

## Spatial distribution of lion kills determined by the water dependency of prey species

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Predation risk from lions (*Panthera leo*) has been linked to habitat characteristics and availability and traits of prey. We separated the effects of vegetation density and the presence of drinking water by analyzing locations of lion kills in relation to rivers with dense vegetation, which offer good lion stalking opportunities, and artificial water points with low vegetation density. The spatial distribution of lion kills was studied at the Klaserie Private Nature Reserve, South Africa. The distance between 215 lion kills and the nearest water source was analyzed using generalized linear models. Lions selected medium-sized prey species. Lion kills were closer to rivers and to artificial water points than expected by random distribution of the kills. Water that attracted prey, and not the vegetation density in riverine areas, increased predation risk, with kills of buffalo (*Syncerus caffer*), kudu (*Tragelaphus strepsiceros*), and wildebeest (*Connochaetes taurinus*) as water-dependent prey species. Traits of prey species, including feeding type (food habits), digestion type (ruminant or nonruminant), or body size, did not explain locations of lion kills, and no seasonal patterns in lion kills were apparent. We argue that the cascading impact of lions on local mammal assemblages is spatially heterogeneous. DOI: 10.1644/09-MAMM-A-392.1.

Key words: body weight, Normalized Difference Vegetation Index (NDVI), *Panthera leo*, prey availability, prey composition, randomization, savanna, vulnerability

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Predation is known to influence the behavior of prey species (Fischhoff et al. 2007; Prins and Iason 1989; Winnie et al. 2008), their density, spatial distribution, and habitat selection (Creel et al. 2005; Valeix et al. 2009), and prey assemblage (Hayward et al. 2007a, 2007b; Mills and Shenk 1992; Mills et al. 1995; Owen-Smith and Mills 2006; Sinclair 1985; Sinclair et al. 2003), and can thereby trigger ecosystem cascades (Carpenter et al. 2008; Ripple and Beschta 2006, 2007). Several studies show that female lions (*Panthera leo*) generally take medium-sized species such as plains zebra (*Equus burchellii*) and blue wildebeest (*Connochaetes taurinus*), whereas males prey on larger species such as African buffalo (*Syncerus caffer*—Funston et al. 1998, 2001; Lehmann et al. 2008; Mills et al. 1995; Owen-Smith and Mills 2008). The smaller-sized impala (*Aepyceros melampus*) generally is negatively selected (Funston and Mills 2006; Hayward et al.

2007a). Hence, prey body mass is a major factor influencing prey selection by lions (Hayward and Kerley 2005). Large differences in the composition of lion prey are due to differences in prey availability, prey mass, lion sex and pride structure, and cultural differences, that is, differences in prey choice between prides through specialization (Funston et al. 2001; Hayward and Kerley 2005; Hayward et al. 2007a), sometimes modified by environmental factors such as rainfall that affect the body condition of prey (Funston and Mills 2006; Mills et al. 1995). Ogotu and Dublin (2004) showed that lion density is correlated positively with prey biomass and that prey availability seems to be more important than habitat



characteristics in determining composition of lion prey (Hayward et al. 2007b; Spong 2002), as is also documented for other carnivores (Murray et al. 1994; Palomares et al. 2001). An ongoing debate exists about the importance of landscape elements, such as erosion gullies, river confluences, kopjes (small rocky hills), and proximity to water, each with different structure and vegetation cover that influence predation risk (Balme et al. 2007; Hopcraft et al. 2005). However, hunting success was only slightly higher in dense vegetation where it is thought to provide cover for stalking lions (Funston et al. 2001; Prins and Iason 1989; Van Orsdol 1984). In the most comprehensive analysis, Hopcraft et al. (2005) showed that certain landscape elements increase predation risk: prey vulnerability is more important to lions than prey availability. The presence of water sources could be beneficial for lions because water attracts prey species that are often closely linked to dense vegetation, especially riverine areas (Rogers and O'Keefe 2003; Van Orsdol 1984; Venter et al. 2003). The presence of natural water sources therefore can influence the location of lion kill sites (Hopcraft et al. 2005). The question remains whether the locations of lion kills are influenced by the availability of water sources, and if this effect is due to the attraction of wildlife to water and hence the higher prey densities there, or if it is caused by the increased cover for stalking lions around these water sources.

We separated the effect of water supply on predation by lions from the effect of cover provided by vegetation associated with rivers. Moreover, we tested for differences in the spatial distribution between kills of different prey species. The distribution of prey species is dependent on such prey traits as water dependency, body size, or feeding type (food habits). The spatial distribution of lion kills in relation to the distribution of their prey, and the traits of the prey species that determine their distribution, are not clear. We analyzed the effect of several traits of prey species on the spatial distribution of lion kills. Water dependency is one of the traits that determines the spatial distribution of lion prey, because prey availability is higher closer to water (De Leeuw et al. 2002). Wildlife species are not distributed randomly over an area; some species (e.g., waterbuck [*Kobus ellipsiprymnus*]) are always found close to water, whereas other species (e.g., giraffe [*Giraffa camelopardalis*]) are less dependent on water (De Leeuw et al. 2002; Redfern et al. 2003). Lion kills of waterbuck are significantly closer to water points than expected based on chance simply because this prey species is not randomly distributed over the landscape. Hence, we expect kills of water-dependent species to be closer to water than kills of species not dependent on water.

Body size and feeding type can influence water dependency of a species (Redfern et al. 2003). Larger species generally have a larger home range to satisfy their requirements (Haskell et al. 2002), so that smaller species would be found closer to water than larger species. Moreover, grazers are more water-dependent than browsers because of the lower water content in grass, and nonruminants would need a larger home range than ruminants of similar size because of their generally larger

intake requirements (Redfern et al. 2003). Hence, kills of smaller, grazing ruminants are expected to be found closer to water than those of larger, browsing nonruminants. Moreover, it has been found that grazers are more associated with artificial water holes and browsers and mixed feeders with natural water sources (Smit et al. 2007); hence we expect that kills of grazers will be closer to artificial water points and those of browsers and mixed feeders closer to rivers.

Seasonal differences also affect the distribution of lion kills (Lehmann et al. 2008). In the wet season the availability of ephemeral water sources increases, and the tendency of prey to enter high-risk areas such as those near water decreases (Hopcraft et al. 2005). Thus, kills are expected to be found farther from water points in the wet season than in the dry season.

## MATERIALS AND METHODS

*Study area.*—To test these hypotheses we analyzed the spatial distribution of lion kills in Klaserie Private Nature Reserve in South Africa (24.203°S, 31.179°E), which forms part of the Associated Private Nature Reserve abutting and contiguous with the Kruger National Park. The study area is dominated by open woodland, with mopane (*Colophospermum mopane*) and red bush willow (*Combretum apiculatum*) as dominant tree species. The mean annual rainfall in the study area was 460 mm/year (1997–2007), of which 80% falls between October and the end of March. The Klaserie River runs through the area and Olifants River forms the northern boundary of the conservation area. Seventy-seven artificial water points and 40 catchment dams provide drinking water over the entire year, over an area of 579 km<sup>2</sup>, so temporal fluctuations in water availability are not significant.

When lion kills were encountered—identified by the presence of lions or lion tracks at the kill site—they were recorded by Klaserie staff members in a central database; data recorded included date, location (global positioning system coordinates), and species. In total, 215 lion kills were found from July 2002 to May 2007 (Fig. 1). Because the reserve is rather small, the road network is very dense, and foot patrols cover the full extent of the reserve, even small carcasses are recorded and the bias for certain species in the lion kill database is minimized.

Water points were classified as artificial (catchment dam, pump, or mill) or natural (one of the rivers). For each location of a lion kill the shortest (straight-line) distance between that location and the nearest artificial and natural water point was calculated using ArcGIS (version 9.2; ESRI Inc., Redlands, California). The resulting set of shortest distances was compared with an equal number of randomly generated shortest distances, calculated from the distance between randomly located points and their nearest artificial and natural water points.

*Statistical analysis.*—The selection by lions for each prey species was calculated using the Jacobs' index *D* (Hayward and Kerley 2005; Krebs 1989), ranging from +1 to -1 for

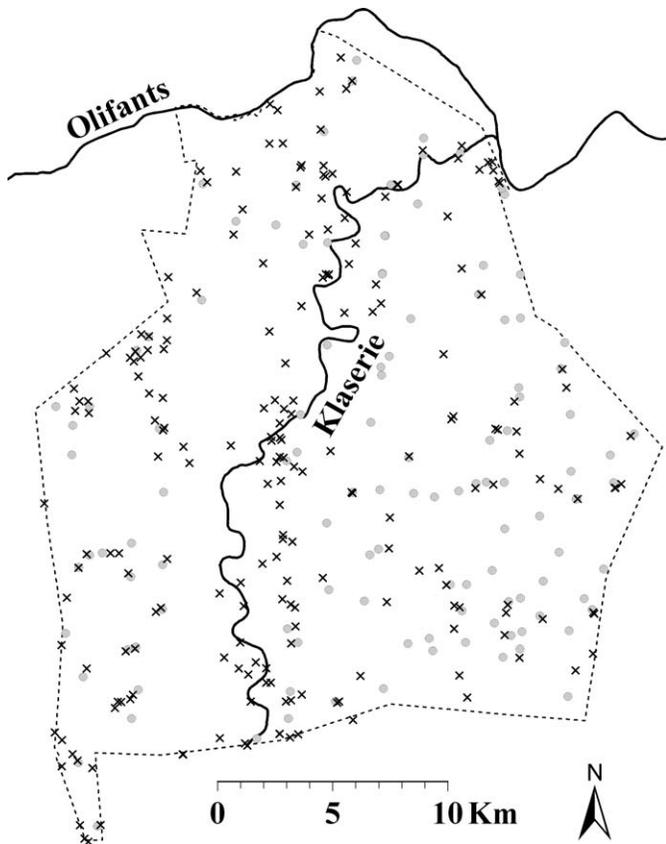


FIG. 1.—Map of the Klaserie Private Nature Reserve showing the lion kill locations (x), the Olifants and Klaserie rivers, and the distribution of the artificial water points and catchment dams (O).

maximum selection and avoidance, respectively. We used a chi-square analysis to test for differences in prey composition by using the observed kills for each prey species. Expected values were calculated based on the average of the annual abundance estimates for each prey species from aerial surveys carried out between 2002 and 2006. This analysis yields chi-square values for each prey species, and the discrepancies between observed and expected values (residuals) were tested for each of the individual species when the overall chi-square test reported significant deviations from expectation (Siegel and Castellan 1988).

We checked for spatial autocorrelation of the distances between kill sites and water with Moran's  $I$ , using SAM version 3 (Rangel et al. 2006). Moran's  $I$  measures the autocorrelation between paired observations in relation to the distance (the "lag" distance) between these observations. The clustering in space of the lion kill locations was tested in ArcGIS, using a Z-test on the average nearest-neighbor distance between lion kills. A generalized linear model, carried out in SPSS version 15 (SPSS Inc., Chicago, Illinois), was applied with shortest distance between lion kill and water source as the dependent variable. The dependent variable was positively skewed; therefore, a gamma distribution with a log-link was used. A Pearson chi-square method was used to calculate the scale parameter, and a sequential Sidak method was used in the multiple comparison tests (Hardin and Hilbe

2007). Type of water source (natural or artificial) or random point was included as a fixed factor, together with several other fixed factors—feeding type, digestion type (ruminant or nonruminant), and season—and the covariates body mass and water dependency. Kills were classified with respect to feeding type (Table 1), digestion type, and body mass. Redfern et al. (2003) calculated the probability of encountering different herbivore species in relation to the distance from water points. We used the odds-ratio, a continuous variable calculated by Redfern et al. (2003), as a proxy for water dependency of the different prey species. This variable is a better classification of the spatial distribution of a species around water than classifying the species as either water-dependent or water-independent. The lower the odds-ratio, the closer to water a species was found. The odds-ratio was available for most species (94% of all 215 kills), but the water dependency of the missing 13 kills (5 species) were estimated using the expert opinion of the Klaserie Warden (for instance, the water dependency of warthog [*Phacochoerus africanus*] is characterized as intermediate to that of impala and water-buck).

We also tested whether kill locations were associated with a different vegetation density than random locations, as expected from the vulnerability hypothesis (Hopcraft et al. 2005). We tested our assumption that vegetation density would be higher around riverine areas compared to artificial water points. An index of the vegetation density, and thereby for stalking opportunities of lions, was obtained using Normalized Difference Vegetation Index (NDVI) data from 19 February 2006, in the middle of the rainy season, from Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER; <https://lpdaac.usgs.gov>, accessed 2 June 2009). Data analysis was done in ArcGIS, selecting only those grid cells (15 × 15 m) where lion kills or random points were located. To compare the difference in vegetation density between artificial water points and sites along natural water sources, we also determined NDVI values at these artificial water points and compared those with an equal number of randomly located sites 150 m from the middle of the river, which was assumed to represent the riverine vegetation. We tested with Mann–Whitney tests whether the NDVI values at lion kill sites were different from those at random sites, and if there were differences in NDVI values between artificial water points and rivers.

## RESULTS

Lions positively selected for buffalo, giraffe, waterbuck, and wildebeest (Table 1). The 3 species with the lowest Jacobs index were the 2 smallest species (impala and porcupine [*Hystrix cristata*]) and the heaviest (white rhinoceros [*Ceratotherium simum*]). Lion kills of elephant (*Loxodonta africana*) were never recorded in Klaserie. Prey composition deviated significantly from prey availability ( $\chi^2_6 = 562.32$ ,  $P < 0.001$ ; Table 2) for prey species that comprised >5% of potential prey numbers. Residual analysis indicated that the

**TABLE 1.**—For lion prey in the Klaserie Nature Reserve, estimated population density (individuals/km<sup>2</sup>, from mean survey values from 2002 to 2006), percentage each species comprised of reported lion kills (2002–2007, *n* = 215), Jacobs' index (*D*) for prey selection (+ values) or avoidance (– values), adult body mass, and digestion and feeding types. The last column was calculated from the distance to water odds-ratio taken from Redfern et al. (2003); the lower the value, the lower the chance of finding the species far from water sources.

Species	Mean density (individuals/km <sup>2</sup> )	Mean density (%)	Lion kills (%)	Jacobs index ( <i>D</i> )	Adult body mass (kg)	Digestion type	Feeding type	Odds-ratio
Buffalo	2.34	14.3	40.5	0.60	481	Ruminant	Grazer	0.78
Crocodile	0.13	0.8	0.5	–0.26	527	Other	Other	0.00 <sup>a</sup>
Giraffe	0.44	2.7	21.4	0.81	1,178	Ruminant	Browser	0.94
Spotted hyena	— <sup>b</sup>		0.5		78	Other	Other	1.00
Impala	9.96	61.1	5.1	–0.93	56	Ruminant	Mixed	0.89
Kudu	0.51	3.1	6.5	0.37	94	Ruminant	Browser	0.89
Lion	0.11	0.7	1.4	0.36	179	Other	Other	0.83 <sup>a</sup>
Porcupine	0.86	5.3	0.5	–0.85	3	Other	Other	1.00 <sup>a</sup>
Warthog	0.21	1.3	2.8	0.38	83	Nonruminant	Other	0.71 <sup>a</sup>
Waterbuck	0.14	0.9	5.1	0.72	193	Ruminant	Grazer	0.52
White rhino	0.17	1.0	0.5	–0.39	2,250	Nonruminant	Grazer	0.97 <sup>a</sup>
Wildebeest	0.16	1.0	5.6	0.71	214	Ruminant	Grazer	1.00
Zebra	0.57	3.5	9.8	0.50	271	Nonruminant	Grazer	0.96
Elephant	0.70	4.3	0	–1.00	Excluded from analysis			

<sup>a</sup> Estimated values.  
<sup>b</sup> Unknown.

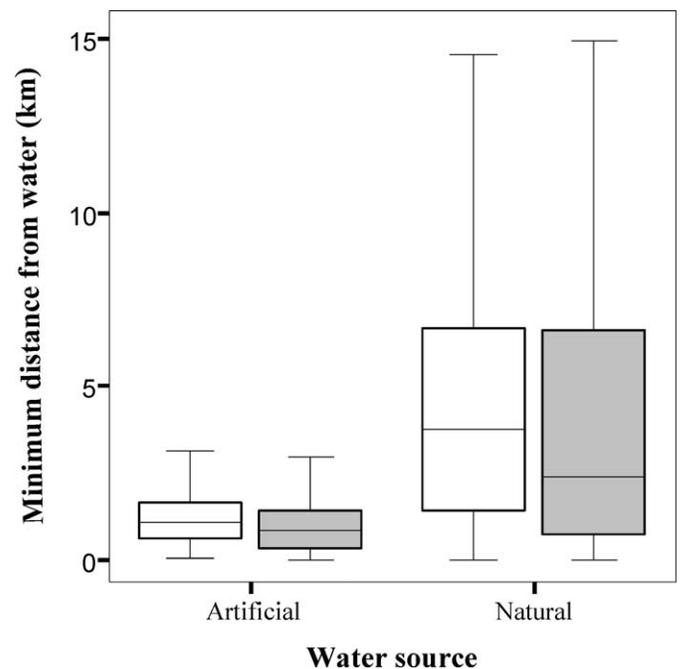
differences between observed and expected values were significant for each species individually (*P* < 0.05), and that lions strongly selected for buffalo and giraffe. Differences in prey selection (Jacobs index) could not be explained by the water dependency of the species (odds-ratio: *r<sub>s</sub>* = –0.123, *n* = 12, *P* > 0.05) or the density of the species (*r<sub>s</sub>* = –0.212, *n* = 12, *P* > 0.05).

Lion kills were spatially clustered and were significantly different from a random distribution (*Z* = –39.67, *P* < 0.01). Spatial autocorrelation did not compromise the analysis (Moran's *I* = 0.036, lag = 3.8 km, *P* > 0.05). Lion kills were significantly closer to water than expected based on a random distribution of the kills (generalized linear model; Wald  $\chi^2_1 = 12.06$ , *P* < 0.001; Fig. 2), and kills were found

**TABLE 2.**—Number of reported kills by lions of prey species that comprise >5% of all reported kills (see Table 1), estimated prey population sizes from 2002 to 2006 surveys, and the expected number of prey killed calculated from the survey proportions, in the Klaserie Nature Reserve. The last 2 columns represent the prey composition at 2 distances from the nearest water source. Composition of prey differed significantly (*P* < 0.01) from availability. Differences between observed and expected values for individual species (\* *P* < 0.05; \*\*\* *P* < 0.001) was based on residual analysis (Siegel and Castellan 1988).

Species	Kills	Estimated population size	Expected kills	Distance from water	
				Close (<5.3 km)	Far (≥5.3 km)
Buffalo	87	1,355	33.5***	50	37
Giraffe	46	256	6.3*	19	27
Impala	11	5,770	142.4***	7	14
Kudu	14	294	7.3***	7	4
Waterbuck	11	82	2.0***	4	10
Wildebeest	12	94	2.3***	9	2
Zebra	21	332	8.2***	5	7
Total	202	8,183	202.0	101	101

closer to artificial water points than to natural river sources (Wald  $\chi^2_1 = 617.74$ , *P* < 0.001). The differences in distances between kill sites and random sites did not differ for artificial water points and natural rivers (Wald  $\chi^2_1 = 0.316$ , *P* > 0.10), indicating that water is the main factor in determining the kill location and that vegetation density around riverine areas does not have any effect on the kill location. No significant effects of digestion type of the prey species (Wald  $\chi^2_1 = 2.635$ , *P* > 0.10), their feeding type (Wald  $\chi^2_2 = 4.88$ , *P* > 0.05), their



**FIG. 2.**—Distance of lion kills (*n* = 215) from water of random locations (white boxes) and lion kill locations (gray boxes). Box plots show ranges (whiskers), 25% and 75% quartiles (boxes), and medians.

body mass (Wald  $\chi^2_1 = 0.95$ ,  $P > 0.05$ ), or season (Wald  $\chi^2_1 = 0.53$ ,  $P > 0.10$ ) on distance of the kills to water points were observed. However, the lower the odds-ratio (representing species with high water dependency), the smaller the distance of the lion kills to water (Wald  $\chi^2_1 = 9.15$ ,  $P < 0.005$ ).

These results indicate that water was the major factor influencing lion prey choice and prey location, and that vegetation cover was unimportant in the selection of the kill site at the scale measured by ASTER. We found that kill sites were indistinguishable from random sites in terms of NDVI (Mann–Whitney test:  $Z = -0.92$ ,  $n1$  and  $n2 = 215$ ,  $P > 0.05$ ). However, artificial water points had, as expected, significantly lower NDVI values than riverine locations ( $Z = -7.941$ ,  $n1$  and  $n2 = 117$ ,  $P < 0.001$ ). Kills of browsers and mixed feeders were not found closer to rivers, and kills of grazers not closer to artificial water holes, so no relationship was observed between feeding type and water source ( $\chi^2_1 = 0.10$ ,  $P > 0.05$ ).

Water dependency of the species affected the kill location, with water-dependent species killed closer to water than species not dependent on water. Therefore, the composition of lion prey (Table 2) was dependent on the proximity to water. To illustrate this effect we identified 2 groups of kills, 1 group relatively close to water and the other group further from water. The demarcation between these 2 groups (5.3 km; Table 2) was chosen so that sample sizes for the groups were equal. Prey composition depended on the distance to the nearest water point ( $\chi^2_6 = 13.84$ ,  $P < 0.05$ ; Table 2), with buffalo, greater kudu (*Tragelaphus strepsiceros*), and wildebeest taken relatively closer to water.

## DISCUSSION

We found that lion kills in Klaserie were located closer to water than expected based on a random distribution of kills. Water-dependent and water-independent species are found at different positions in the landscape, with water-dependent species closer to water (Redfern et al. 2003), which influenced the composition of lion prey. Water dependency of the prey species and the distance of the kills to water were negatively associated. Prey species are attracted to water, and lions exploit this nonrandom distribution. Difference in vegetation density is not an important feature to distinguish kill sites at this scale of analysis. Thus, our study shows that prey availability is more important than prey vulnerability, consistent with the predictions of Ogutu and Dublin (2004) and inconsistent with the findings of Hopcraft et al. (2005). We were able to separate the confounding effect of vegetation differences around water holes and water supply. We demonstrated that it was not vegetation density around natural water sources that increases predation risk for prey species but the actual presence of water, which was attracting prey species (Redfern et al. 2003; Smit et al. 2007). The herd size and structure, behavior, and time of drinking by prey, and the presence of other herbivores are important factors in decreasing predation risk when drinking (Valeix et al. 2008).

Buffalo, zebra, and wildebeest modify their activity patterns and habitat use in relation to lion predation risk (Fischhoff et al. 2007; Prins and Iason 1989; Sinclair and Arcese 1995; Winnie et al. 2008). Valeix et al. (2008) showed that species modify their activity, herd size, and drinking frequency at water holes, probably in response to the higher predation risks perceived there.

Body mass, feeding type, or digestion type of the prey species were not related to the distance from the kills to water. This is in agreement with Redfern et al. (2003), who also found no relationship between the distribution of prey and these traits. We expected to find kills of browsers and impala (the only mixed feeder species) closer to rivers and grazers closer to artificial water points (Smit et al. 2007), but feeding type was not related to the type of the water source that was closest to the kill site. Apparently, herbivores are distributed over Klaserie indifferent of their feeding type. Perhaps the high density of water points and the year-round supply of water, creating a low gradient in water availability, are the reasons that these factors were unimportant in determining the distribution of herbivores. This also might explain why we did not find the seasonal pattern in lion kills documented in other studies (Patterson et al. 2004; Van Bommel et al. 2007) where lions exhibited a seasonal pattern in prey selection as a response to the lower availability of prey in the rainy season when prey species are spread over a larger area and no longer concentrate around limited water points.

Several studies found that the composition of lion prey is determined mainly by prey body mass (Funston et al. 1998, 2001; Hayward and Kerley 2005; Lehmann et al. 2008; Mills et al. 1995; Owen-Smith and Mills 2008). Our results indicate a similar prey selection, with species such as zebra, wildebeest, and waterbuck as the positively selected species. The larger buffalo also was selected, but in general, larger species were avoided. Selection or avoidance of prey in our study is similar for all species to the results obtained by Hayward and Kerley (2005), except for the porcupine, which was negatively selected in our study. We found no relationship between selection–avoidance of prey and the water dependency of prey. In summary, lion predation is skewed toward medium-sized species and is distributed nonrandomly over the landscape, and water-dependent prey species are killed closer to water than are water-independent species. Our results are surprising because the density of water sources is very high in Klaserie (100% of the Klaserie area is within 3 km from a water point), in contrast with Kruger National Park where 92% of the area is within 5 km of water (Redfern et al. 2003). Hence, water availability in Klaserie is not strongly constraining the distribution of prey species. We expect that in areas with a larger water availability gradient, the dependency of prey species on water will influence their predation risk more strongly.

Our finding that lion kills are closer to water than expected on the basis of a random distribution could affect not only prey distribution (Valeix et al. 2009) but also the local community structure of the mammal assemblage (Mills and Shenk 1992;

Owen-Smith and Mills 2006; Power 2002). Moreover, impacts of lion predation differ among prey species, with medium-sized species being selected (Owen-Smith and Mills 2008; Sinclair et al. 2003). We found that lion predation pressure is not distributed uniformly over the area but is higher closer to water holes. Also, other landscape elements can increase predation risk by lions, such as erosion gullies, the availability of kopjes (Hopcraft et al. 2005), or the vegetation structure (Fischhoff et al. 2007; Prins and Iason 1989; Sinclair and Arcese 1995). Hence, the impact of lions on population sizes of species in local assemblages has a spatial component. Valeix et al. (2009) showed that species react to the spatial heterogeneity in lion predation pressure, with browsers shifting to more open areas as an antipredator strategy but grazers being less affected. Browsing and grazing species, especially impala (Prins and Van Der Jeugd 1993) or wildebeest (Holdo et al. 2009; Sinclair 2003), might have a keystone role in the composition of savanna systems (Van Langevelde et al. 2003), and therefore local differences in community assemblages can lead to important changes at the system level through cascading effects, such as has been reported elsewhere as a result of predation (Carpenter et al. 2008; Ripple and Beschta 2006, 2007; Schmitz et al. 2006).

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