

Water dependence structures predation risk for large herbivores in insular protected areas

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Abstract

Predator avoidance strategies vary across the ungulate guild. Population-level responses to the presence of large predators to a large extent depend on how well ecological conditions suit the particular predator avoidance strategies of a species. Predation risk from ambush predators, e.g. lions negatively correlates with distance from surface water, but only at scales comparable to the foraging range of lions. Prey species with low surface water requirements spend less time close to surface water, and their predator avoidance revolves around selecting predator-free zones. Arguably, spatial segregation would be further encouraged by competition from water-dependent conspecifics. The scarcity of predator-free zones in confined spaces raises the expectation that they are exposed to a high predation risk relative to species more dependent on surface water. Based on this premise, we argue that lion introductions to insular conservation areas of limited size, compromise diverse ungulate communities. We do an across-species comparison of the long-run population growth of a selection of prey species across fourteen small conservation areas. Study areas are categorised according to those harbouring apex predators (lions) and those that do not. Our findings suggest species differentially respond to the presence of lions, with negative responses biased towards species with low surface water requirements. In smaller conservation areas harbouring lions, reducing surface water frequency might prove key to the successful conservation of water-independent large herbivores.

Keywords: *Panthera leo*; Prey selection; Spatial scale; Prey refuge; Anti-predator strategies

Introduction

As apex predators, lions (*Panthera leo*) are considered keystone species, with the highest predation impact on prey populations of all large carnivores across their geographical range (Martin and Owen-Smith 2016), often limiting prey densities below levels determined by resource availability (see Hopcraft et al. 2012). Negative responses of prey populations to temporal increases in lion density are therefore frequently reported in open systems, and perhaps more commonly, in insular systems following lion reintroductions (see Hunter 1998; Harrington et al. 1999; Power 2002; Tambling and Du Toit 2005; Georgiadis et al. 2007). Lions generally prefer medium-sized prey with a clear preference for some species, e.g. blue

wildebeest (*Connochaetes taurinus*) and plains zebra (*E. quagga*), (Hayward and Kerley 2005). Yet, negative responses to the presence of lions are frequently reported for species not highly selected for by lions, e.g. sable antelope (*Hippotragus niger*) (Owen-Smith et al. 2012; Chirima et al. 2013; Crossmary et al. 2016), roan antelope (*Hippotragus equines*) (Harrington et al. 1999), and hartebeest antelope (*Alcelaphus buselaphus*) (Ng'weno et al. 2017) which suggests prey selection is highly context dependent (Crossmary et al. 2016; Riginos 2015).

The importance of spatial refuges in reducing predation risk has received considerable attention in the literature (Valeix et al. 2009a, b; Thaker et al. 2011; Martin et al. 2015; Riginos 2015; Schmidt and Kuijper 2015; Moll et al. 2016; Prugh et al. 2019). While trade-offs between resource acquisition and predation risk occur across multiple spatio-temporal scales (Lima 2002; Valeix et al. 2009a, b), there seems to be some agreement that prey, to reduce predation risk, select habitat at landscape scales (see Hebblewhite et al. 2005; Hebblewhite and Merrill 2009). Proximity to surface water increases predation risk (de Boer et al. 2010), predisposing highly water-dependent species to increased predation risk (but see Martin and Owen-Smith 2016). Species also select habitats along a disturbance gradient, e.g. blue wildebeest prefer highly disturbed heavily grazed shortgrass habitats while hartebeest prefers virtually unutilized tallgrass communities (Spencer 1995), with the latter, typically found further from water points (Smit et al. 2007). Based on this premise, spatial segregation among prey species, therefore, should increase with conservation area (Cain et al. 2012; see Schmidt and Kuijper 2015) affording prey species of low surface water requirements relatively predator-free zones. Apparent competition, i.e. where competition between prey species occurs via relative differences in susceptibility to predation, rather than via direct competition for resources (Van de Koppel et al. 2005; Owen-Smith and Mills 2008; DeCesare et al. 2010; Davidson et al. 2012) underscores the importance of different spatial requirements among prey species to escape predation. Nonetheless, increased predation risk associated with surface water proximity is mediated by the habitat occupied by the prey species, e.g. thick vegetation increases predation risk by ambush predators (Martin and Owen-Smith 2016). Yet, negative responses to increased lion presence in the literature appear biased towards species with relatively low surface water requirements, suggesting reduced conservation area limits their options to escape predation.

Most South African conservation areas are typically small (< 100,000 ha) relative to sites on which Hayward and Kerley (2005) based their lion prey preferences. Here, we compare the long-run mean population growth of four prey species in small conservation areas (see methods section for the size range of study sites) to the presence of the lion as the focal apex predator. We specifically evaluate whether prey species with low surface water requirements, e.g. hartebeest and eland (Woodall and Skinner 1993) exhibit lower long-run population growth when lions are present compared to when they are not. We further determine if this is apparent for species with high surface water requirements e.g. blue wildebeest and zebra (Hayward and Hayward 2012; Kihwele et al. 2020). This partitioning needs some qualification though. Surface water dependence, of course, follows a gradient (see Veldhuis et al. 2019; Kihwele et al. 2020). Blue wildebeest and eland appear to fall somewhere in between high dependence and independence in terms of absolute water requirements but the latter can reduce their surface water dependence effectively by selecting succulent food (Kihwele et al. 2020). For the sake of brevity, we, therefore, refer to wildebeest as water dependent, and eland as water independent.

We further considered area size and rainfall as two potential confounding factors in the study, considering their widely acknowledged importance in ecology. Increased area size affords

large herbivores a broader scope for obtaining resources generally (Owen-Smith 2014). Any negative prey responses to lion exposure (which are mostly biased towards relatively large areas) would, therefore, suggest exposure to lions is the key driver. Rainfall in turn dictates primary production, i.e. resource availability (Coe et al. 1976) and a negative response following lion exposure, but coinciding with a drought period, would complicate the interpretation of a negative response to lion exposure.

We expect prey preferences reported in the Hayward and Kerley (2005) study for species of low surface water requirements (water-independent species) to poorly predict responses to lion exposure in smaller conservation areas. We further predict that area size and rainfall are not important in the context of the current study.

Materials and methods

Study sites

To draw comparisons between estimated long-run population growth for prey species with low surface water requirements (hereafter water independent) and two prey species highly dependent on surface water (hereafter water dependent), several sites for which extensive count data of game populations were available, were collated. We only selected sites where the four focal prey species co-occur. These were partitioned into those containing lions and those which do not (Table 1). The majority of study sites lack kill data, and consequently, the limited kill data available were not considered for this study. The two water-dependent prey species involved blue wildebeest and or black wildebeest and zebra (mountain *E. zebra* or plains zebra) depending on whichever species occur), and water-independent prey included eland and hartebeest. Sites without lions included Mokala-, Vaalbos- (later de-proclaimed), Golden Gate (Golden Gate Section and QwaQwa Section)-, Camdeboo National Parks (NP), and Bloemhof-, Botsalano-, Mafikeng-, and Molopo Nature Reserves (NR). Sites with consistent long-run lion presence included Madikwe GR, Addo NP, and Marakele NP. Pilanesberg NP and Mountain Zebra NP could be partitioned into two stages: a pre- and post-lion introduction phase (Table 2). The study sites cover a range of ecological conditions, most notably varying rainfall, vegetation, and area size. The study sites located within the Savanna biome include the Game Reserves Bloemhof Dam, Botsalano, Madikwe, Mafikeng, Molopo and the National Parks Marakele, Mokala, and the now decommissioned Vaalbos. Mean annual rainfall varies from around 330 to 650 along a west–east axis. The Mountain Zebra and Camdeboo National Parks are located in the Nama Karoo biome, with a mean annual rainfall of around 400 mm and 350 mm respectively. The Golden Gate sections are located within the Grassland biome, with a mean annual rainfall of around 760 mm per annum region. The Addo Elephant National Park is located in the Albany Thicket biome, with a mean annual rainfall of around 450 mm per annum (see NASA POWER 2018; Mucina and Rutherford 2006).

Table 1 Predator profile of each study site included in our analysis

Site	Size (km ⁻²)	Lion density (100 km ⁻²)	Wild dog density (100 km ⁻²)	Spotted Hyena	Cheetah density (100 km ⁻²)	Pre and post lion phase
Addo-Kuzuko ^a	400	0.92			0.82	
Bloemhof ^b	250					
Botsalano ^b	58					
Camdeboo ^a	194					
Golden Gate ^a	116					
Golden Gate Qua Qua ^a	224					
Madikwe ^b	650	4.06	2.4	x	x	
Mafikeng ^b	48					
Marakele ^a	650	1.5		x	x	
Mountain Zebra ^a	284	1				x
Mokala ^a	196					
Molopo ^b	240				x	
Pilanesberg ^b	572	5.85	7.7		x	x
Vaalbos ^a	230					

We assumed leopard and black-backed jackal occur at all study sites and are therefore not included

^aNational Parks

^bNorth West Parks

^xpresent, but densities unknown

Table 2 Mean long-run population growth estimates (*r*) derived from exponential models fitted to time-series count data of prey populations

Species	<i>n</i> (years)	<i>R</i> ²	Lions	Site	<i>r</i>
Hartebeest	7	0.32	No Lions	Pilanesberg NR	0.03
Hartebeest	14	0.75	No Lions	Golden Gate NP	0.08
Hartebeest	10	0.64	No Lions	Qwa Qwa section	0.10
Hartebeest	17	0.62	No Lions	Vaalbos NP	0.14
Hartebeest	12	0.76	No Lions	Mokala NP	0.16
Hartebeest	26	0.80	No Lions	Camdeboo NP	0.12
Hartebeest	15	0.94	No Lions	Mountain Zebra NP	0.20
Hartebeest	18	0.49	No Lions	Molopo NR	0.10
Hartebeest	18	0.79	No Lions	Mafikeng NR	0.03
Hartebeest	18	0.63	No Lions	Bloemhof NR	0.21
Hartebeest	18	0.67	No Lions	Botsalano NR	0.08
Hartebeest	22	0.89	Lions	Pilanesberg NR	-0.18
Hartebeest	14	0.73	Lions	Madikwe NR	-0.16
Hartebeest	11	-0.47**	Lions	Addo NP	-0.17
Hartebeest	13	0.88	Lions	Marakele NP	-0.04
Hartebeest	8	0.99	Lions	Mountain Zebra NP	-0.06
Eland	12	0.7	No Lions	Pilanesberg NR	0.10
Eland	15	-1.76**	No Lions	Golden gate	0.14
Eland	10	0.24	No Lions	Qwa Qwa section	0.19

Eland	17	0.47	No Lions	Vaalbos NP	0.15
Eland	12	0.52	No Lions	Mokala NP	0.10
Eland	12	0.71	No Lions	Camdeboo NP	0.10
Eland	16	0.81	No Lions	Mountain Zebra NP	0.12
Eland	18	0.65	No Lions	Molopo NR	0.17
Eland	18	0.86	No Lions	Mafikeng NR	0.09
Eland	18	0.12	No Lions	Bloemhof NR	0.02
Eland	18	0.58	No Lions	Botsalano NR	0.10
Eland	13	0.55	Lions	Pilanesberg NR	-0.15
Eland	20	0.93	Lions	Madikwe NR	-0.22
Eland	11	0.7	Lions	Addo NP	0.11
Eland	13	0.72	Lions	Marakele NP	-0.04
Eland	8	0.43	Lions	Mountain Zebra NP	-0.08
Wildebeest		*	No Lions	Pilanesberg NR	0.11
Wildebeest	15	0.57	No Lions	Golden Gate NP	0.08
Wildebeest	8	0.93	No Lions	Qwa Qwa section	0.14
Wildebeest	12	0.14	No Lions	Vaalbos NP	0.11
Wildebeest	10	0.84	No Lions	Mokala NP	0.10
Wildebeest	26	0.27	No Lions	Camdeboo NP	0.13
Wildebeest	15	0.98	No Lions	Mountain Zebra NP	0.26
Wildebeest	18	0.72	No Lions	Molopo NR	0.21
Wildebeest	18	0.67	No Lions	Mafikeng NR	0.10
Wildebeest	18	0.53	No Lions	Bloemhof NR	0.26
Wildebeest	18	0.48	No Lions	Botsalano NR	0.18
Wildebeest	16	0.8	Lions	Pilanesberg NR	-0.11
Wildebeest	20	0.25	Lions	Madikwe NR	-0.01
Wildebeest	11	0.16	Lions	Addo NP	-0.11
Wildebeest	13	0.25	Lions	Marakele NP	0.11
Wildebeest	8	0.42	Lions	Mountain Zebra NP	0.09
Zebra	12	0.82	No Lions	Pilanesberg NR	0.17
Zebra	15	0.54	No Lions	Golden Gate NP	0.04
Zebra	8	0.86	No Lions	Qwa Qwa section	0.11
Zebra	13	0.47	No Lions	Vaalbos NP	0.14
Zebra	11	0.97	No Lions	Mokala NP	0.19
Zebra	28	0.77	No Lions	Camdeboo NP	0.07
Zebra	15	0.97	No Lions	Mountain Zebra NP	0.10

Zebra	18	0.31	No Lions	Molopo NR	0.18
Zebra	18	0.52	No Lions	Mafikeng NR	0.13
Zebra	18	0.52	No Lions	Bloemhof NR	0.13
Zebra	18	0.57	No Lions	Botsalano NR	0.09
Zebra	10	0.55	Lions	Pilanesberg NR	0.01
Zebra	20	0.79	Lions	Madikwe NR	0.04
Zebra	11	0.06	Lions	Addo NP	-0.04
Zebra	13	0.66	Lions	Marakele NP	0.09
Zebra	8	0.75	Lions	Mountain Zebra NP	0.09

* Estimates derived from Tambling and Du Toit (2005)

** Negative R^2 values suggest an exponential model is a poor model to describe the time series and these estimates were, thus, excluded from main analysis (Table 3)

Study sites ranged in size from 28,400 to 65,000 ha where lions were reintroduced, and from 4800 to 57,200 ha with no lions, all of which are fenced. By comparison, sites included in the study by Hayward and Kerley (2005) mostly comprised large open systems across Africa.

Census data

We collated the time series of population sizes of our four focal species from our study sites. North West Parks authorities follow typical protocols used in small reserves by conducting annual triplicate aerial censuses using 800 m wide transects. SANParks follow the same protocol of conducting total counts but not in triplicate, with a consequent larger margin of error. Authorities, thus, make use of aerial surveys covering the total area of a reserve but do not use formal statistical analyses that account for sampling errors (North West Parks, National Parks Board, unpublished data) or biases (Seber 1982). We cannot correct for errors and biases and, thus, consider the data as a time series of the minimum number of individuals known to be alive at the time of a survey. We considered such time series adequate for estimating long-run population growth responses of prey species, because of the consistency in survey methodology over time.

Estimating long-run population growth

We used the population growth responses of prey populations to the presence or absence of lions as crude indicators of the effect of predation, but we report lion densities to aid the interpretation of the results. We constructed population growth models for each prey species (Gotelli 2001). Our models took the form of a discrete-time exponential model that corrects for annual introductions and removals of individuals of species between surveys

$$N_{t+1} = (N_t + N_{i,t \rightarrow t+1} - N_{r,t \rightarrow t+1})\lambda + \varepsilon,$$

where λ is finite population growth, N_{t+1} is the population size at time $t + 1$, N_t is the population size at time t , $N_{i,t \rightarrow t+1}$ is the number of individuals that managers introduced from time t to time $t + 1$, $N_{r,t \rightarrow t+1}$ is the number of individuals that managers removed from time t to time $t + 1$, and ε represents error. Note that removals did not target specific sexes or ages and focused on herds that comprised both sexes and ages in varying proportions. Similarly, introductions did not target specific ages or sexes. Our models, thus, do not account for varying ages and sexes explicitly.

We estimated population growth (r), using maximum likelihood approaches (Edwards 1972; Microsoft Excel macro provided by Hood 2005) and assessed whether our approach was reasonable based on R^2 values. Estimates of mean R^2 values varied across data sets and somewhat between species, with hartebeest ($R^2 = 0.65$), eland ($R^2 = 0.6$), wildebeest ($R^2 = 0.53$), and zebra ($R^2 = 0.63$). We calculated the R^2 values as follows:

$$R^2 = 1 - \text{SSE}/\text{SST},$$

with SSE the Sum-of-Squares-Error, and SST the Total-Sum-of-Squares of the NULL model. Data sets inconsistent with exponential models included those of wildebeest counts at Pilanesberg National Park before the introduction of lions. This most likely stems from missing data regarding wildebeest introductions and removals (North West Parks unpublished data). We, therefore, obtained estimates of wildebeest population growth of Pilanesberg from a previous study (Tambling and Du Toit 2005). Exponential models were also inconsistent with hartebeest counts at Addo National Park (Kuzuko section where lions were present), and eland counts (Golden Gate National Park where lions were absent). These results were, therefore, excluded from the main analysis, while the R^2 values included for the analysis ranged from 0.12 to 0.98. The number of surveys from which population growth was derived, the degree of fit to exponential models, and area size are summarised in Table 2.

Estimating species population growth response to lion predation

For sites with time-series spanning periods of lion absence and later lion presence, we separated species-specific data into a pre- and post-lion introduction phase. To centralise population growth around zero, point estimates were \log_e -transformed, and data were organised according to whether exposed to lion presence or not. We constructed a simple linear model, comprising two categorical explanatory variables—predation (absence or presence) and prey species, as well as their interaction term. We report our findings at the 0.05 level of significance. Thus, our model is constructed as follows:

$$r \sim X + Y + X * Y + \varepsilon,$$

with $r = \log_e$ (population growth), X =predationstatus, Y =preyspecies and ε =error.

The analysis was done in R version 3.1.6 (R Core Team 2013).

Accounting for potentially confounding factors

To assess the potential effect of area size, we inspected the correlation, if any, between long-run population growth and area size for each species individually for sites with no lions. We expected that population growth correlates with area size. Note that lions were introduced into predominantly large conservation areas in the context of this study. For potential rainfall effects, we only assessed whether a negative population response could possibly be due to drought conditions, i.e. we do not explore the overall effect of rainfall on population growth. The long-run mean annual rainfall of a pre- and post-lion introduction phase is therefore compared.

Results

We collated 64 species-specific data sets in 14 small protected areas (Table 2) but censored two because of data issues. For areas with lions, we had four datasets for hartebeest, five for eland, five for wildebeest and five for zebra. In areas without lions, we had 11 datasets for hartebeest, 10 for eland, 11 for wildebeest and 11 for zebra. The range in years covered by the 62 data sets was 7–28 years. Estimated population growth (r) ranged from -0.22 to 0.26 , with the two water-independent prey species having the greatest range (eland -0.022 to 0.190 ; hartebeest -0.18 to 0.21).

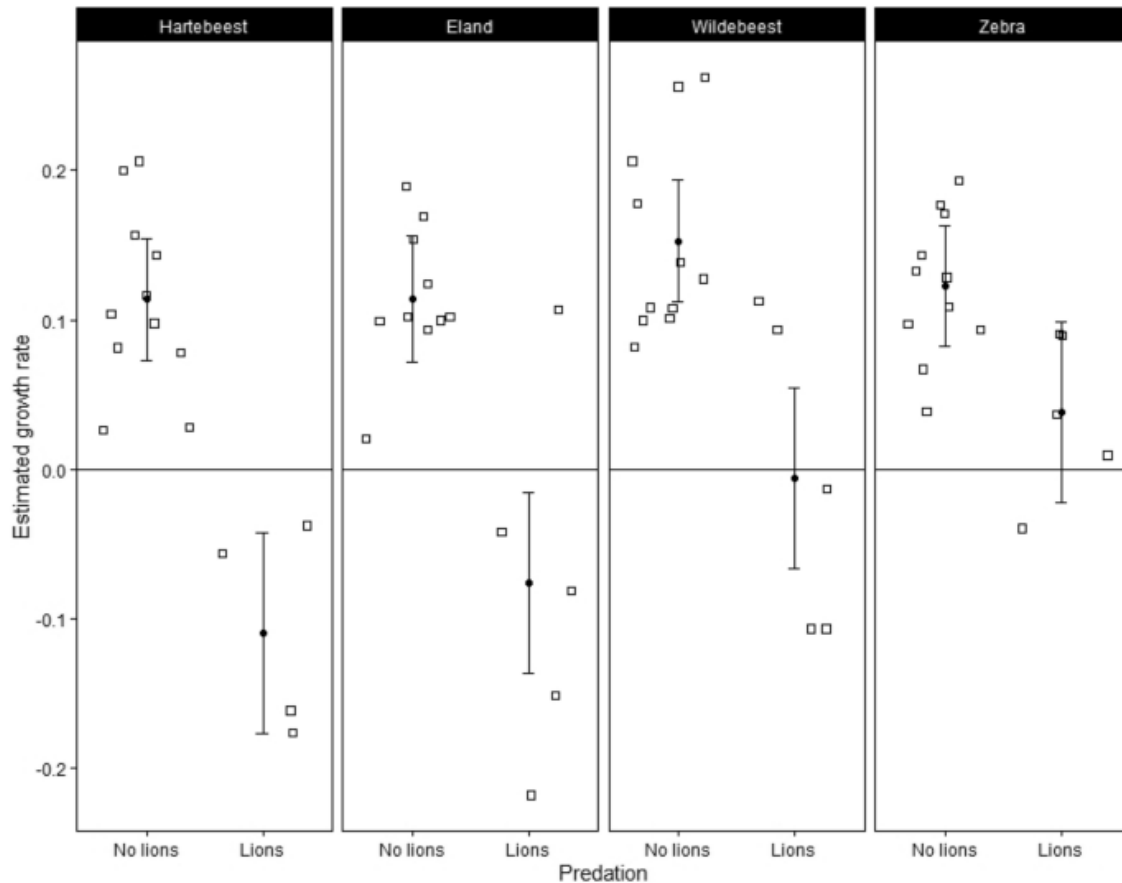


Fig. 1. Point estimates with 95 percent confidence intervals of long-run mean population growth r of two water-independent (hartebeest and eland) and two water-dependent (wildebeest and zebra) prey species in conservation areas with, and without lions

Figure 1 illustrates the variable population growth across study sites. The mean estimated population growth for species without lion presence differed slightly, ranging in increasing order from 0.11 (SE 0.02) for hartebeest, 0.12 (SE 0.01) for eland, 0.12 (SE 0.01) for zebra, and 0.15 (SE 0.02) for wildebeest, but does not significantly differ from one another.

Hartebeest populations in the presence of lions all showed decreasing trends, with population growth ranging from -0.04 to -0.18 (Fig. 1; Table 3) with a mean of -0.12 (SE 0.03). In those same reserves, four out of five eland populations had decreasing trends, with estimates ranging from 0.11 to -0.22 , and a mean of -0.08 (SE 0.06). Among wildebeest populations in the presence of lions, three out of five populations were declining, with estimates ranging

from 0.11 to -0.11 , and a mean of -0.01 (SE 0.05). For zebra populations in the presence of lions, one out of five populations showed a decreasing trend, with population growth estimates ranging from 0.09 to -0.04 and a mean of 0.04 (SE 0.02) (Fig. 1; Table 2). Hartebeest populations, therefore, seemed most affected by the presence of lions, followed by eland. The hartebeest negative response to the presence of lions is significant ($p < 0.001$; Table 3; Fig. 1). The same result was found for eland ($p < 0.001$). For wildebeest ($p = 0.85$) and zebra ($p = 0.22$), the presence of lions did not induce a significant negative response (Table 3).

Table 3 Summary output of the relative influence of lion presence, and prey species, on long-run prey population growth rates

Model	Coefficient \pm SE	<i>t</i>	<i>p</i>
No lions*hartebeest	0.114 \pm 0.02	5.49	<0.001
Lions*hartebeest	-0.110 \pm 0.03	-3.2	<0.001
No lions*eland	0.114 \pm 0.02	5.25	<0.001
Lions*eland	-0.08 \pm 0.03	-2.48	<0.05
No Lions*wildebeest	0.153 \pm 0.02	7.38	<0.001
Lions*wildebeest	-0.006 \pm 0.03	-0.19	0.85
No lions*zebra	0.123 \pm 0.02	5.93	<0.001
Lions*zebra	0.038 \pm 0.03	1.23	0.22

Figure 2 illustrates the site-specific prey species' responses to the presence of lions. Addo Elephant National Park provides an interesting anomaly, with the positive growth of the eland population contrasting with the negative growth of wildebeest and zebra. Note that long-term rainfall of the Zebra National Park during the post-lion introduction phase (368 ± 90 mm; $n = 5$) is lower than during the phase preceding lion introductions (436 ± 119 mm; $n = 5$), while for Pilanesberg mean annual rainfall for the post-lion reintroduction phase were similar to the long-term mean.

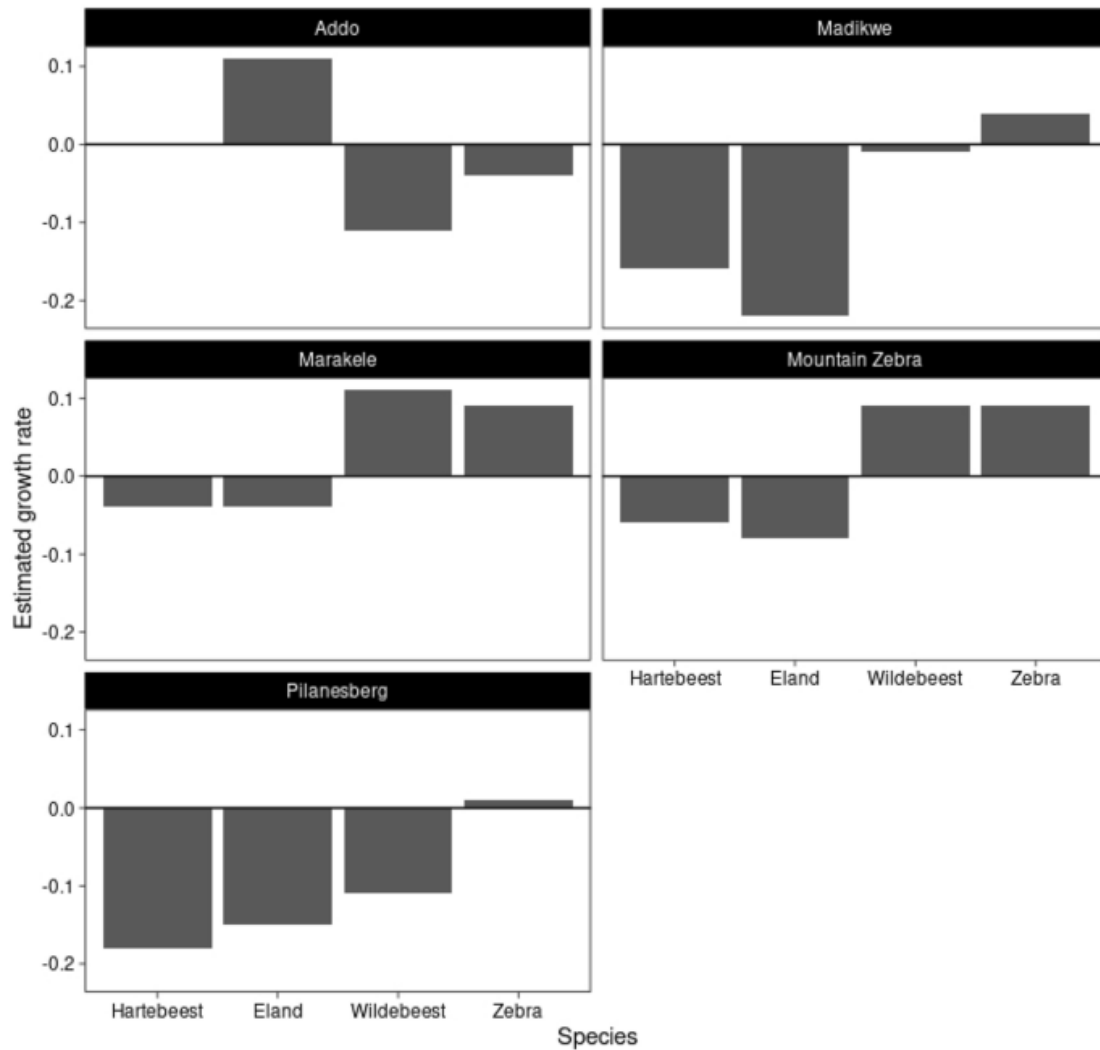


Fig. 2. Long-run population growth of prey species at sites where lions were introduced. Hartebeest population growth has been omitted from Addo Elephant National Park due to the poor fit of time-series data to an exponential population growth model

The area size is a confounding factor, with hartebeest population growth showing a correlation with area size at sites with no lions (Fig. 3). This becomes particularly evident when Pilanesberg is removed from the analysis. For other species, a correlation is less apparent.

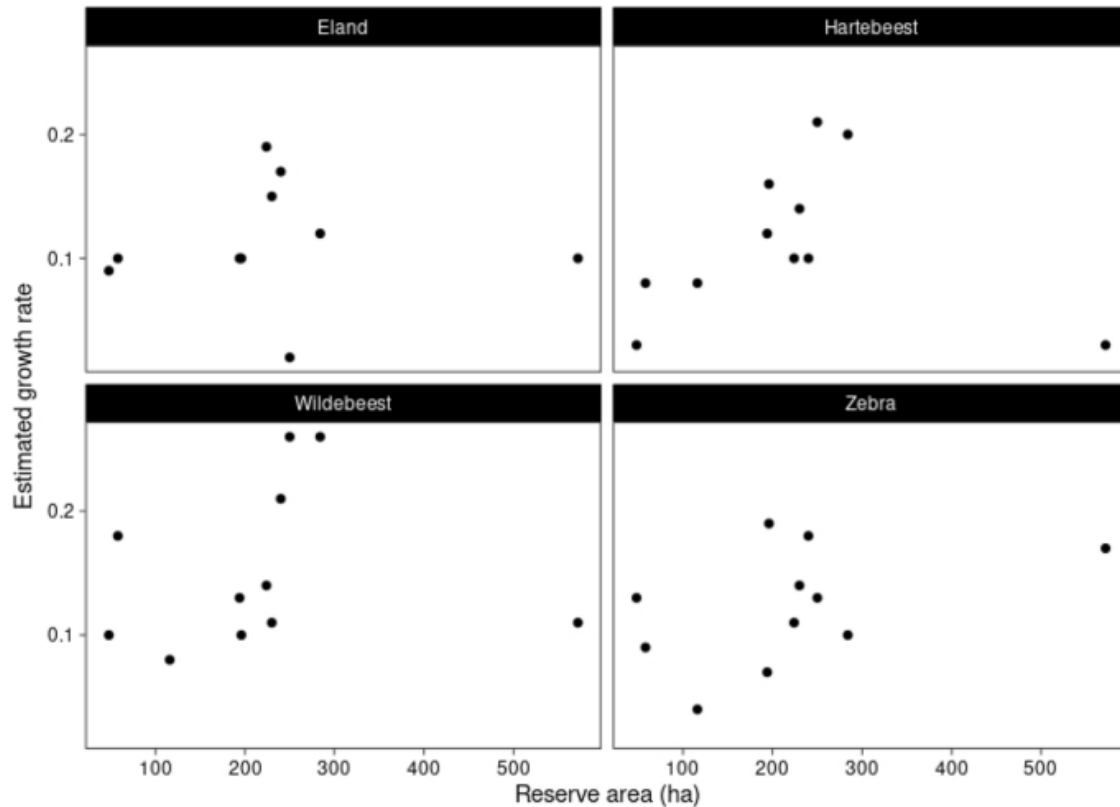


Fig. 3. Population growth in relation to area size in the absence of lions. If Pilanesberg on the far right is seen as an outlier, for hartebeest there is a strong positive correlation between area size and population growth. For other species, this positive correlation is less apparent

Discussion

Our findings demonstrate differing population responses to the presence of lions for hartebeest and eland (water independent) than for wildebeest and zebra (water dependent). The negative response to the presence of lions was most evident for hartebeest and eland populations, and least evident for wildebeest and zebra populations. This is consistent with the idea that in small insular systems, water availability gradients shape refuge availability, with water-independent species affected more so than water-dependent species. Similar declines for water-independent species have nevertheless been reported also for open systems (Chirima et al. 2013; Harrington et al. 1999; Crosmary et al. 2016; Ng’weno et al. 2017) not necessarily related to surface water frequency. Space use in larger open systems is perhaps more nuanced, i.e. additional trade-offs occur to firstly balance water and forage requirements (Ogutu et al. 2014), but simultaneously to avoid predation. Surface water too sparsely distributed might introduce additional travelling costs if resources become depleted (Crosmary et al. 2016; Ogutu et al. 2014). Also, similar declines have been reported for water-dependent species, e.g. the wildebeest population declined in Kruger National Park following prolonged above-average rainfall, which in turn increased ambush opportunities for lions (Smuts 1975). In the context of the current study, forage limitations are likely to be of secondary importance, given that populations are managed through regular removals. However, at a reduced spatial scale, hartebeest preference for tallgrass communities, and

associated increased ambush opportunities by lions, might predispose them to increased predation risk. Furthermore, the pre- and post-lion treatments at Pilanesberg and Mountain Zebra National Park sites closely follow the overall findings, providing further support for our overall findings. Note, however, that the mean long-term rainfall for the Zebra National Park was low during the post-lion introduction phase compared to the phase preceding lion introductions. While this suggests a cautionary note, both eland and hartebeest are drought-tolerant species (Veldhuis et al. 2019) whereas wildebeest and zebra are not.

We cannot rule out the potential impact of mesopredators or other large co-occurring predators on prey populations. For example, black-backed jackal (*Canis mesomalis*) selects for hartebeest new-born relative to wildebeest new-born, at least under game ranch settings where lions are absent (Klare et al. 2010), which possibly links to the fact that they hide their young for a period after birth (Skinner and Chimimba 2005). This likely explains the marginally more variable, and slightly lower mean population growth across sites (with no lions) for hartebeest when compared with the other study species. Broadly speaking though, the population growth for the study species in sites where lions are absent are very similar (Fig. 1), including the pre-lion phase at Pilanesberg and Mountain Zebra National Park. Leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*), and spotted hyena (*Crocuta crocuta*) predation most likely do not sufficiently differentiate between prey species to warrant inclusion into our modelling approach. Worth noting also is that for Madikwe, where lions and wild dog reintroductions coincided, a clear pre- and post-lion phase cannot be distinguished but predation data (North West Parks data unpublished data) suggest hartebeest contribute very little to wild dog kills and substantially to lion kills at Madikwe.

Area size effects on population fitness provide interesting scope for further research (Fig. 3). Wherever lions are absent, and with Pilanesberg considered an outlier, the correlation between hartebeest growth and area size suggests area size affords reduced competition between coexisting species, dictated possibly by differing surface water requirements and thermoregulatory abilities (Veldhuis et al. 2019). If anything, this adds credence to our notion that negative responses of hartebeest and eland are driven primarily by lion introductions in predominantly large areas. The poor fit of Pilanesberg possibly relates to the presence of a broader suite of large predators than found elsewhere.

The lack of kill data limits the scope of this study somewhat, so direct and indirect effects (see Valeix et al. 2009a, b; Clinchy et al. 2013) of predation could not be assessed. Furthermore, data on space use by coexisting species would add further insight into how species balance forage acquisition with predation risk across sites differing in vegetation structure. Such a study would possibly explain the anomalous response of prey species to lion introductions in the Albany thicket of Addo Elephant National Park (Fig. 2). Lack of open habitat most likely predisposed wildebeest and zebra to increased predation risk relative to water-independent species.

In summary, our findings are consistent with our expectation that water-independent species are more sensitive to predation risk at the spatial scales imposed by small conservation areas. We posit that this potentially relates, at least for hartebeest, to their preference for tallgrass communities where greater ambush opportunities predispose them to higher predation risk. We acknowledge that additional time-series data on prey densities, as well as those for lions, across a broad spectrum of ecological settings, are required to provide further insights into predator-prey dynamics at small spatial scales. We furthermore agree with previous authors

(Veldhuis et al. 2019; Kihwele et al. 2020) that decreasing surface water availability should be an important mitigating measure wherever the conservation of water-independent species is a priority.

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Conflict of interest

The authors declare that they have no competing financial interests.

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