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Smaller ungulates are first to incur imminent extirpation from an African protected area

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ABSTRACT

It is commonly assumed that larger species are more vulnerable to extinction because of their low population densities and slow time to recover from setbacks. We report that, contrary to this expectation, it is the smaller ungulate species that first reached the brink of local extirpation within a 950 km^2 fenced protected area, the Hluhluwe-iMfolozi Park. Moreover, earlier records show that most of these species had formerly been extremely common within the park region. Neither habitat change, competition for resources or exposure to predation provided a consistent sole explanation for the drastic population crashes shown by five smaller ungulate species (body mass 10–45 kg). We suggest that smaller species can be more vulnerable to local extinction as a consequence of their narrower habitat occupation and hence restricted spatial distribution. Nevertheless all of the threatened species thrive widely outside the protected area. Our findings show that smaller rather than larger species can be most at risk of local extirpation when confined within protected areas. Hence more attention needs to be given to conserving such species within broader regional landscapes.

1. Introduction

It has for long been recognized that protected areas will inevitably lose species because of the stochastic dynamics of the populations that they contain (Soule et al., 1979). Assessments have generally found that large body size is a leading predictor of extinction risk (Pimm et al., 1988; McKinney, 1997; Cardillo et al., 2005; Davidson et al., 2009; Dirzo et al., 2014; Hilbers et al., 2016). Larger animals should be especially vulnerable because of their greater space requirements (Damuth, 1987; but see Cotgreave, 1993; Reynolds, 2004), and slower rates of population recovery from setbacks. Furthermore, big mammals are particularly vulnerable to human overkill, and convincing evidence shows that the presence of modern human hunters was the key factor precipitating large mammal extinctions towards the end of the Pleistocene (Johnson, 2002; Koch and Barnovsky, 2006; Bartlett et al., 2016). But prioritization of terrestrial megafauna (i.e. herbivores weighing more than 40 kg and carnivores weighing more than 15 kg) for conservation action and funding (Ripple et al., 2016) may be at the expense of smaller species equally or more deserving of attention (Ford et al., 2017).

Drawing on an unusually long series of abundance estimates, we report that, contrary to expectations, it is five of the smaller antelope species (body mass 10–60 kg) that have reached the brink of local extirpation within a long-standing protected area, and not the larger ungulates. Four of them had been among the most abundant ungulates in the region with local populations numbering in the thousands. The most recent population estimates within the park boundaries have fallen to fewer than 25 animals in four cases. A sixth small antelope that was not formerly common has become locally extinct. The extirpation of these six species would reduce the complement of ungulate species contained within the protected area from 20 to 14, i.e. a reduction by 30% of its species richness of large herbivores. Only one of the ungulates larger than 100 kg in body mass is approaching similar levels of rarity, with a total population reduced to fewer than 200 individuals. These results challenge the widely accepted assumption that large bodied species are more at risk of extinction.

The protected area exhibiting this scenario is the Hluhluwe-iMfolozi Park (HiP), proclaimed as separate Umfolozi and Hluhluwe Game Reserves in 1897 and situated in the south-eastern KwaZulu-Natal province of South Africa (Cromsigt et al., 2017). The park boundaries, completely fenced since the early 1970s, enclose an area of nearly 950 km^2 and contain a full complement of Africa's megaherbivores along with populations of most medium-large ungulates. All large predators have been restored: lions (*Panthera leo*) and cheetahs

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(*Acinonyx jubatus*) during the 1960s and wild dogs (*Lycaon pictus*) during the 1980s (Somers et al., 2017). Leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*) had remained present. Conservation measures had seemingly represented an outstanding success story, particularly with regard to the recovery of the white rhinoceros (*Ceratotherium simum*; Owen-Smith, 1988; Linklater and Shrader, 2017).

Potential mechanisms that may have contributed to the drastic downward trends of the smaller antelope species include (a) habitat change, (b) interspecific competition, and (3) predation, plus potential interactions among them. Over the period when these populations declined, HiP experienced increases in woody plant cover (Staver and Beckett, 2017), expanding populations of two introduced antelope species (Le Roux et al., 2017), and re-introduced large carnivores. In this report, we (1) document the population changes over 80 years shown by various large herbivores based on estimates from different sources, (2) assess relationships with body size, and (3) evaluate the implications of the evidence for particular mechanisms from associated patterns in time or space.

2. Methods

The herbivore population estimates that were available to us were drawn from various sources subject to different approximations and biases (Le Roux et al., 2017). The earliest were derived from records of animals shot during an attempted game elimination campaign undertaken when one of the original game reserves was under management of the veterinary authority. Following the transfer of control to the conservation authority, plus consolidation of the protected area, repeated aerial counts were undertaken, later replaced by biennial ground counts corrected for visibility bias. The ungulate species covered by these counts are listed in Table 1 along with their scientific names, body mass, dietary categories and habitat type primarily occupied.

Table 1
Ungulate species mentioned in the text, their feeding types and habitat associations. Body mass is the mean adult female mass from Owen-Smith (1988).

Species	Scientific name	Body mass	Feeding type	Habitat
African elephant	*Loxodonta africana*	2800	Mixed	Broad
White rhino	*Ceratotherium simum*	1600	Grazer	Broad
Giraffe	*Giraffa camelopardalis*	825	Browser	Broad
African buffalo	*Syncerus caffer*	520	Grazer	Broad
Black rhino	*Diceros bicornis*	1000	Browser	Broad
Zebra	*Equus quagga*	300	Grazer	Broad
Wildebeest	*Connochaetes taurinus*	220	Grazer	Open short grass
Waterbuck	*Kobus ellipsiprymnus*	180	Grazer	Near rivers
Greater kudu	*Tragelaphus strepsiceros*	170	Browser	Wooded savanna
Bushpig	*Potamochoerus larvatus*	70	Omnivore	Forest and bush
Nyala	*Tragelaphus angasii*	63	Mixed	Woodland
Warthog	*Phacochoerus africanus*	58	Grazer	Broad
Common reedbuck	*Redunca arundinum*	45	Grazer	Tall grass
Impala	*Aepyceros melampus*	44	Mixed	Broad
Bushbuck	*Tragelaphus scriptus*	37	Browser	Forest patches
Mountain reedbuck	*Redunca fulvorufulus*	26	Grazer	Open hillslopes
Grey duiker	*Sylvicapra grimmia*	17	Browser	Bush patches
Red duiker	*Cephalophus natalensis*	14	Browser	Forest
Klipspringer	*Oreotragus oreotragus*	13	Browser	Rocky outcrops
Steenbok	*Raphicerus campestris*	11	Browser	Dry bush

2.1. Game elimination campaigns

Game elimination campaigns were aimed at combatting the transmission of the disease nagana or trypanosomiasis from wild ungulates to cattle, firstly by shooting all wild ungulates in regions surrounding the proclaimed game reserves and later by eradicating wild ungulates serving as hosts of the tsetse flies (*Glossina* spp.) transmitting the blood parasites within the Umfolozi Game Reserve (GR) and environs. Mentis (1970) documented the numbers of animals of various species killed in these two campaigns. The first one extended from June 1929 to November 1930 and encompassed buffer zones adjoining the Umfolozi GR, including sections that later became incorporated within the enlarged protected area. Bourquin and Hitchins (1979) provided further records of animals destroyed within buffer zones adjoining Hluhluwe GR. The combined area of these buffer zones amounted to around 1400 km^2, and extended further south and west than the current HiP boundaries (Mentis, 1970). Animals killed during this brief campaign provide minimal estimates of the animals present around that time within the area covered.

A further game elimination program was conducted after the Umfolozi GR had been placed under the control of the veterinary authority, starting in 1942 and ending in 1950. The shooting was ended after it became clear that it was ineffective in reducing numbers of the smaller antelope species that also served as hosts for tsetse flies, in particular grey duiker and bushbuck. Because of the extended period covered, tallies of animals destroyed need to be adjusted for continuing recruitment into the respective populations in order to estimate the effective population sizes of the various species at the start of this period. This correction was made by Mentis (1970) taking into account the reproductive potential of the various species (his Table 9). The area encompassing Umfolozi GR together with its buffer zones at that time covered 1150 km^2 (Mentis, 1970). Buffer zones adjoining Hluhluwe GR where further animals were killed added perhaps an additional 250 km^2, yielding a total area of 1400 km^2. We adjusted the population totals estimated by Mentis (1970) to represent the 950 km^2 total area of the subsequent protected area, i.e. multiplying them by 950/1400. For white rhinos, which were excluded from the shooting campaign, we used the estimated number counted from the ground at that time within the protected area, as reported by Player and Feely (1960). Few animals were shot within the Hluhluwe Game Reserve which was mostly free of tsetse flies and remained protected. Both impala and nyala were introduced there by the park warden during the 1930s from nearby populations of these two species. Giraffe were introduced during the 1960s and elephant during the 1980s (Le Roux et al., 2017).

2.2. Aerial and ground surveys

From 1954 onwards, intrinsic changes in herbivore populations within the park boundaries have been managed by animal removals undertaken by the conservation authority, initially lethally by shooting to counteract perceived overgrazing, but later by live capture and sales. However, the species affected in this way were restricted to several of the larger ungulates, from impala size upwards. None of the small antelope species currently at risk of imminent extirpation was subjected to removals.

To estimate population totals during the period 1967–1972, after the two game reserves had been managed by the conservation authority for nearly two decades (te Beest et al., 2017), we used the aerial count totals obtained by fixed-wing aircraft in 1967 and helicopter in 1970 and 1972 (Brooks and Macdonald, 1983). Aerial counts under-estimate true populations by varying degrees depending on the visibility from the air of the species concerned. They become quite unreliable for species smaller than impala. For these more cryptic species we turned to ground-based observations. These were made during 1968–71 in four regions providing representative coverage of Umfolozi Game Reserve within a combined survey area of 28 km^2 (Owen-Smith, 1973). Density