Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use

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Abstract. Predators may influence their prey populations not only through direct lethal effects, but also through indirect behavioral changes. Here, we combined spatiotemporal fine-scale data from GPS radio collars on lions with habitat use information on 11 African herbivores in Hwange National Park (Zimbabwe) to test whether the risk of predation by lions influenced the distribution of herbivores in the landscape. Effects of long-term risk of predation (likelihood of lion presence calculated over four months) and short-term risk of predation (actual presence of lions in the vicinity in the preceding 24 hours) were contrasted. The long-term risk of predation by lions appeared to influence the distributions of all browsers across the landscape, but not of grazers. This result strongly suggests that browsers and grazers, which face different ecological constraints, are influenced at different spatial and temporal scales in the variation of the risk of predation by lions. The results also show that all herbivores tend to use more open habitats preferentially when lions are in their vicinity, probably an effective anti-predator behavior against such an ambush predator. Behaviorally induced effects of lions may therefore contribute significantly to structuring African herbivore communities, and hence possibly their effects on savanna ecosystems.

Key words: African large herbivores; ecology of fear; habitat selection; Hwange National Park, Zimbabwe; landscape of risk; lion; Panthera leo; *resource selection function.*

Introduction

The role of predation is most commonly measured through the direct lethal effects of predators on prey numbers. However the indirect effects of predation, such as the alteration of prey behavior, may also be important in prey ecology (Lima and Dill 1990, Lima 1998). Behavioral responses to predation include spatial redistribution (Ripple and Beschta 2004), selection of specific habitat structure (Creel et al. 2005, Wirsing et al. 2007), temporal and spatial changes in activity patterns (Fenn and Macdonald 1995), increased vigilance and reduced foraging time (Abramsky et al. 2002), or changes in group size (Lima 1995). Selection should favor individuals which optimize reduction of predation risk against its associated costs, e.g., vigilance against reduction in intake rate (Illius and Fitzgibbon 1994). Indirect effects of predation are thus expected to have an impact on the fitness of prey individuals, and hence on prey demography. Indeed, as emphasized by a meta-analysis of invertebrates, predators can have a greater effect on their prey's demography through behaviorally

mediated effects than through direct consumption (Preisser et al. 2005). There is also evidence that indirect effects of predation influence populations of large herbivores (Creel et al. 2007). Most studies on predator–prey relationships have resorted to using indirect proxies of predation risk (e.g., distance to cover, vigilance). Consequently, one limitation on understanding of behavioral responses to predation is that accurate data on prey behavior are rarely complemented by comparable information on their predators (Lima 2002). There is generally a need to go beyond traditional investigations of predator–prey relationships conducted at a small spatial scale through direct observations (e.g., Ferguson et al. 1988, Hernández and Laundré 2005). Furthermore, in the context of the landscape of fear (Laundré et al. 2001), there is a need for multi-species approaches that go beyond single predator–prey pairs, as most studies come from temperate systems with a few herbivore and predator species (e.g., Ferguson et al. 1988), to understand how ecological constraints may mediate predation-related behavioral responses. In addition, even though it would be adaptive for prey to vary their behavior in accord with perception of risk, both temporally and spatially and at multiple scales, little is known about the differences between behavioral responses to immediate vs. longer-term variation in the risk of predation (but see Creel and Winnie 2005).

PLATE 1. (Top) In the context of the "ecology of fear," an impala is running away from two lions (photo credit: Gavin St Leger). (Bottom) An alert young male lion is a potential danger for herbivores (photo credit: Courteney Johnson).

In this study, we have investigated the influence of the risk of predation by lions (*Panthera leo*) on the behavior of 11 species of African large herbivores (see Plate 1). Lions contribute to the major share of herbivores killed across a wide body size range (Owen-Smith and Mills 2008) and consequently should have a detectable influence on the behavior of most herbivores. To investigate whether the risk of predation by lions is a structuring force in African savanna herbivore communities, we tested two hypotheses. First, herbivore distribution in the landscape is influenced by the risk of predation by lions, and herbivores avoid areas characterized by high risk of predation. Second, the selection of habitat structure by herbivores should be influenced by the perceived risk of predation, because habitat structure affects visibility and hence capacity to detect a predator, ease of escape from a predator (Lima 1992), and camouflage and ambush opportunities for predators (Hopcraft et al. 2005). In order to gain insights into the spatial and temporal scales on which herbivores base their anti-predator behavior, we tested the two hypotheses using an index of long-term risk of predation by lions (seasonal landscape of risk representing the likelihood of lion presence calculated over four months). The second hypothesis was tested using an index of short-term risk of predation by lions (presence/absence of lions in the vicinity in the last 24 hours). We investigated whether the risk of predation by lions influenced habitat selection mainly for their preferred prey species. However, a multitude a factors may

TABLE 1. Results from the logistic regression modeling the probability of selecting a site.

Taxon	Significant variable	Estimate	χ^2	df	P
Grazers					
Buffalo (450 kg)	distance to water	-0.0001 ± 0.0001	3.22	1, 117	0.0572
Roan (220 kg)	distance to water	$\mathbf{-0.0003 \pm 0.0001}$	**4.92**	**1, 43**	**0.0265**
Zebra (200 kg)	distance to water	$\mathbf{-0.0002 \pm 0.0001}$	**14.58**	**1, 454**	**0.0001**
	habitat type	**G > B and W**	**6.75**	**2, 454**	**0.0342**
Sable (185 kg)	distance to water	-0.0002 ± 0.0001	3.34	1, 101	0.0675
Wildebeest (165 kg)	distance to water	$\mathbf{-0.0006 \pm 0.0002}$	**11.97**	**1, 74**	**0.0005**
	habitat type	**G > B and W**	**7.10**	**2, 74**	**0.0287**
Warthog (45 kg)	distance to water	$\mathbf{-0.0003 \pm 0.0001}$	**29.27**	**1, 387**	**<0.0001**
	habitat type	**B < G and W**	**9.91**	**2, 387**	**0.0070**
Water-dependent browsers					
Giraffe (750 kg)	distance to water	0.0001 ± 0.0001	0.16	1, 718	0.6874
	habitat type	G > B > W	18.03	2, 718	0.0001
	long-term predation risk	8.73 ± 18.76	0.22	1, 718	0.6417
	long-term predation risk × distance to water	$\mathbf{-0.0229 \pm 0.0102}$	**5.06**	**1, 718**	**0.0245**
Kudu (135 kg)	distance to water	0.0001 ± 0.0001	0.09	1, 620	0.7657
	long-term predation risk	47.47 ± 17.35	7.49	1, 620	0.0062
	long-term predation risk × distance to water	$\mathbf{-0.0254 \pm 0.0114}$	**4.97**	**1, 620**	**0.0258**
Impala (45 kg)	distance to water	0.0001 ± 0.0001	0.07	1, 811	0.7950
	habitat type	B < W and G	31.21	2, 811	<0.0001
	long-term predation risk	72.87 ± 17.65	17.04	1, 811	<0.0001
	long-term predation risk × distance to water	$\mathbf{-0.0311 \pm 0.0102}$	**9.34**	**1, 811**	**0.0022**
Water-independent browsers					
Duiker (15 kg)	long-term predation risk	$\mathbf{-50.43 \pm 19.23}$	**6.88**	**1, 247**	**0.0087**
Steenbok (8 kg)	habitat type	B and G > W	66.32	2, 1105	<0.0001
	long-term predation risk	$\mathbf{-97.43 \pm 16.69}$	**34.07**	**1, 1105**	**<0.0001**

Notes: The average body mass (unit mass as per Cumming and Cumming [2003]) of each species is indicated. Results are presented as estimate (±SE). For habitat type, G represents grassland, B bushland, and W woodland; G > B and W indicates a significantly higher probability of selecting a site in grassland habitat. Boldface type indicates results of interest for the interpretation. There was no significant effect of long-term predation risk × habitat type; thus no results are presented here. See also Fig. 2 for interpretation of the interaction results for water-dependent browsers.

influence predator–prey relationships. As herbivore body size and diet may affect habitat use and anti-predator strategy (Jarman 1974, Fritz and Loison 2006), we also investigated whether herbivore behavioral responses to the risk of predation were dictated, at least partly, by body size and/or diet (browsers and grazers were contrasted).

METHODS

Study site

Hwange National Park (HNP) covers ~15 000 km^2 of semiarid dystrophic (low nutrient soil) savanna in northwestern Zimbabwe (19°00′ S, 26°30′ E). The vegetation is primarily woodland and bushland savanna, with plant communities dominated by *Colophospermum mopane*, *Combretum* spp., *Acacia* spp., *Baikiaea plurijuga*, and *Terminalia sericea* (Rogers 1993). The long-term mean annual rainfall is 606 mm, which falls primarily between October and April. The surface water available to animals is found in natural as well as artificial waterholes. The study area is located in the northern region of HNP (~7000 km^2) where lion density is estimated around 2.7 lions/100 km^2 (Loveridge et al. 2007b). We studied the influence of the risk of predation by lions on six grazers (African buffalo *Syncerus caffer*, roan antelope *Hippotragus equines*, sable antelope *Hippotragus niger*, warthog *Phacochoerus aethiopicus*,

blue wildebeest *Connochaetes taurinus*, and plain zebra *Equus quagga*) and five browsers (common duiker *Sylvicapra grimmia*, giraffe *Giraffa camelopardalis*, impala *Aepyceros melampus* (impala is a mixed-feeder but is a browser in the dry season), greater kudu *Tragelaphus strepsiceros*, and steenbok *Raphicerus campestris*). There is substantial variation in average body size among these 11 species (see Table 1). Duiker and steenbok are species that do not need to drink regularly as they meet their water requirements from their food, and these are independent of access to surface water (Skinner and Smithers 1998). In HNP, the top five species utilized by lions appear to be buffalo (33% of kills), kudu (18%), giraffe (9%), zebra (6%), and elephant *Loxodonta africana* calves (6%), accounting together for 72% of lion kills (Loveridge et al. 2007a). Spotted hyena *Crocuta Crocuta* is another common large predator of HNP, with an estimated density of 8.5 hyaenas/100 km^2 (Drouet-Hoguet 2007). Fecal analyses revealed some dietary overlap with lions, with elephant calves (15%), kudu (12%), duiker (11%), buffalo (9%), wildebeest (8%), steenbok (8%), and giraffe (7%) accounting for 70% of hyena diet (Drouet-Hoguet 2007). No accurate data on the spatial ecology of hyenas were available to allow us to consider hyenas in this study. However, lions contribute to the major share of herbivores killed across a wide body size range (Owen-Smith and Mills 2008) and consequently were
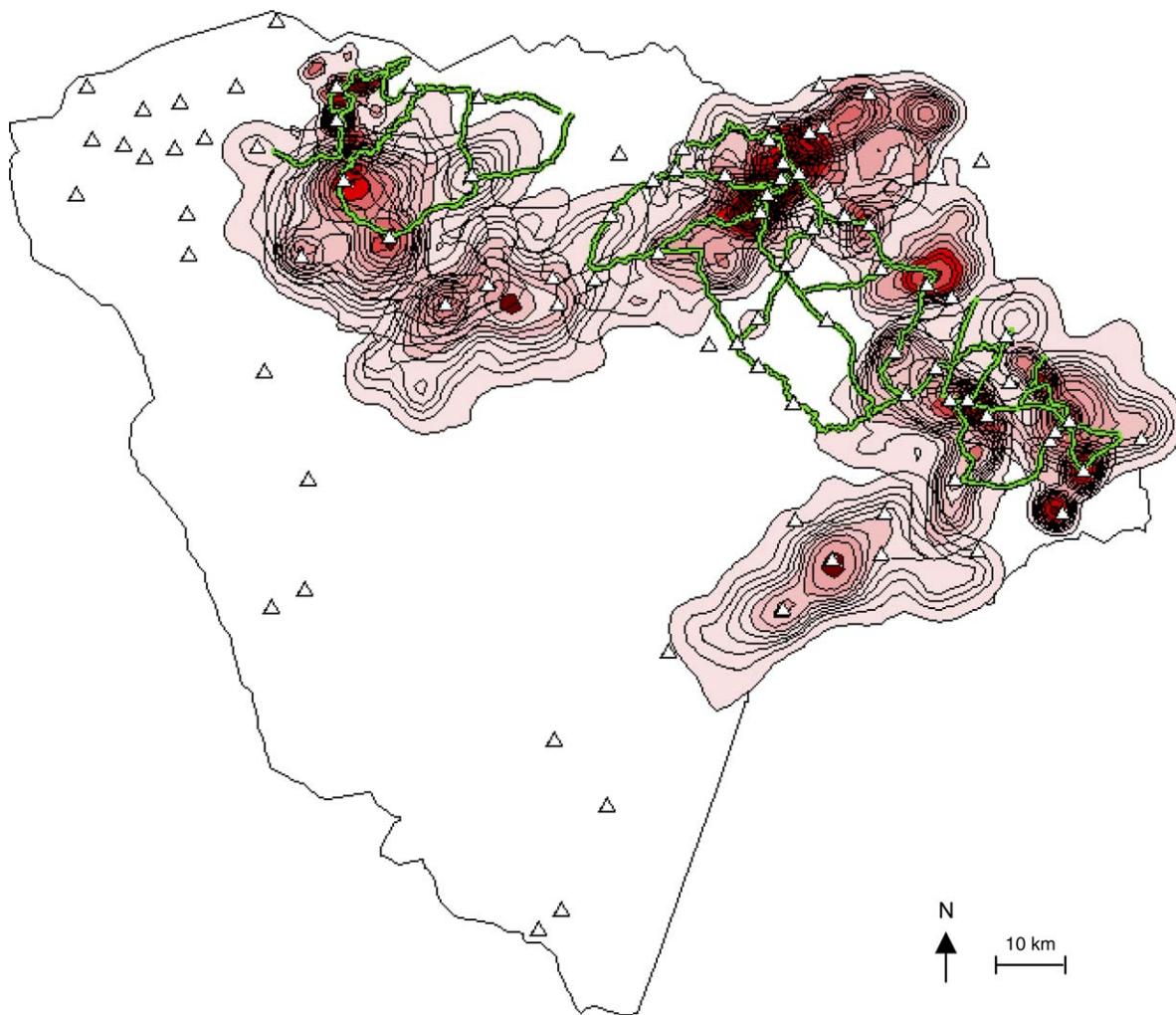
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Fig. 1. Map showing the landscape of long-term predation risk for the period July–October 2005. The contour lines represent the 10% isopleths. The darker an area, the higher the probability of lion presence. Green lines represent the transects along which herbivores were monitored. White triangles represent the main waterholes (artificial).

expected to have a detectable influence on the behavior of most herbivores.

Data

From 2002 to 2005, lions were closely monitored in the study area, of which 17 female and 10 male adults were fitted with GPS Simplex radio-collars (female, 900 g; male, 950 g; Televilt Positioning AB, Lindesberg, Sweden; see Loveridge et al. [2007b] for details). Most lion groups were collared in the study area (80% of the lion groups seen in the study area included one collared individual during the study period). Preliminary analyses revealed that lionesses from the same pride stay together most of the time in HNP, with females from a pride sighted together in 89.2% ± 7.4% of sightings. Positional data from the GPS radio collars were downloaded regularly, and animals' locations were available for 2003, 2004, and 2005. For each individual,

one location was available hourly from 18:00 hours to 07:00 hours, plus fixes at 09:00 hours and 16:00 hours. Herbivore distributions were monitored along road transects (Fig. 1). Monitoring sessions were carried out in May–June (beginning of the dry season) and September–October (end of the dry season). For each herbivore sighting, we used ArcView 3.2 (Environmental Systems Research Institute, Redlands, California, USA) to extract habitat type (grassland, bushland, or wood-land) from the vegetation map layer (Rogers 1993), and measure the distance to the closest waterhole (hereafter, distance to water).

Long-term and short-term risk of predation

While there are factors other than lion presence that define the riskiness of a site (e.g., activity of other predators, habitat characteristics), the short-term and long-term risk of predation are here taken to mean the

short-term and long-term probability of lion presence. Short-term risk of predation was estimated by the presence of lions in the area of the herbivore sighting (<2 km) in the preceding 24 hours as revealed by fine scale spatiotemporal data collected by the lion GPS radio collars. For the analyses related to this short-term risk of predation, only areas where we could be confident of the movements of the majority of lion groups were considered. We contrasted situations characterized by "lion present" and "lion not detected," a conservative approach insofar as the effects of undetected lions work against our hypotheses. We approximated the long-term risk of predation at a location by an index proportional to the probability of lion presence at this location, calculated over four months. We correlated the preceding four months of lion spatial data with each period of herbivore observation. Herbivore observations were made in May–June and September–October each year, and so lion spatial data from March to June and from July to October were used, respectively. We calculated consecutive 10% kernel isopleths, using the reference smoothing factor h_{ref} as recommended by Hemson et al. (2005), for each individual lion using Ranges 7 (version 0.811 [South and Kenward 2006]). Where gaps in the data set occurred, owing to poor satellite detection, we used averaged isopleths over all the locations available for individuals who were confirmed to be alive and present in the area during the specified period. We then approximated the probability of a lion presence by $0.10/(A_i - A_{i-1})$; with A_i being the area of the surface of isopleths i and 0.10 because 10% of all locations are located between two consecutive isopleths. Six seasonal landscapes of risk were produced (March–June 2003, 2004, and 2005; July–October 2003, 2004, and 2005; example in Fig. 1).

Analyses

We used logistic regressions to develop resource selection functions (RSF; proportional to the probability of use of a resource by an animal [Manly et al. 1993]) for each herbivore species. The dependent variable is 1 for herbivore sightings. It is 0 for control points located every 2 km on all transects. Control points represent the range of what was available to herbivores. We modeled the probability of selecting a site (1 vs. 0) as a function of the distance to water, the habitat type, the long-term predation risk, the interaction between habitat type and long-term predation risk and the interaction between distance to water and long-term predation risk. To avoid any bias linked to the probability of detection of an animal depending on habitat type, we used only the observations located within 100 m of the transects (number of observations for buffalo = 53, for duiker = 103, for giraffe = 347, for impala = 386, for kudu = 311, for roan = 18, for sable = 49, for steenbok = 449, for warthog = 189, for wildebeest = 78, and for zebra = 206). Reference points for available sites for a given herbivore
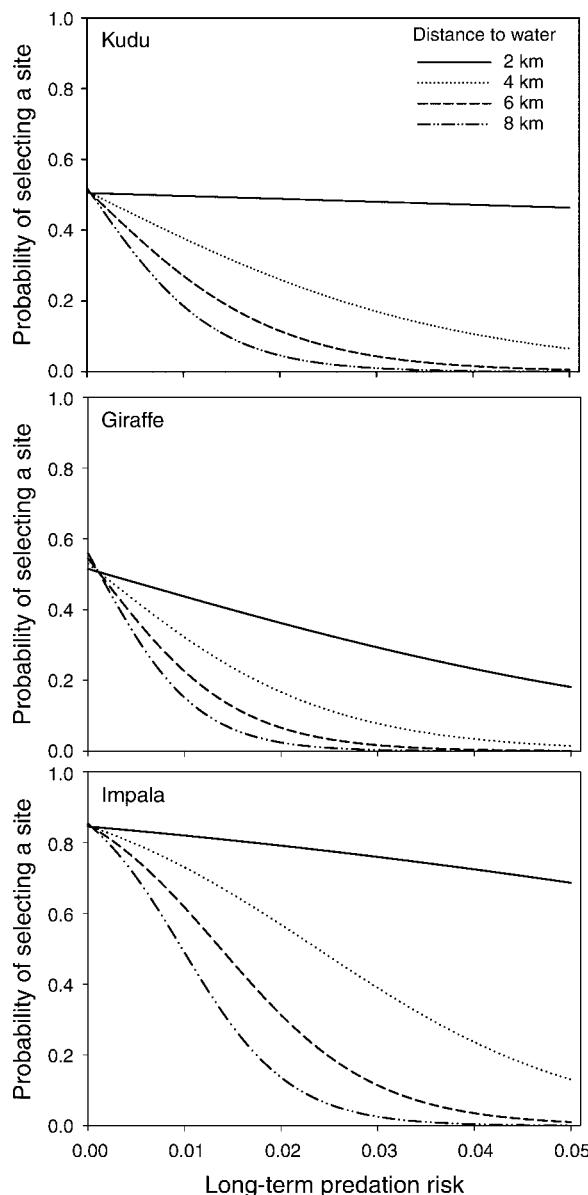

FIG. 2. Relationship between the long-term predation risk (proportional to the likelihood of lion presence) and the probability of selecting a site (results from logistic regressions) for the three water-dependent browsers. The interaction long-term predation risk × distance to water was significant for all at $P < 0.05$.

species in the analyses were randomly selected from the pool transect points to achieve a 1:1 ratio of used-to-available sites. Statistical analyses used generalized linear models performed with SAS software (version 9.0; SAS Institute 2002), using the LOGISTIC procedure. Backward variable selection was used with successive removal of non-significant variables. We performed a likelihood ratio test to assess whether the general models significantly differed from a model with a random distribution of used and available site charac-
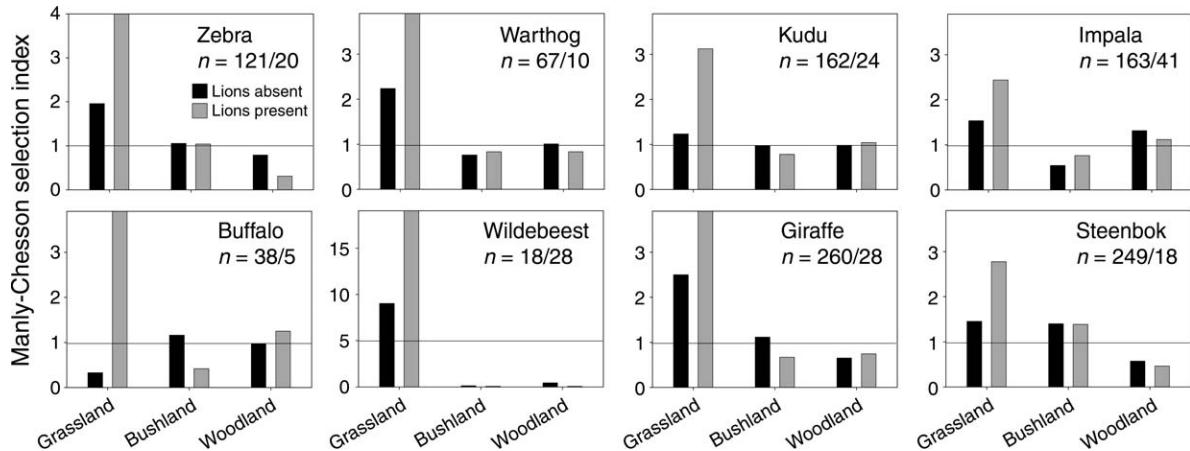
FIG. 3. Comparison of the Manly-Chesson selection index of each habitat type between the sites where lions were absent in the preceding 24 hours (black bars) and the sites where lions were present (gray bars). Roan, sable, and duiker were excluded because fewer than five observations were available for one category. Index values above 1 indicate preference, values below 1 indicate avoidance, and values equal to 1 indicate use in proportion of availability. The two *n* values represent the number of herbivore sightings in sites where lions were absent in the preceding 24 hours (first number) and the number of herbivore sightings in sites where lions were present in the preceding 24 hours (second number).

teristics. We also performed a Hosmer and Lemeshow goodness-of-fit test to evaluate whether the fitted models were adequate for describing the data (Hosmer and Lemeshow 2000).

We then tested for variation in habitat use between sites where lions had been present in the past 24 hours and sites where lions were not detected. RSF were nonsignificant ($P > 0.1$ for all species) due to the low number of observations with lions in the vicinity per habitat category. However, consistent trends across species were found, as revealed by the Manly-Chesson selection index, which is the proportional use divided by the proportional availability of each habitat (Manly et al. 1972, Chesson 1978). This index value is <1 or >1 if the habitat is respectively avoided or selected. We used only the observations further than 1km from a waterhole in this approach, because habitat availability is strongly modified in the vicinity of waterholes.

RESULTS

For all grazers, site selection was not associated with the long-term predation risk but was mainly influenced by distance to water and/or habitat type. They favored use of open areas and/or use of areas close to waterholes (Table 1). For all water-dependent browsers, site selection was influenced by the interaction between distance to water and long-term predation risk, with the probability of selecting a site decreasing as the long-term predation risk increased for a given distance to water (Table 1, Fig. 2, Appendix). For all water-independent browsers, site selection was negatively associated with the long-term predation risk (Table 1). For all species, the interaction between the long-term predation risk and habitat type did not have a significant effect on site selection (Table 1). All logistic regressions were significant (likelihood ratio test: $P < 0.05$) and they provided

good fits (Hosmer and Lemeshow goodness-of-fit test: $P > 0.05$) for all species except kudu and warthog ($P = 0.004$). Manly-Chesson indices suggested that short-term predation risk may influence habitat preference for all species, which appeared to shift to greater use of grassland when lions were in the vicinity (Fig. 3). Buffalo, giraffe, and to a lesser extent kudu, which appear to be the main prey species for lions in HNP (Loveridge et al. 2007a), also appeared to avoid bushland when lions were in the vicinity (Fig. 3).

DISCUSSION

Our results suggest that the risk of predation by lions influences the behavior of African herbivores. They also show that diet rather than prey preference and body size influences these relationships. Indeed, browsers and grazers appear to be influenced by different spatial and temporal scales in the variation of the risk of predation by lions. Whereas the distributions of all browsers across the landscape were negatively associated with the long-term risk of lion presence (as assessed by our proxy), those of grazers did not. The scale of decision making in herbivores can be viewed as a hierarchical process ranging from the bite to the landscape (Senft et al. 1987). It may differ between browsers and grazers since food resources tend to be distributed in different ways (Gordon 2003). In HNP, the vegetation is primarily woodland and bushland, and open grassland areas are scarce and often associated with waterhole areas (Rogers 1993). Consequently, foraging areas are scarcer for grazers. Additionally, the distribution of herbivores in the landscape is constrained by the distribution of surface water, and this constraint is stronger for water-dependent grazers (Western 1975, Redfern et al. 2003). In HNP, surface-water sources are limited and often available in few waterholes (see Fig. 1). Due to the distribution of

grasslands and waterholes in HNP, grazers have no option but to use habitats mostly located in the vicinity of the few waterholes and grasslands. These areas often correspond to areas of high long-term predation risk. Because their suitable habitats are mostly restricted to risky environments, we suggest that grazer's anti-predator strategy (use of safer habitat, stronger vigilance behavior) is essentially based on responses to pulses of predation risk; i.e., when lions are in the vicinity (Lima and Bednekoff 1999). Our results also suggest that the behavioral response of grazers to high immediate predation risks involve shifts in the habitat structure they use (see also Fischhoff et al. 2007).

In HNP, spatial distribution of browsers is less constrained than that of grazers because they are less water-dependent (duiker and steenbok are even water independent) and most of the park is covered by woodland and bushland (Rogers 1993). Interestingly, water-dependent browsers avoid risky areas mainly when they are far from water. This suggests that they may rely on other behavioral responses in the vicinity of waterholes, as suggested for grazers. Our results suggest that decision making by browsers is influenced by predator movements over the larger ecological landscape. This probably arises through the experience browsers have of lion encounters over the past months, or through their response to the odor of lions (Kats and Dill 1998). This results in avoidance of risky areas where possible. In this case, non-lethal effects of predators on prey populations are expressed in terms of large-scale patterns in the use of space by prey (see also Doncaster [1994] for hedgehogs and badgers, Ripple and Beschta [2004] for elk and wolves).

Whereas the long-term risk of predation by lions appeared to influence the landscape areas selected by browsers, it did not influence the habitat types selected by any herbivore. However, our results reveal how African herbivores use habitats in risk-sensitive ways over short-time periods when lions are in the vicinity. These results are consistent with lion hunting strategy (opportunist stalk-and-ambush hunters [Hopcraft et al. 2005; see Plate 1]), and anti-predation strategy of some prey. For instance, buffalo and giraffe avoid bushland and favor open areas where vigilance behavior and flight are facilitated (Jarman 1974, Fritz and Loison 2006). Other studies have already emphasized that prey select micro-habitats that allow escape from predators (Wirsing et al. 2007). Independently from their strategy, most species favored use of open grassland areas when lions were in the vicinity, probably owing to a greater detection of lion movements. Contrary to larger herbivores, smaller herbivores can be preyed upon by almost all carnivores (Owen-Smith and Mills 2008), and the risk of being predated by other predators (spotted hyena, leopard, painted dog, cheetah) may therefore also affect habitat use. Nonetheless, our study detected a pattern in prey behavior correlated to the use of sites by lions. Our results generally reinforce the idea that predator–prey interac-

tions influence habitat use, and that habitat features are crucial when assessing predator–prey interactions.

Our results encourage a more thorough exploration of predation as a major determinant of ecological niche. Clearly, spatial variability in the risk of predation and its consequences on fitness has been under-estimated (Lind and Cresswell 2005). For large herbivores, the long-term costs of anti-predator behavior (decrease in feeding activity due to increased level of vigilance, shift to safer but poorer habitats) may lead to decreased body-condition, lower fecundity for females or lowered competitive ability for males (e.g., Creel et al. 2007). By constraining distribution in the landscape for browsers and influencing habitat selection for many herbivores, lions may have greater effects on their prey dynamics than would be predicted on the basis of direct predation only. Consequently, as observed in other ecosystems, predation might affect ecosystem functioning by influencing the distribution and intensity of herbivore pressure, hence creating trophic cascades (Ripple and Beschta 2004). The differential results between grazers and browsers suggest that the diversity of dietary type, and probably body size, within the herbivore community may also generate different ecosystem responses to indirect predation risk.

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APPENDIX

Relationship between the long-term predation risk and the probability of selecting a site (results from logistic regressions) for the three water-dependent browsers (*Ecological Archives* E090-003-A1).