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African Lion and Spotted Hyaena Changes in Kruger National Park, South Africa

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Abstract: Prey biomass, diversity, and availability dictate predator abundances and niche structure. Increased prey biomass and availability predicts that two apex predators, African lions and spotted hyaenas, should increase in abundance. Although elephant and rhino carcasses generated by poachers released prey biomass not previously available, individual lion prides or spotted hyaena clans may only have an additional fresh carcass for less than two weeks in a year. This predicts that predator changes primarily associate with prey biomass changes. We used a case study in Kruger National Park and showed that although African lion and spotted hyaena numbers increased, it did not associate with better availability of rhinoceros and elephant carcasses. Increases in the number of adult lionesses, instead, were linked with rises in prey biomass given competition with spotted hyaenas. Biomass of poached rhinoceros and elephant carcasses made trivial contributions to bottom-up changes in apex predator populations. Poachers, however, may induce top-down trophic cascades through the removal of keystone grazing and browsing species.

Introduction

Large predator guilds in intact African savannas typically comprise African lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), leopards (*Panthera pardalis*), brown hyaenas (*Hyaena brunnea*), cheetahs (*Acinonyx jubatus*), and wild dogs (*Lycaon pictus*). Competition and dietary niche packing often dictate the exact composition of a specific large predator guild.[1] Prey diversity and biomass are thus key drivers of predator dynamics in African savannas.[2] The influence of prey as a key resource predicts that changes in prey biomass should lead to changes in predator dynamics. Increases in prey should thus lead to increases in population sizes of large predator populations.

The large predator guild is relatively intact in the Kruger National Park (Kruger), a transitional savannah in South Africa.[3] A robust lion population, resilient to the emergence of bovine tuberculosis, dictates dynamics of the large predator guild.[4] Lions primarily compete with spotted hyaenas, another robust large predator with a dynamic population.[5] Although leopards spatially respond to where lions are, Kruger has an established leopard population.[6] Brown hyaenas are largely absent with only few records for Kruger. Cheetahs and wild dogs—the least dominant of the large carnivores—have small populations, with the wild dogs in particular recovering from a dramatic population decline.[7]

Kruger recorded substantial herbivore increases since the stopping of direct population control of several species, the restoration of natural water gradients through closure of boreholes and dams, and the restoration of natural food gradients through the dropping of fences.[8] In addition, the poaching of African elephants (*Loxodonta africana*) and rhinoceroses (white rhino--*Ceretotherium simum*, and black rhino--*Diceros bicornis*) may be a catalyst for a trophic cascade involving large predators.[9] Prey of African lions and spotted hyaenas does

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not typically include adult mega-herbivores like elephants and rhinos.[10] Both lions and spotted hyaenas, however, scavenge carcasses of any species if available.[11] Wide-scale poaching of elephants and rhinos may thus release prey biomass not available to lions and spotted hyaenas. Both these mechanisms reflect increased prey biomass and availability.

The killing of elephants and rhinos, however, are not distributed uniformly across the Kruger landscape. For instance, rhino poaching is most intense in southern Kruger (i.e. Marula Region), an area 9138 km^2 in size.[12] Even so, the number of rhinos and elephants killed per day on average is spread across the individual home ranges of a lion or spotted hyaena. Given that poachers killed 2.09 to 2.32 rhinos per day by the end of 2015 in southern Kruger, lions have a 1.2 percent to 4.5 percent chance of a new and fresh rhino carcass at any day, or 4.6 to 16.3 days per year, within a home range (range 52.2 km^2 to 175.9 km^2).[13] Spotted hyaenas have a 0.7 percent to 3.8 percent chance, or 3.7 to 13.7 days per year, given their territories (range 25 km^2 to 130 km^2).[14] At best, both lions and spotted hyaenas have reduced energetic prey capture costs for approximately two weeks a year. Energy expenditure to hunt has consequences for predator vital rates.[15] It is, however, unlikely that this is realized for lions and spotted hyaenas at a population level in Kruger.

We thus test two expectations. Given the increased overall available prey biomass, we expect that lion and spotted hyaena populations increased. The relative low additional prey biomass due to elephant and rhino poaching predicts that lion and spotted hyaena changes should primarily associate with changes in normal prey biomass. We use our results to reflect on potential atypical trophic cascades induced by poaching.[16]

Methods

Study Area

Kruger comprises thirty-five landscape types resulting from granite and gneiss deposits separated by Karoo sediment. In the southern parts, wooded savanna comprising *Sclerocarya caffra* and *Acacia nigrescens* dominates the basalts, while mixed *Combretum* spp. and *Acacia* spp. are the key species on granites. Northern parts comprise primarily *Colophospermum mopane* woodlands. Kruger is in the low-lying savanna of South Africa and covers 19,485 km^2 with annual rainfall exceeding 450 mm.[17]

Data Collection

We collated information on lion and spotted hyaena abundances for 2005-06 and 2008.[18] During July to September 2015, we surveyed 239 sample stations located throughout Kruger using similar techniques as before.[19] Sample stations had at least 10km spacing between them. At each sample station, we played a buffalo calf-in-distress recording continuously for one hour and recorded lions and spotted hyaenas that responded to the recording.

To define natural prey availability, we extracted census data for 1998 to 2016 from SANParks's data depository for the main herbivore species eaten by lions and spotted hyaenas.[20] Aerial surveys use distance sampling to estimate population sizes and confidence intervals for impala (*Aepyceros melampus*), giraffe (*Giraffa camelopardalis*), zebra (*Equus burchelli*), blue wildebeest (*Connochaetus taurinus*), kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus elipsiprymnus*), and warthog (*Phacochoerus aethiopicus*).[21] For buffalo (*Syncerus caffer*), authorities use total counts.[22] Estimates thus serve as minimum known to be alive at the time of a survey.

For the period 2005 to 2015, we also extracted annual poaching and natural death incidences of rhinos and elephants across Kruger from SANParks' data repository.[23] Kruger comprises twenty-two administrative units or sections. Rangers regularly patrol sections on foot and from aerial-based platforms. They use indicators such a vulture activity and tracks of poachers to locate carcasses. Rangers record the geographic locality, most likely cause of death, and state of decay that provides an estimate of the time since death. This allows backdating the date of death for each carcass.[24]

Data Analysis - Predator Abundance Changes

Estimated population sizes and 95 percent confidence intervals for lions came from the Jolly estimator adapted for lions.[25] This uses effective area sampled by a call-up station (circle with radius of 4.3±0.9km, mean±SD) and response rates of lions without (0.73±0.08 of groups present) and with (0.29±0.08 of groups present) cubs. The lion survey of 2008 introduced variance associated with distances of stations from water on total lion estimates.[26] Estimates of adult females, however, were unbiased then.[27] Furthermore, adult females are the key demographic component. We thus used the number of adult females as the response variable. For spotted hyaenas, we used the Jolly estimator adapted for hyaenas.[28] Call-up stations sample a radius of 2.12±0.16 km, with 0.68±0.01 of adult and sub-adult individuals responding.

To evaluate overall change in Kruger, we calculated exponential growth between survey years for both species. We randomly extracted a value from the statistic distribution of estimates in the two years of comparison and calculated the annual exponential growth from one estimate to the next estimate. We repeated the procedure 100,000 times, from which we extracted the median value as a point estimate of the exponential growth. The 2.5% and 97.5% percentiles provided estimates of the lower and upper confidence interval respectively. We concluded significant change if the 95% confidence intervals excluded zero.

Data Analysis - Drivers of Changes in Lions and Spotted Hyaenas

Several explanatory variables influence changes in apex predator abundance. We used the previous zonation of Kruger to evaluate the influence of various explanatory variables on predator changes.[29] This provided us with six zones of varying levels of prey biomass (Fig. 1). In addition, we defined response variables as well as explanatory variables for the 2005-2008 as well as the 2008-2015 periods for these zones. The number of adult females at the start of a period was an explanatory variable for changes in lions and spotted hyaenas. Change in adult and sub-adult individuals was our response variable. The number of adult and sub-adults at the start of a period served as an explanatory variable for both changes in lions and spotted hyaenas. We estimated exponential growth per annum as response variables of lion and spotted hyaena changes within each zone over the two focal periods.

We focused on population changes for lions and spotted hyaenas between 2005/2006 and 2008 as well as 2008 and 2015 as response variables per zone. Food resources, partitioned into natural prey, poached carcasses, and natural carcasses, were included as explanatory variables. Next, we considered intra-specific interactions and used species-specific abundance estimates at the start of each time interval for lions and spotted hyaenas as an additional explanatory variable. Finally, we focused on competition between lions and spotted hyaenas and included lion changes as an explanatory variable for changes in spotted hyaenas and *vice versa*.

Interactions with external drivers can also explain changes in predator abundances. Previous studies concluded little influence of bovine tuberculosis (*Mycobacterium bovis*) on predator dynamics in lions or spotted hyaenas.[30] We thus did not include bovine tuberculosis incidence as an explanatory variable. Herbivores live at higher densities on the basalts than the granites. In addition, densities are lower in the dry north of Kruger irrespective of substrate. Herbivore numbers increased over the study period.[31] The six zones thus had different herbivore densities and hence prey biomass across space and time.

Using extracted estimates, we calculated the biomass of eight key prey species comprising >95 percent of lion and hyaena prey in Kruger.[32] We multiplied each species' estimated abundance by the average adult female body mass.[33] For the 2005 to 2008 period, we used the annual biomass from 2005 to 2008 to estimate average annual prey biomass for that period. Annual biomass estimates from 2009 to 2015 provide the average annual prey biomass for the 2008 to 2015 period.

To estimate biomass provided by black rhino, white rhino, and elephant carcasses, we extracted the annual number of carcasses found within each of the six zones.[34] Note, our analyses combined black and white rhinos. We assigned cause of death as poached or natural, and estimated average annual biomass (average adult female body weight multiplied by number of carcasses) from poached individuals and deaths through natural causes for each zone and each of the two study periods.

Having defined response and explanatory variables, we used generalized linear modelling to evaluate changes in lions and spotted hyaenas. Candidate models included all combinations of explanatory variables. We standardized each response variable to range from zero to one. This reduced bias influence of a specific variable. We used model selection and the AICc metric to identify the most likely models.[35] All models less than two different from the model with the smallest AICc were included as models explaining the changes in lions or spotted hyaenas. We specifically used the AICc metric because we were conscious of the small sample size and the influence that has on model selection. To check the importance of a specific variable, we calculated the relative variable importance as the sum of the calculated Akaike weights of all the models in the set containing a particular variable.[36]

Our analyses highlighted that competitive interactions play a key role in defining changes of lions and spotted hyaenas. We thus calculated the residual of changes in lions using the linear relationship with changes in spotted hyaenas. We used linear regression of these residuals against all other explanatory variables to elucidate factors that associate with changes in abundance once we accounted for competition. We used Microsoft Excel for all analyses.

Results

Predator Abundance Changes

During 2005-06, 413 (95 percent CI: 371-455) adult female lions lived in Kruger. The 2008 estimate was similar when 411 (343 to 479) adult females lived in Kruger. By 2015, we recorded 604 (515-693) adult females living in Kruger. Overall, 1803 (1715-1891) lions lived in Kruger during 2015. The spotted hyaena estimate during 2005-06 of 3348 (3131-3566) did overlap with the 2008 estimate when 3667 (3443-3891) individuals lived in Kruger. During 2015, 7339 (6998-7680) sub-adult and adult spotted hyaenas lived in Kruger.

Between 2005-06 and 2008, the number of adult female lions did not change across Kruger (0.01, 95% CI: -0.07 – 0.06), but increased from 2008 to 2015 (0.06, 95 percent CI: 0.02 – 0.09). These changes were not consistent across the six zones of Kruger (Fig. 1). Spotted hyaenas also did not change (0.03, 95 percent CI: -0.07 – 0.15) between 2005-06 and 2008.

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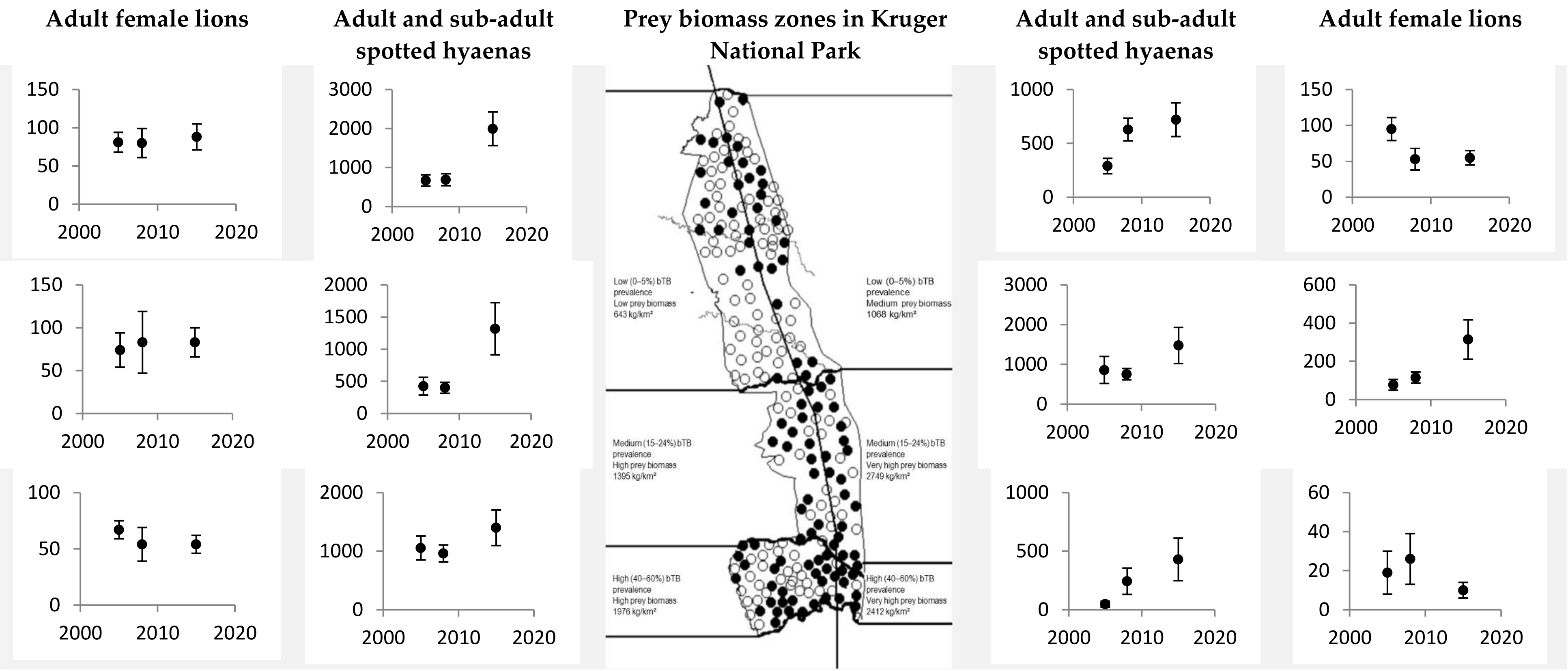

Figure 1. Estimates of adult female lions as well as adult and sub-adult spotted hyaenas derived from call-up localities (map: circles are call-up localities, dark are an example of responses for lions during 2005/2006[37]) during the survey periods from 2005 to 2015. We indicate the six prey biomass zones used in our analyses and the estimates of adult female lions and adult and sub-adult spotted hyaenas for each of these zones. Error bars represent 95% confidence intervals of the estimates.

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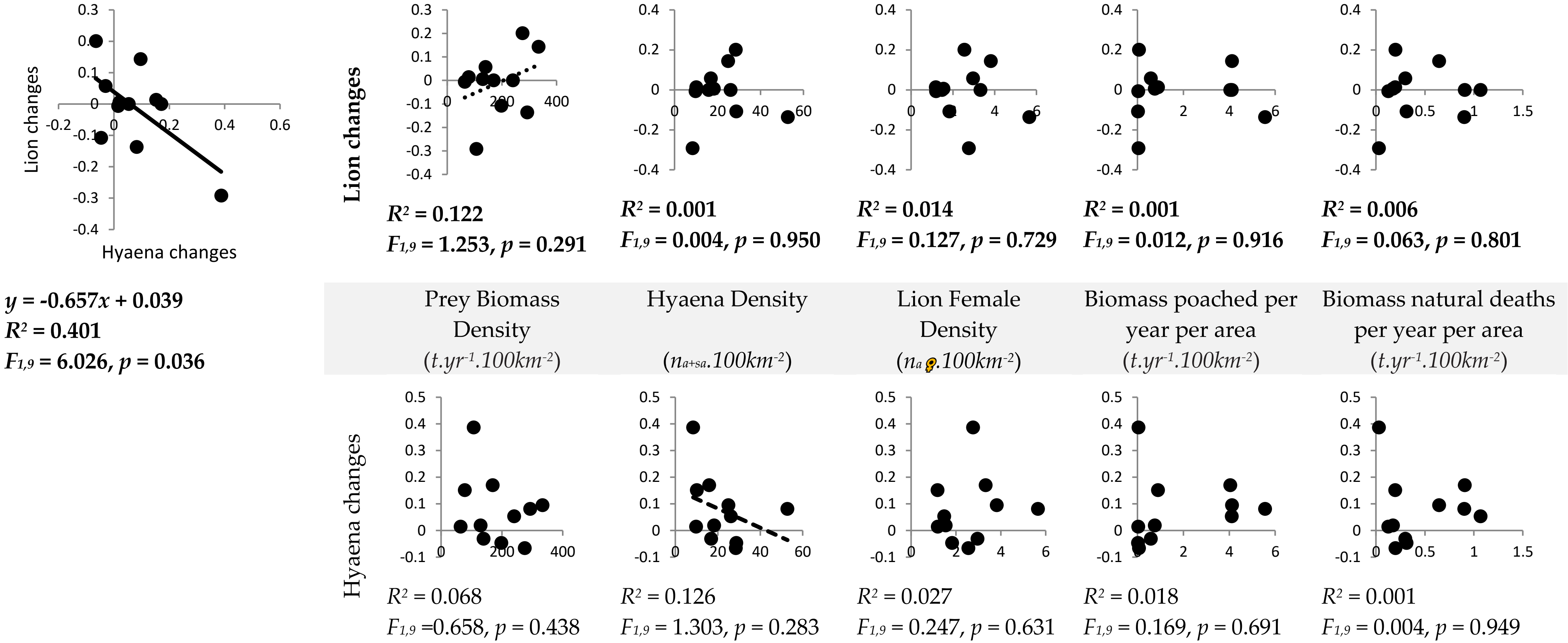

$y = -0.657x + 0.039$
$R^2 = 0.401$
$F_{1,9} = 6.026, p = 0.036$

Prey Biomass Density $(t.yr^{-1}.100km^{-2})$
Lion changes: $R^2 = 0.122$, $F_{1,9} = 1.253, p = 0.291$
Hyaena changes: $R^2 = 0.068$, $F_{1,9} = 0.658, p = 0.438$

Hyaena Density $(n_{a+sa}.100km^{-2})$
Lion changes: $R^2 = 0.001$, $F_{1,9} = 0.004, p = 0.950$
Hyaena changes: $R^2 = 0.126$, $F_{1,9} = 1.303, p = 0.283$

Lion Female Density $(n_{a♀}.100km^{-2})$
Lion changes: $R^2 = 0.014$, $F_{1,9} = 0.127, p = 0.729$
Hyaena changes: $R^2 = 0.027$, $F_{1,9} = 0.247, p = 0.631$

Biomass poached per year per area $(t.yr^{-1}.100km^{-2})$
Lion changes: $R^2 = 0.001$, $F_{1,9} = 0.012, p = 0.916$
Hyaena changes: $R^2 = 0.018$, $F_{1,9} = 0.169, p = 0.691$

Biomass natural deaths per year per area $(t.yr^{-1}.100km^{-2})$
Lion changes: $R^2 = 0.006$, $F_{1,9} = 0.063, p = 0.801$
Hyaena changes: $R^2 = 0.001$, $F_{1,9} = 0.004, p = 0.949$

Figure 2. Univariate relationships recorded between changes in lions (changes in adult female lions) and spotted hyaenas (changes in adult and sub-adult hyaenas) and a number of independent variables. We provide linear regression results and highlight significant relationships with a solid line. We also highlight those relationships with $R^2 > 0.1$ with a broken line

From 2008 to 2015, spotted hyaenas increased significantly (0.10, 95 percent CI: 0.06 – 0.14). These changes were also not consistent across the six zones (Figure 1)

Drivers of Changes in Lions and Spotted Hyaenas

The strongest relationship explaining carnivore changes reflected on a competitive interaction. Lion changes were inversely related to spotted hyaena changes and vice versa (Figure 2). Note that annual biomass from poached individuals per unit area did not play a role in explaining changes in lions or spotted hyaenas.

Eleven models were included for lions across the six zones and two time-periods (Table 1). Changes in spotted hyaenas carried a combined Akaike weight of 0.22 in the 54.5 percent of models that included this variable. All other variables were part of only 18.2 percent of the selected models. The second relative important variable was prey biomass (combined Akaike Weight = 0.10), while spotted hyaena abundance, lion abundance, poached carcass biomass and natural carcass biomass had combined Akaike weights of 0.09 each.

For changes in spotted hyaenas, our analyses identified thirteen models (Table 1). Changes in lions were included in 42.9 percent for which the combined Akaike weight was 0.19. Hyaena abundance (combined Akaike weight = 0.16) and prey biomass (combined Akaike weight = 0.15) were part of 28.6 percent of the selected models. Lion abundance (combined Akaike weight = 0.12) and poached carcass biomass (combined Akaike weight = 0.12) were present in 21.4 percent of the models, with natural carcass biomass (combined Akaike weight = 0.06) in only 14.3 percent.

Table 1. Candidate Models Used in Our Analyses (A. Adult Female Lions. B. Adult and Sub-Adult Spotted Hyaenas)

A. Adult Female Lions

Variables included	R^2	RSS	AIC_c	Delta	Likelihood	Weight
HC	0.43	578.92	1.54	0.00	1.00	0.07
PBD	0.33	674.81	1.63	0.09	0.96	0.07
HD	0.25	760.18	1.69	0.15	0.93	0.06
PYA	0.07	941.09	1.80	0.26	0.88	0.06
LFD	0.05	954.71	1.81	0.27	0.87	0.06
NYA	0.05	961.83	1.81	0.27	0.87	0.06
HC+PBD	0.59	417.00	3.32	1.78	0.41	0.03
HC+LFD	0.58	422.70	3.33	1.79	0.41	0.03
HC+PYA	0.53	471.84	3.41	1.87	0.39	0.03
HC+NYA	0.45	551.30	3.51	1.97	0.37	0.03
HC+HD	0.44	564.50	3.52	1.98	0.37	0.03

B. Adult and Sub-Adult Spotted Hyaenas

Variables included	R^2	RSS	AIC_c	Delta	Likelihood	Weight
LC	0.43	607.66	1.57	0.00	1.00	0.07
HD	0.38	657.34	1.61	0.05	0.98	0.07
LFD	0.06	999.46	1.83	0.26	0.88	0.06
PBD	0.01	999.46	1.83	0.26	0.88	0.06
PYA	0.01	1046.66	1.85	0.28	0.87	0.06
NYA	0.01	1051.98	1.85	0.29	0.87	0.06
LC+LFD	0.58	442.52	3.36	1.80	0.41	0.03
HD+PBD	0.57	456.93	3.38	1.82	0.40	0.03
LC+HD	0.54	488.13	3.43	1.86	0.39	0.03
LC+PYA	0.50	524.77	3.47	1.91	0.38	0.03
LFD+HD	0.50	525.24	3.48	1.91	0.38	0.03
PYA+PBD	0.46	575.10	3.53	1.97	0.37	0.03
LC+PBD	0.44	597.25	3.55	1.99	0.37	0.03

Key: HC – change in adult and sub-adult spotted hyaenas, LC – change in adult female lions, PBD – prey biomass density, HD – spotted hyaena density, PYA – biomass of rhinos poached per annum per unit area, LFD – adult female lion density and NYA – biomass of rhinos that died naturally per annum per unit area. We present only the chosen models.

Competitive interactions between spotted hyaenas and lions dominated the selected models. Residuals of lion changes after we accounted for the effect of spotted hyaenas, related to prey biomass (Figure 3).[38] Residual lion changes had no associations with the other variables.[39] Residuals of spotted hyaena changes after removing the effect of lions, did not relate to any of the remaining variables.[40]

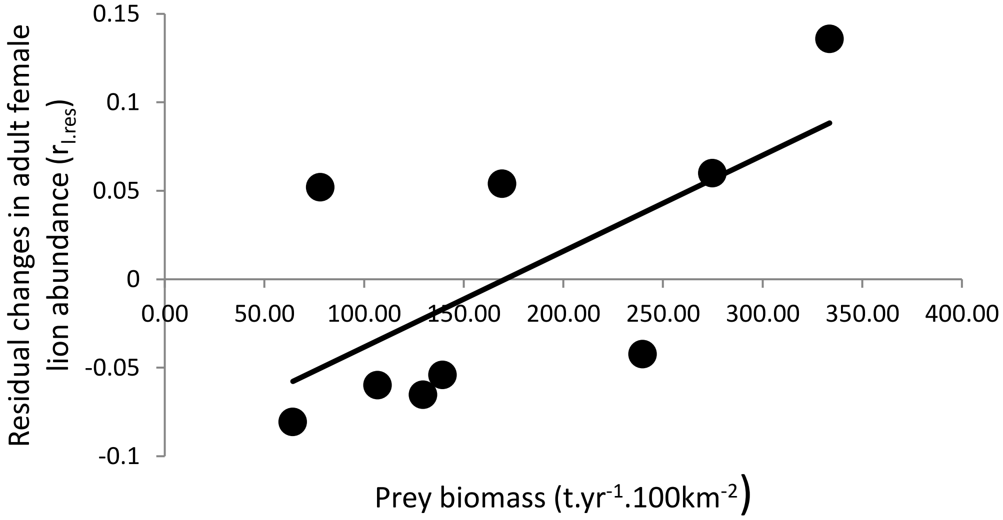

Figure 3. The relationship between changes in adult female lions and prey biomass once we accounted for the effect of competitive interactions with spotted hyaenas.

Discussion

Large predator dynamics and consequent trends in undisturbed populations typically associate with the dynamics of their prey.[41] Over the study period, we recorded significant increases both in lions and spotted hyaenas. We, however, could not find evidence that lions and spotted hyaenas in Kruger had higher abundances or population growth rates after food increases due to rhino and elephant poaching. Increases instead associated with natural prey biomass increases.

Predator switching to different prey items can impact our results—in such instances predators may not increase in abundance.[42] Some aspects highlight that this was unlikely. First, we recorded a significant increase in both lion and spotted hyaena abundances. Second, although changes in lion diets that studies recorded before associated with environmental conditions and bovine infection status of prey, previous studies found no evidence of rhino or elephant forming part of lion diet during 2010 to 2012.[43] During this period, poachers killed 1449 rhinos comprising both black and white rhinos. Note no elephants were poached then.

[44] We acknowledge that the absence of hard evidence of lions and spotted hyaenas changing their diet over our study period provide constraints. Even so, prey biomass increased substantially. It is likely that even if lions and spotted hyaenas changed diet, the impact on our results is negligible.

The dynamics of top predators in Kruger associate with natural prey biomass and interspecific interactions.[45] We noted that models included prey biomass that dictated lion dynamics, while intra-specific competition with spotted hyaenas dictated how well they responded to prey. Typically, lion abundances increase when the preferred ungulate prey biomass increases. For spotted hyaenas, competition with lions played a key role. Prey overlap between lions and spotted hyaenas in Kruger predicts competition between lions and spotted hyaenas.[46] Lions are the dominant competitor, hence the difference in the importance of prey and competition noted between lions and spotted hyaenas.

Note that potential effects of the disease bovine tuberculosis for both lions as well as spotted hyaenas is most likely negligible. Previous studies highlighted little predicted consequences for lions.[47] We thus do not expect bovine tuberculosis influences in the present study. Other diseases, synergistic effects of multiple diseases, or droughts can influence the dynamics of species. We are not aware of any other wide-spread disease incidences, and Kruger had above average rainfall during our study.[48]

Impacts of human disturbances that disrupt the food chain of which large predators form part may carry inconsistent consequences.[49] Lion numbers across Africa have declined with as few as 20,000 remaining.[50] Global trends for spotted hyaenas are uncertain. It is likely that top predators like lions and spotted hyaenas experience similar stressors such as habitat encroachment, bush-meat trade, retribution killing, and by-kill from poaching.[51]

Wildlife trafficking is one of the key global environmental change drivers that threatens many species.[52] Poachers who provide illegal wildlife goods linked to a species directly affect the extinction probability of that species. One exception is when poachers increase food available to top predators.[53] These may have consequences for predator populations because unavailable prey items become available.

The low influence of rhino and elephant carcasses on lion and spotted hyaena abundances contrasted the predictions made previously of poacher induced increases in top predator abundances because more food becomes available.[54] Above average rainfall in Kruger over our study period may have had consequences for natural prey biomass of lions and spotted hyaenas. Indeed, previous analyses highlighted that overall herbivore biomass increased.[55]

Even though the two top predators did not respond to more rhino and elephant carcasses, poachers may induce other cascade consequences along the food chain.[56] Rhinos create grazing lawns that influence grazing and fire regimes within Kruger.[57] Poaching effects on rhino distribution and abundance could lead to top-down cascades—in other words reduced rhinos may lead to reduced grazing lawns that then have impacts on several grazing antelopes.[58] The presence of historic man in Kruger could have induced some of these negligible disturbance effects on rhino distribution and populations.[59] It is unlikely though that these would have been at the intensity that recent poaching imposes. Our study does not negate that authorities need policies and implementation plans that reduce illegal human-disturbances in protected areas.

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Notes

1 Owen-Smith and Mills 2008
2 Mills et al. 1995; Moleón et al. 2015
3 Owen-Smith and Mills 2008
4 Ferreira and Funston 2010
5 Ferreira and Funston 2016
6 Maputla 2014; Maputla et al. 2015
7 Marnewick et al. 2014
8 van Wilgen et al. 2016; Smit et al. 2020
9 Everatt et al. 2016
10 Owen-Smith and Mills 2008
11 Perreira et al. 2014
12 Ferreira et al. 2015
13 Data available from the SANParks Environmental Crime Investigation Database, Ken Maggs, (ken.maggs@sanparks.org). Maruping 2015; Lion home-range characteristics used LoCoh, Kernel Tools (Powel 2012) and Animal Movements found in Hawth’s Tools (http://www.spatialecology.com/htools) [Accessed: 2012, 30 March] with the smoothing factor h*ref* (Hemson et al. 2005). Data comprises 300 to 850 GPS fixes for 32 lionesses to help define 90% and 50% isopleth kernels, $k = \sqrt{n}$ were used to calculate the seasonal total and core range respectively, where k is kernel isopleth and n is the number of fixes in the set.
14 Henschel 1986; Minimum polygons using information of individuals followed for extended periods over four seasons.
15 Laundré 2014
16 Everatt et al. 2016
17 Ferreira and Funston 2010
18 Ferreira and Funston 2010; Young-Overton, Funston and Ferreira 2014; Ferreira and Funston 2016
19 Ferreira and Funston 2010
20 Data available from the SANParks Data Repository, Judith Botha, judith.botha@sanparks.org; Owen-Smith and Mills 2008; The study collated records of the carcasses of all animals found dead and the cause of death collected by rangers from 1936 to 1946 and 1954 to 1995. From 49453 carcasses, only 6% had causes other than kills by predators including lions, spotted hyenas, leopards (*Panthera pardus*), cheetah (*Acinonyx jubatus*) and African wild dog (*Lycaon pictus*).

21 Kruger et al. 2008
22 Mills et al., 1995
23 Data available from the SANParks Environmental Crime Investigation Database, Ken Maggs, ken.maggs@sanparks.org
24 Personal communication, Ken Maggs, ken.maggs@sanparks.org
25 Ferreira and Funston 2010
26 Young-Overton et al. 2014
27 Young-Overton et al. 2014
28 Ferreira and Funston 2016
29 Ferreira and Funston 2010; Substrate, vegetation and climate helped to define zones. Herbivores have higher densities on fertile basalts in the east than on western granites; and lower densities in the dryer north than the wetter south of Kruger. Two large perennial rivers further dictated zoning. The Olifants and Sabie Rivers are perennial and act as effective barrier for most prey species. This lead to six zones with varying levels of prey biomass and prevalence of bovine tuberculosis prey.
30 Ferreira and Funston 2010; Ferreira and Funston 2016
31 Smit et al. 2020
32 Owen-Smith and Mills 2008
33 Skinner and Chimimba 2005
34 Data available from the SANParks Environmental Crime Investigation Database, Ken Maggs, ken.maggs@sanparks.org
35 Johnson and Omland 2004
36 Burnham and Anderson 2002
37 Ferreira and Funston 2010
38 rl = -0.823rh+0.086, F1,7=15.15, P<0.01, R2=0.68, where rl is changes in adult female lioness abundances and rh changes in adult and sub-adult spotted hyaena abundances; rl.res = 0.001pn – 0.093, F1,7=5.35, P<0.05, R2=0.43 where rl.res is residual lion abundances and pn is natural prey biomass
39 lion abundance: F1,7=2.94, P=0.13, R2=0.29; poached carcass biomass: F1,7=2.29, P=0.17, R2=0.25; adult and sub-adult spotted hyaena abundance: F1,7=1.61, P=0.24, R2=0.19; and natural death carcass biomass: F1,7=0.82, P=0.40, R2=0.10
40 rh = -0.831rl+0.099, F1,7=15.15, P<0.01, R2=0.68 rl is changes in adult female lioness abundances and rh changes in adult and sub-adult spotted hyaena abundances; lion abundance: F1,7=3.16, P=0.11, R2=0.31; poached carcass biomass: F1,7=1.80, P=0.22, R2=0.21; prey biomass: F1,7=1.25, P=0.30, R2=0.15; natural death carcass biomass: F1,7=0.41, P=0.55, R2=0.05; and spotted hyaena abundance: F1,7=0.01, P=0.92, R2=0.01
41 Mills et al. 1995; Moleón et al. 2015; Owen-Smith and Mills 2008
42 Perreira et al. 2014; Moleón et al. 2015
43 Maruping-Mzileni et al. 2017; Researchers collected scats and kill data for lions from 2010 to 2012. Kill data came from direct observations of 32 study prides. Clusters of satellite fixes (i.e. 3 consecutive 8 hour interval fixes within 100 m) derived from at least one lion fitted with a satellite transmitter allowed researchers to visit a kill site and identify the prey. Collection of scats was opportunistic during the study period. The combined records from kills and scats was sufficient to define lion diet (Trites and Joy 2005).
44 Data available from the SANParks Environmental Crime Investigation Database, Ken Maggs, ken.maggs@sanparks.org
45 Ferreira and Funston 2010; Ferreira and Funston 2016; Owen-Smith and Mills 2008

46 Owen-Smith and Mills 2008
47 Ferreira and Funston 2010; Ferreira and Funston 2016; Kosmala et al. 2016
48 van Wilgen et al. 2016
49 Worm and Paine 2016
50 Bauer et al. 2016
51 Ripple et al. 2014
52 Rosen and Smith 2010
53 Everatt et al. 2016
54 Ferreira and Funston 2010; Ferreira and Funston 2016
55 van Wilgen et al. 2016; Smit et al. 2020
56 Everatt et al. 2016
57 Cromsigt and Beest 2014
58 Ferreira et al. 2015
59 Carruthers 1995