and/or survival in the sensitive age/sex classes with high nutrient requirements (lactating females and juveniles, i.e. foals and yearlings), and in the period of poor resources (the dry season). Most of the animals were less fat in the dry seasons than the wet seasons, this was particularly true for the foals and yearlings and among these the females (Fig. 2 and Table 1). However, animals in the sensitive age classes (juveniles) were only slightly less fat in the dry season. The scores of the stallions and mares did not vary, averaging 4 ('Fleshy') in both dry and wet seasons (Fig. 2). The condition of the lactating females, with high nutrient requirements, was the same as when their requirements were low ('Fat', score 4 ½, see Appendices 2a & 2b). These results are, therefore, not consistent with the expectations for resource-limitation.

Equid populations typically show clear declines in condition in the lean seasons and especially when lactating. For instance, in the resource-limited horses on Shackleford Banks, USA, where predation is absent, lactating females were classed 'Very thin' (score 2.0), and non-lactating females were better (score 3.1, Rubenstein 1986). Overall, the average condition of the horses on Shackleford Banks was 2.8 i.e. below 'Moderate' (3), and therefore much worse than the Hwange zebras. In another resource-limited horse population on Sable Island, Canada, even in the summers, none were fat and all were in moderate condition or thinner (Medill & al. 2023). In contrast, the Hwange zebras were always in body condition considered ideal for breeding domestic mares ('Moderate' Condition 3) or fatter (see American Quarter Horse Association <https://www.aqha.com/-/body-condition-score>).

Therefore, BCS did not vary strongly between seasons, age classes or the breeding state of females, and the variations observed are unlikely to affect reproduction or survival of adults or juveniles. The data for Hwange covers dry years and wet ones, hence, this conclusion is robust in all conditions encountered during these years. We therefore reject the expectations of the resource-limitation hypothesis and consider that zebras in Hwange have had abundant resources, so they must have been limited by process(es) other than resource-limitation.

### *Predator-limitation*

For predator-limitation, we expected offtake to be high enough to limit the population. Lion and leopard abundances were not high and zebras represented not more than 5% of the prey consumed by these carnivores, resulting in estimated offtakes of 14.7 zebras per year for lions and 7.7 zebras per year for leopards. A key result of this analysis is that hyaenas are by far the most abundant predators in the Hwange system, occurring at a density of 0.113 hyaenas/km<sup>2</sup> (excluding cubs), seven times as abundant as lions, and zebras are an important prey for them since they occur in 11.4% of the scats and are the third most important prey among the medium and small species (Périquet & al. 2015). As a result, the offtake by hyaenas, estimated as 104 zebras per year in the study area, is much higher than the offtakes by lions and leopards, and we estimate that together the three species took 126 zebras per year (see Table 2). The estimated zebra population in the study area was 724, so 126 animals (consumed by all three carnivores) represent 17.5% of the zebra population. The potential annual rate of increase for zebra is estimated at 22.3% (from Sinclair 2003, equation 3.1), 161 animals. If the predators were responsible for the death of 126 (it was not possible to attach confidence limits to this figure as the errors could not always be estimated e.g. for daily food consumption by the predators), and some additional zebras were poached, we conclude that the offtake by predation is great enough to limit the zebra population.

This is a tentative conclusion owing to the uncertainty in all the variables. However, the derived offtake uses conservative values for predator densities, the proportions of zebras in the diets and body mass at death, so the impact of predation may be greater than estimated. For instance, we could have used 150 kg for body mass at death by hyaenas since hyaenas generally kill prey smaller than 150 kg (Kruuk 1972; Cooper 1990; Mills 1990) when they hunt alone or in small packs, as in Hwange (2-4 individuals, Périquet & al. 2015). Had we done so, the estimated offtake by predation, 22.3%, would have been the same as the estimated maximum rate of increase, 22.3% of the zebra population.

Additionally, limitation of the Hwange population by predation is consistent with:

- (i) the fact that the demographic process limiting the Hwange zebra population is mortality in first and second-year animals. Accessible prey for leopards is 1-100kg (Sinclair & al. 2003); lions take a large proportion of juvenile zebras in all seasons (Davidson & al. 2013) and most of the offtake by hyaenas is likely to be juveniles (foals and yearlings) since hyaenas generally kill prey smaller than 150 kg (Kruuk 1972; Cooper 1990; Mills 1990), close to half the body mass of adult zebras,

when they hunt alone or in small packs, as in Hwange (2-4 individuals, Périquet & al. 2015).

- (ii) Zebras in Hwange foal all the year, so small zebras are always available, unlike many alternative prey species like wildebeest and impala which calve seasonally. Juveniles are therefore likely to provide many of the zebra kills throughout the year for all these carnivores, which fits with the fact that the demographic process involved is the mortality of juveniles.
- (iii) Predation as a limiting factor has been suggested in studies of three other zebra populations. In the Serengeti, zebras are limited by low foal survival, apparently due to predation (Grange & al. 2004). In Kruger National Park, the zebra population stabilised after increasing, due to lower survival of both juveniles and adults (Owen-Smith & Mason 2005) from lion predation (Mills & Shenk 1992). Thirdly, in Ngorongoro crater, Kruuk (1972) considered that the zebra population was limited by hyaenas which consumed  $\approx 9\%$  of the zebras annually, matching recruitment.
- (iv) The predator/prey ratio in Hwange is as high or higher than in systems where zebras are predator-limited like Ngorongoro and Kruger (see Fritz & al. 2011).
- (v) Other sources of mortality do not appear to limit the zebra population: social factors could reduce recruitment rates in zebras, as males cause some foetal and foal mortality in feral horses (Berger 1986) and males kill foals in captive zebras (Pluhacek & Bartos 2000). However, in Hwange, if male infanticide occurs it must be rare, and there are no important consequences for foal survival (Vitet & al. 2021). Zebras are not susceptible to foot-and-mouth disease or rinderpest, and though they can carry African horse sickness, they do not show clinical symptoms (Radcliffe & Osofsky 2002). Macroparasites can affect the condition of animals like zebras but are never lethal (Turner & Getz 2010). There is no record of anthrax or clinical symptoms from other diseases in the Hwange zebras, and no cases of morbidity in zebras have been found by researchers and many Park rangers in the field, which suggests that parasites and/or pathogens do not limit the population.

Our results align with Hopcraft, Olf & Sinclair (2010) who concluded that "... an evaluation of mortality in juvenile age classes might show that predation by a single predator, with low capture rates, could still impose strong population regulation, especially for larger species."

Two kinds of information would be useful to test the generality of these results from Hwange: data on zebra numbers in areas where predator populations decline, and data on zebra body

condition in areas with little or no predation or anthropogenic mortality, especially during droughts.

### *Conclusion*

In this study of a savannah ecosystem with unusually complete data, we found that this population of large herbivores was not 'bottom-up' limited by their resources as predicted by the Hopcraft model (Hopcraft, Olf & Sinclair 2010). They maintained good body condition regardless of season and even when their nutrient requirements were high, in lactation. Conservatively, estimated offtake by three large predators, particularly by hyaenas, suggests that predation could limit the population. This conclusion supports emerging knowledge about the contribution of predation by smaller predators to prey population dynamics, through expanding their prey base to juveniles of larger prey species (Clements & al. 2014, Annear & al. 2023).

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### **Data Availability Statement**

The data on body condition used for this study are available from Simon Chamaille-Jammes ([simon.chamaille@cefe.cnrs.fr](mailto:simon.chamaille@cefe.cnrs.fr)) on reasonable request.

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### **Conflict of interest disclosure**

The Authors declare that they have no conflict of interest.

## Ethics approval statement

The results reported here are observational and did not involve handling animals. This study was carried out with research permits from the Zimbabwe Parks and Wildlife Management Authority (ZimParks). It is part of a long-term cooperation, started in 1999, between the ZimParks, Oxford University (team leader A.J. Loveridge) and the French CNRS (team leader H. Fritz). The field work was done in collaboration with the research staff of Hwange National Park.

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## FIGURES, TABLES, APPENDICES

### FIGURES (in text)

**Fig. 1.** The density of zebras (+/- 95% CL) in the study area (1261 km<sup>2</sup>) estimated from road counts. Green triangles indicate the results from the wet season, and red circles results from the dry season.

**Fig. 2.** Body condition in plains zebras in Hwange National Park, using a 9-point body condition score scaling from 5 ('Extremely fat') to 1 ('Poor'), with intermediate values for animals whose condition falls between these (see Appendix 1). Mean values +/- 1 SD. **Age classes** are 'Foal' (1<sup>st</sup> year), 'Yearling' (2<sup>nd</sup> year), 'Subadult' (3<sup>rd</sup> and 4<sup>th</sup> years) and 'Adult' (5<sup>th</sup> year and older). The **seasons** are wet and dry seasons for the years 2008-17.

**TABLES** (in an attached file)

**Table 1.** A cumulative link model for ordinal regression on the variations of body condition in Fig.2.

**Age classes** are 'Foals' 1<sup>st</sup> year, 'Yearlings' 2<sup>nd</sup> year, 'Subadult', 3<sup>rd</sup> and 4<sup>th</sup> years and 'Adult' 5<sup>th</sup> year and older.

The **seasons** are wet season and dry.

	Df	Chi.sq	Probability
AgeClass	3	43.12	2.32e-09 ***
Sex	1	2.02	0.156
Season	1	9.98	0.002 **
AgeClass:Sex	3	6.27	0.099
AgeClass:Season	3	11.28	0.010 *
Sex:Season	1	0.05	0.816
AgeClass:Sex:Season	3	11.39	0.0010 **
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**Table 2.** The offtake of zebras by the three major predators in the zebra study area, calculated for 2004-2019.

For the sources see **Material and Methods Predation.**

<u>Densities</u>		<u>Zebra average body mass at death (kg)</u>		<u>For lions and hyaenas</u>	
<u>Hyaenas (excluding cubs)</u>	0.113		200		
<u>Lions (excluding cubs)</u>	0.015		45		<u>For leopards</u>
<u>Leopards (excluding cubs)</u>	0.020	<u>Study area (km<sup>2</sup>)</u>	1261		
<u>Zebras</u>	0.574				
<u>Food required</u>					
<u>Consumption by</u>	<u>per day/ind. (kg)</u>	<u>Predators (number of individuals)</u>	<u>%Zebras in diet</u>	<u>Biomass of zebra eaten/year (kg)</u>	<u>Zebras killed/year. (number)</u>
<u>Hyaenas</u>	3.51	142	11,4	20811	104
<u>Lion adults+subadults</u>	8.5	19	5	2934	14.7
<u>Leopards</u>	3.78	25	1	348	7.73
Total number zebras killed / year					126
% zebras killed / year					17.5
<u>Estimated number of zebras in the study area</u>					724
<u>Potential rate of increase (%)</u>					22.3
<u>Potential annual increase</u>					161

## **APPENDICES** (in 2 attached files)

**Appendix 1.** Scoring of body condition.

**Appendix 2.** The median condition scores (potentially 5 = Extremely Fat to 1 = Poor) of adult female zebras in two states of nutrient requirements (High = when lactating; Low = when not lactating or one year after the birth of a foal if the foal was still present). Each record is the median of monthly observations for a female in one session of the years 2006-10.

**2a. *Females with replicate data in each state of requirements***

**2b. *Females with no replicate data for one state of requirements***