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# Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates

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**Abstract.** Studies that focus on single predator–prey interactions can be inadequate for understanding antipredator responses in multi-predator systems. Yet there is still a general lack of information about the strategies of prey to minimize predation risk from multiple predators at the landscape level. Here we examined the distribution of seven African ungulate species in the fenced Karongwe Game Reserve (KGR), South Africa, as a function of predation risk from all large carnivore species (lion, leopard, cheetah, African wild dog, and spotted hyena). Using observed kill data, we generated ungulate-specific predictions of relative predation risk and of riskiness of habitats. To determine how ungulates minimize predation risk at the landscape level, we explicitly tested five hypotheses consisting of strategies that reduce the probability of encountering predators, and the probability of being killed. All ungulate species avoided risky habitats, and most selected safer habitats, thus reducing their probability of being killed. To reduce the probability of encountering predators, most of the smaller prey species (impala, warthog, waterbuck, kudu) avoided the space use of all predators, while the larger species (wildebeest, zebra, giraffe) only avoided areas where lion and leopard space use were high. The strength of avoidance for the space use of predators generally did not correspond to the relative predation threat from those predators. Instead, ungulates used a simpler behavioral rule of avoiding the activity areas of sit-and-pursue predators (lion and leopard), but not those of cursorial predators (cheetah and African wild dog). In general, selection and avoidance of habitats was stronger than avoidance of the predator activity areas. We expect similar decision rules to drive the distribution pattern of ungulates in other African savannas and in other multi-predator systems, especially where predators differ in their hunting modes.

**Key words:** African ungulates; antipredator strategies; conditional logistic regression; habitat selection; Karongwe Game Reserve, South Africa; large carnivore; multi-predator–prey systems; predator hunting mode; spatial distribution; utilization distribution.

## INTRODUCTION

The spatial patterns of animals are driven primarily by the distribution of resources and the presence of predators (Lima 1998, Sih 2005). However, these factors can differ in their magnitude of effect (Preisser et al. 2005), especially since the spatial distribution of resources can be relatively stable, at least over the timescales of spatial decision making, while predation risk almost never is (Sih 2005). Thus, although prey may have a reliable knowledge of the current spatial distribution of resources, perception of the spatial and temporal distribution of predation risk must be updated more frequently.

Prey respond to predation risk at the landscape level with a range of behavioral tactics, including temporal and spatial changes in activity patterns and selection of safer habitats (reviewed in Lima 1998). Predation risk,

however, can depend on the structural complexity of the environment, which can affect the probability of prey encounter and kills (Hebblewhite et al. 2005), and the effectiveness of antipredator strategies (Andruskiw et al. 2008). For example, the hunting efficiency of wolves (*Canis lupus*), a coursing predator, in Yellowstone National Park is influenced by the amount of open grassland adjacent to streams (Kauffman et al. 2007). But areas where prey are most likely to encounter predators may not be where they are most likely to be killed, and this difference can depend on the habitat (Hebblewhite et al. 2005), as well as the space use and hunting mode of the predator (Atwood et al. 2009).

In a landscape where predators are spatially anchored by nests or territories, prey can avoid these areas of predictable high predator activity (Thomson et al. 2006). For example, Pied Flycatchers (*Ficedula hypoleuca*) avoid nesting in forest patches occupied by the more dangerous Pygmy Owl (*Glaucidium passerinum*) (Morosinotto et al. 2009). Avoidance of spatially anchored predators is common in avian systems, and

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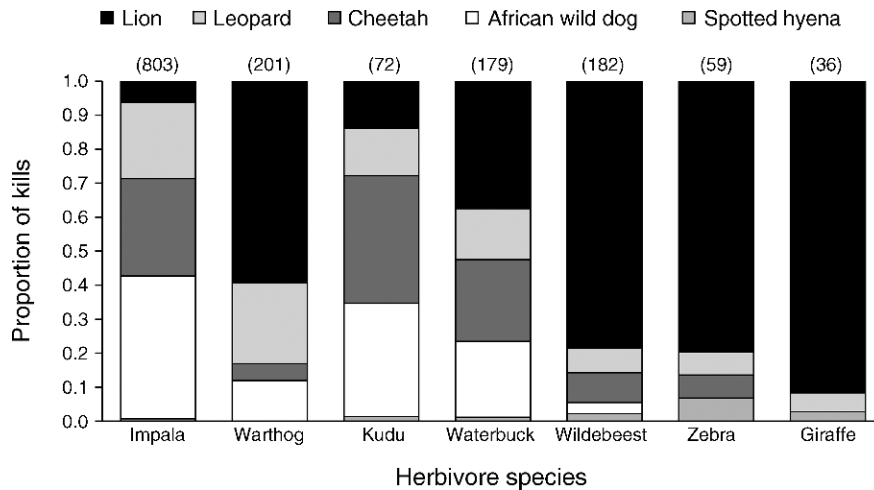


FIG. 1. Proportion of kills by lion, leopard, cheetah, African wild dog, and spotted hyena of seven ungulate species in Karongwe Game Reserve (KGR), South Africa. The total number of recorded kills for each species over a four-year period (August 2001–September 2005) is reported in parentheses above each bar.

we suggest that mammalian prey may also utilize such a landscape-level antipredator strategy. The territory and space use of sit-and-pursue hunters are more stable and predictable over time than the more variable space-use pattern of actively hunting or cursorial predators (Preisser et al. 2007). Given that cues (e.g., encounter rate) from sit-and-pursue predators provide more information about local predation risk (Lima and Bednekoff 1999), antipredator responses are often stronger in response to sit-and-pursue predators than cursorial predators (Schmitz 2005, Preisser et al. 2007). Despite the support for this hypothesis in invertebrates and fish (Preisser et al. 2007), tests of the effect of predator hunting mode on antipredator behavior are surprisingly rare in mammalian systems (but see Atwood et al. 2009).

Furthermore, prey rarely are in single-predator environments and are expected to evaluate the relative predation risk from multiple predators simultaneously (Sih et al. 1998, Lima 2002). In localized and controlled conditions, prey show threat-sensitive predator avoidance, where antipredator responses are matched to the degree of threat (e.g., Persons and Rypstra 2001, Mathot et al. 2009, Morosinotto et al. 2009, Thaker et al. 2010). However, this hypothesis has rarely been tested at the landscape level, where the spatial pattern of predation risk is dynamic (Lima 2002). To understand spatially explicit antipredator decisions, most studies construct landscapes of fear (Laundré et al. 2001, Searle et al. 2008). This method relies on prey consistently and overtly responding to predation risk, but in a multi-predator environment, fails to differentiate the relative predation risk of each predator (but see Willems and Hill 2009). In addition, landscapes based on prey perception fail to distinguish between antipredator responses to avoid encountering predators and antipredator responses to avoid risky habitats. Minimizing

predation risk in a multi-predator environment may likely involve avoiding predators as well as avoiding habitats where most kills are made, depending on the reliability of knowledge of these relative predation risk parameters across the landscape (Lima and Bednekoff 1999).

Here, we explain the distribution of seven ungulate species in a fenced reserve in South Africa as a function of relative predation risk. We used four years (2001–2005) of kill and carcass records for lion (*Panthera leo*), leopard (*P. pardus*), cheetah (*Acinonyx jubatus*), African wild dog (*Lycyaon pictus*), and spotted hyena (*Crocuta crocuta*) in this closed system to determine relative predation impact for each ungulate species (Fig. 1; see Lehmann et al. 2008 for details on methods). From the location of these kills, we determined the relative riskiness of the different habitat types for each ungulate species (based on Manly-Chesson selectivity index; Fig. 2). These predator- and habitat-specific measures of mortality were used to test the following hypotheses of how ungulates can avoid predation risk in a landscape of multiple predators: (1) ungulates avoid areas that are heavily utilized by their main predators (highest contribution to mortality); (2) ungulates avoid areas that are heavily utilized by all predators, where the degree of avoidance is related to the level of predation threat from that predator; (3) ungulates avoid areas that are heavily utilized by sit-and-pursue predators (lion, leopard), more than they avoid areas utilized by less predictable cursorial predators (African wild dog, cheetah); (4) ungulates avoid risky habitats, where the probability of kills are high; and (5) ungulates select safer habitats, where the probability of kills are low.

The first three hypotheses are strategies to reduce the probability of encountering predators (see Plate 1), and the last two hypotheses are strategies to reduce the probability of being killed. Antipredator strategies are

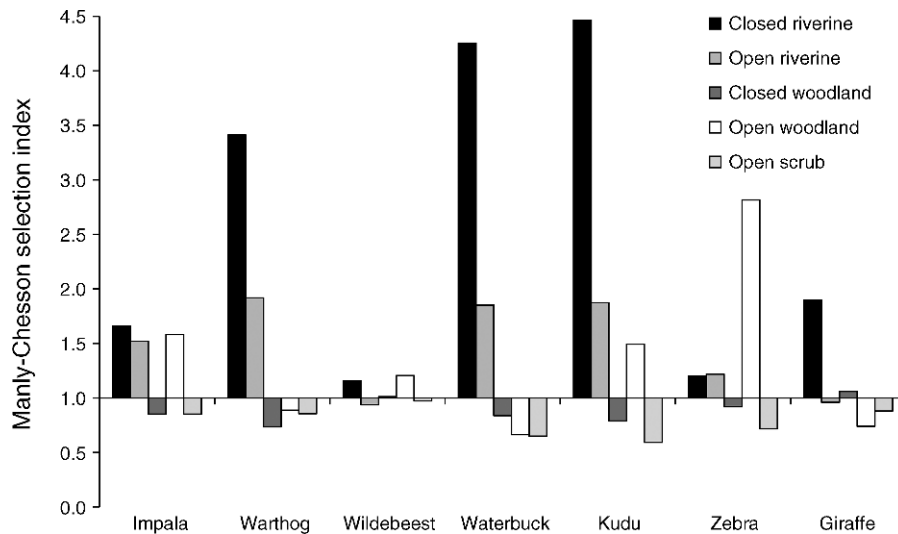


FIG. 2. Manly-Chesson selection index for proportion of kills over a four-year period (August 2001–September 2005) by all predators in each habitat type. Index values  $>1$  indicate that more kills were made, values  $<1$  indicate that fewer kills were made, and values  $= 1$  indicate that kills were made in proportion to the availability of habitat.

likely to involve a combination of directly avoiding the space use of predators and avoiding risky habitats, and therefore, we also tested combinations of variables from the four main hypotheses. Thus, we provide the first comprehensive landscape-level examination of the distribution of each ungulate species as a function of different strategies to avoid predation risk from multiple predators.

#### METHODS

This study was conducted in Karongwe Game Reserve (KGR; center  $24^{\circ}13' S$  and  $30^{\circ}36' E$ ), located in the Limpopo Province, South Africa (Fig. 3). This reserve is an  $85 \text{ km}^2$  conservancy within the Granite lowveld bioregion of the Savanna Biome (Mucina and Rutherford 2006). Mean annual rainfall is  $515 \pm 70$  mm, mean  $\pm$  SE, and falls mainly from October to February. Water availability is not limited, as animals have access to natural rivers as well as artificial waterholes across the whole reserve throughout the year (Fig. 3). We used a habitat map of KGR based on a supervised classification of Landsat Enhanced Thematic Mapper + imagery (year 2000 imagery, available online)<sup>4</sup> that categorized the vegetation into five habitat types: (1) closed woodland (54.4% of area) consisting mainly of *Combretum* and *Mopane* woodlands with closed tree canopies; (2) open woodland (24.1%) consisting mainly of *Acacia* spp. with separated tree canopies; (3) open riverine (15.8%) consisting of open canopy forest with thick understory along drainage lines; (4) closed riverine (1.6%) consisting of gallery forests along rivers; and (5)

open scrub (4.1%) consisting of old agricultural lands now reverting to open scrub habitat (Fig. 3).

#### Ungulate presence

Ungulate presence on the landscape was determined by drive counts throughout KGR in 2004–2005. During this period, the reserve was sampled four times for five consecutive days each: 29 November–3 December 2004 (rainy season), 16–20 March 2005 (end of rainy season), 2–6 June 2005 (dry season), and 1–5 September 2005 (end of dry season). This road strip census procedure (detailed in Hirst 1969) was conducted by two teams, each of which travelled half the reserve roads daily (80 km total) and recorded the positions (latitude/longitude coordinates) of all ungulates sighted using a handheld Global Positioning System. The start and end points of each drive were alternated daily to ameliorate time bias. Twelve ungulate species were recorded in KGR, but for this study we focused on the seven most common species: impala (*Aepyceros melampus*;  $\approx 1027$  individuals in the reserve from annual aerial census during the study period), blue wildebeest (*Connochaetes taurinus*;  $\approx 211$ ), waterbuck (*Kobus ellipsiprymnus*;  $\approx 167$ ), Burchell's zebra (*Equus burchelli*;  $\approx 156$ ), kudu (*Tragelaphus strepsiceros*;  $\approx 136$ ), warthog (*Phacochoerus africanus*;  $\approx 126$ ), and giraffe (*Giraffa camelopardalis*;  $\approx 70$ ).

#### Predator space use

During this study period, KGR had five large carnivores; lion, leopard, cheetah, African wild dog, and spotted hyena. African wild dog were removed in April 2005, and thus were only present for the first two ungulate counts. Almost all the adult predators were fitted with VHF transmitters (Telonics SB2 Transmitter,

<sup>4</sup> (<https://zulu.ssc.nasa.gov/mrsid/>)

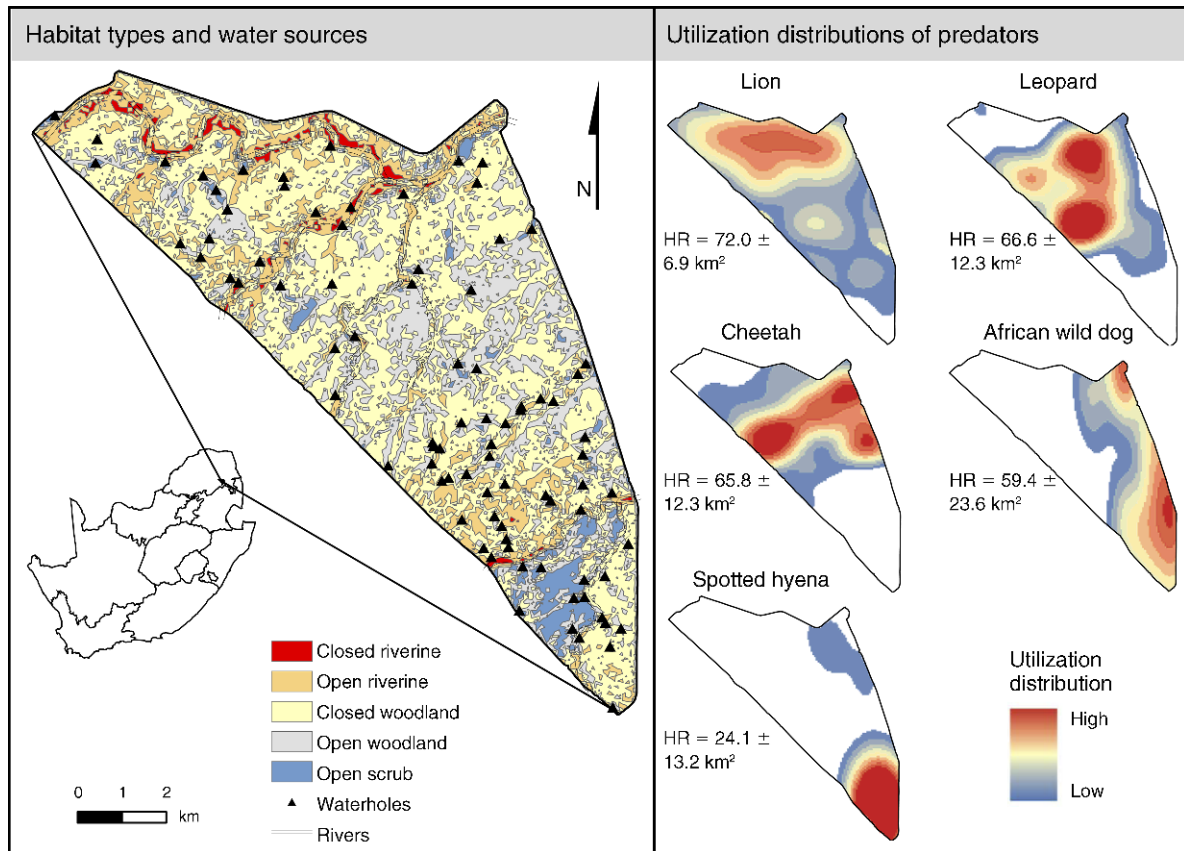


FIG. 3. Map of Karongwe Game Reserve, South Africa, showing the five habitat types, locations of water sources, and utilization distributions (UD) of lion ( $n = 1023$  location points), leopard ( $n = 904$ ), cheetah ( $n = 1920$ ), African wild dog ( $n = 252$ ), and spotted hyena ( $n = 468$ ). For illustration, we only show predator UD that span the period from 31 October to 29 November 2004, but we report home range (HR) sizes (mean  $\pm$  SE) for all four sample periods.

Africa Wildlife Tracking, Pretoria, South Africa) during the study period ( $n = 4$  lion [of 5 total], 4 cheetah [of 5], 4 leopard [of 4], 2 African wild dog [of 4], 2 spotted hyena [of 4]). Diurnal and nocturnal locations for all predators were collected multiple times (2–48 points) daily. However, to correct for inconsistencies in sampling, we used two to four daily locations, obtained by homing-in between 05:00–10:30 and 15:30–20:30 hours. Non-collared individuals were almost always (>90% of the time) associated with collared individuals.

We constructed predator-specific landscapes of predation risk based on locations of predators over a 30-day period preceding each ungulate drive count. We expected this 30-day period of predator locations to sufficiently represent normal home-ranging activity (Garton et al. 2001) without seasonal variation. Since we were interested in species-specific predation risk, we pooled locations for all individuals of the same predator species. As a result, we used a mean of 914 points ( $\pm 644$  SD) per species to calculate utilization distributions (UD) for each predator (Fig. 3) using a 95% fixed-kernel estimator with least-squares cross-validation bandwidth selection (Gitzen et al. 2006) using Home Range Tools

in ArcGIS 9.3 (Environmental Systems Research Institute 2008). Thus, we created a time-specific probabilistic measure of space use (Millsbaugh et al. 2006) for each of the five carnivore species at the landscape level (Fig. 3).

#### *Modeling ungulate presence*

To determine the parameters that best explained the presence of ungulates on the landscape, we developed models using a paired or conditional logistic regression analysis (Hosmer and Lemeshow 2000, Compton et al. 2002). We compared measures of predation risk at each ungulate point location (1) to an equal number of randomly generated reference points (0) within the reserve. We extracted the values of predator UD, habitat types, and distance to the boundary fence for all ungulate locations and paired random locations in ArcGIS 9.3. Predator UD were calculated specifically for each drive count and thus the probability of occurrence was conditional upon the specific time period of sampling (i.e., we paired random points with used locations for the same time period). Given that this study was conducted in a closed ecosystem, the



PLATE 1. To minimize this kind of encounter with their main predator, wildebeest avoid areas that are highly utilized by lions. Photo credit: Vicky Gladwin.

boundary fence may have potentially affected the spatial distributions of some ungulates. Niemann (2010) found a greater proportion of African wild dog kills (of impala and warthog only) near fences in KGR, but fences had no influence on the location of kills for lions (Lehmann et al. 2008), cheetah, or leopard (C. Owen, *unpublished data*). Therefore, we included distance to the fence as a variable only for models of impala and warthog distribution that also had African wild dog UDs as a predictor.

The probability of selecting a site (1 vs. 0) was modeled with a conditional logistic regression analysis using the COXREG procedure in SPSS 15.0 (SPSS 2006), so that the attributes at each point location were matched to attributes at a reference location for the same time period. Habitat types were included in the models as dummy variables, and all other predictor variables were square root-transformed for analyses. All predictor variables were tested for multicollinearity (tolerance levels  $> 0.79$  for all variables), and closed woodland was excluded from analysis due to high multicollinearity ( $< 0.01$ ).

We used an information-theoretic approach to test a priori models that best explain the presence of each ungulate species in the landscape. The global model for each ungulate species included all habitat and predator

space-use parameters. We then constructed candidate models for each ungulate species, testing the five main hypotheses and combinations of hypotheses for minimizing predation risk. Based on the relative predation impact for the seven ungulate species (Fig. 1), we considered predators that contribute to at least 35% of kills to be main predators. We also excluded the space use of spotted hyena from candidate models for all ungulate species except zebra because spotted hyena contributed to  $< 3\%$  of predation-related mortality in KGR. We present a priori model structures for each hypothesis in Appendix A.

We used Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) to assess model weights ( $w_i$ ), and ranked candidate models using  $\Delta AIC_c$  (Burnham and Anderson 2002). To account for model selection uncertainty, estimates of the coefficients of main effect parameters in all models with  $\Delta AIC_c \leq 2$  were averaged (Burnham and Anderson 2002). We report the effect of each predictor variable on the response variable with model-averaged parameter estimates (Appendix B). The magnitude of effect of each predictor variable on the response variable was determined with odds ratios ( $e^b$ ), which indicates the change in the odds of the response variable for every unit increase in the predictor variable (Allison 1999, Hosmer and Lemeshow 2000). An odds

TABLE 1. Best-supported models predicting the presence of each ungulate species on the landscape in Karongwe Game Reserve, South Africa.

Model	$K$	$AIC_c$	$w_i$
Impala ( $n = 3098$ occurrence points)			
All predators <sub>(LN+LP+CH+WD)</sub> + risky habitat <sub>(CR+OR+OW)</sub>	8	3638.90	0.99
Warthog ( $n = 242$ )			
All predators <sub>(LN+LP+CH+WD)</sub> + risky habitat <sub>(CR+OR)</sub> + safer habitat <sub>(OS)</sub>	8	275.17	0.74
Wildebeest ( $n = 516$ )			
Sit-and-pursue predators <sub>(LN+LP)</sub> + risky habitat <sub>(CR)</sub> + safer habitat <sub>(OS)</sub>	5	570.91	0.81
Waterbuck ( $n = 259$ )			
Global model (all parameters)	10	276.40	0.99
Kudu ( $n = 262$ )			
All predators <sub>(LN+LP+CH+WD)</sub>	5	332.88	0.34
Sit-and-pursue predators <sub>(LN+LP)</sub> + safer habitat <sub>(OS)</sub>	4	333.58	0.24
Sit-and-pursue predators <sub>(LN+LP)</sub> + risky habitat <sub>(CR)</sub>	4	334.75	0.13
Zebra ( $n = 385$ )			
Sit-and-pursue predators <sub>(LN+LP)</sub> + risky habitat <sub>(CR+OR+OW)</sub>	6	457.22	0.78
Giraffe ( $n = 246$ )			
Sit-and-pursue predators <sub>(LN+LP)</sub> + safer habitat <sub>(OR+OW+OS)</sub>	6	316.87	0.43
Sit-and-pursue predators <sub>(LN+LP)</sub> + risky habitat <sub>(CR)</sub> + safer habitat <sub>(OR+OW+OS)</sub>	7	316.99	0.40

Notes: Shown are models with  $\Delta AIC_c \leq 2$ , based on a conditional logistic regression analysis. Reported are the number of parameters ( $K$ , including residual variance  $\sigma^2$ ), Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ), and Akaike's model weight ( $w_i$ ). Abbreviations for utilization distributions of predators are: lion, LN; leopard, LP; cheetah, CH; and African wild dog, WD. Habitat type abbreviations are: closed riverine, CR; open riverine, OR; open woodland, OW; and open shrub, OS.

ratio of 1 indicates no effect of the variable and odds ratios greater than 1 indicate greater effect, such that an odds ratio of 10 indicates the odds being 10 times more likely. Note, however, that this effect is not linear for odds ratios  $< 1$ ; for example, an odds ratio of 0.1 indicates that the odds are 10 times less likely. For each ungulate species, we used a  $k$ -fold cross validation for case-control design to evaluate model robustness as proposed by Boyce et al. (2002). Cross-validated Spearman-rank correlations were calculated between 10 equal-interval bin ranks of ungulate presence and frequencies for five model "test-training" sets (at a 20% testing ratio). Models with good predictive ability have a high, positive cross-validated Spearman rank correlation value ( $r_s$ ) on a scale of  $-1$  to  $1$ .

## RESULTS

The presence of warthog and impala on the landscape were best explained by a single top model (warthog  $w_i = 0.74$ , impala  $w_i = 0.99$ ; Table 1), which included an avoidance of the space use of all known predators (lion, leopard, cheetah, African wild dog) and of risky habitats. The distribution of warthog supported the prediction that the space use of predators were avoided in order of predation threat. The odds of occurrence of warthog in a particular area was 2.05 times lower with every unit increase in lion UD (Fig. 4a), which was expected since lion were the primary predator of warthog in KGR (59% of all warthog killed by lion; Fig. 1). The degree of avoidance of leopard, African wild dog, and cheetah (Fig. 4a) was in the order of relative predation risk (Fig. 1). Impala did not show threat-

sensitive avoidance of predation risk. More than 42% of impala were killed by African wild dog, while only 6% were killed by lion (Fig. 1), yet impala were 1.49 times less likely to be present in areas with higher lion UDs, but only 1.07 times less likely to be present in areas of higher African wild dog UDs (Fig. 4b). The odds of occurrence for impala and warthog also decreased in closed riverine, open riverine, and open woodland (impala only) habitats (Fig. 4a, b), which were all risky habitats for these species (Fig. 2). The odds of warthog presence also increased by 1.22 times in open scrub habitats (Fig. 4a), which was one of the habitats where the probability of being killed was low (Fig. 2).

Top models that best explained the presence of wildebeest ( $w_i = 0.81$ ), zebra ( $w_i = 0.78$ ), and giraffe ( $w_i = 0.83$ ) on the landscape all included avoidance of sit-and-pursue predators, avoidance of risky habitats, and selection of safer habitats (Table 1). The odds of occurrence for all three ungulate species in an area was 1.18–1.58 times lower for every unit increase in lion UDs, and 1.20–1.44 times lower for every increase in leopard UDs (Fig. 5a–c), despite the fact that lion alone contributed to  $>75\%$  of mortality for each of these species. These three ungulate species also avoided closed riverine and open woodland (zebra only) habitats, which were risky habitats with the highest relative proportion of kills (Fig. 2). Relatively safer habitats (Fig. 2), such as open scrub and open woodland (giraffe only), were also selected (Fig. 5a–c). Selection of open riverine habitat by giraffe was weak (odd ratio  $\pm 95\%$  confidence intervals include 1), despite being included in the top model.

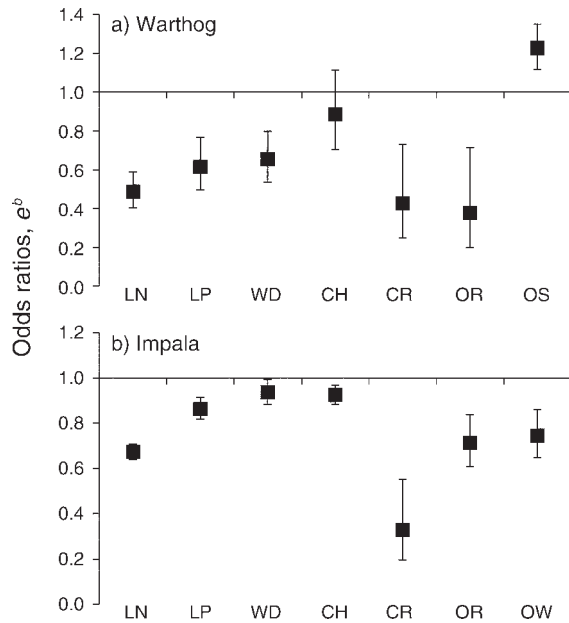


FIG. 4. Odds ratios ( $e^b$ ) and 95% confidence intervals for the model-averaged parameters in the highest ranked models predicting the presence of (a) warthog and (b) impala in KGR. Parameters are utilization distributions of lion (LN), leopard (LP), African wild dog (WD), and cheetah (CH), and closed riverine (CR), open riverine (OR), open woodland (OW), and open scrub (OS) habitats. Odds ratios  $<1$  indicate an avoidance, while those  $>1$  indicate a preference.

The presence of kudu on the landscape was best explained by three top models, which included two of the hypothesized strategies for reducing predator encounters, and selection of some habitats (model-averaged  $w_i = 0.71$ ; Table 1). The odds of kudu occurrence on the landscape decreased by 1.3 times with high African wild dog UD, but increased by 1.44 times with increasing lion UD (Fig. 6a). Kudu were also 1.32 times less likely to occur in risky closed riverine habitat, and were 1.61 times more likely to occur in the relatively safer open scrub habitat (Fig. 6a). Although included in one of the three top models, the space use of leopard and cheetah were poor predictors of kudu presence on the landscape (odds ratio  $\pm$  95% confidence intervals include 1).

The presence of waterbuck on the landscape was explained by the global model, which included all the predictor variables ( $w_i = 0.99$ ; Table 1). The space use of the predators had poor support in predicting waterbuck presence on the landscape (Fig. 6b). As expected, waterbuck were more likely to occur in the relatively safer open woodland and open scrub habitats, but contrary to expectation, waterbuck also selected the riskier open riverine habitat (Fig. 6b).

The predictive capacity of the models explaining presence of all seven species on the landscape was strong ( $r_s > 0.941$ ,  $P < 0.001$ ; see Appendix C for species-specific values).

## DISCUSSION

Many studies have shown that ungulate distributions are a function of predation risk from a single dominant predator in the landscape (Creel et al. 2005, Kittle et al. 2008, Valeix et al. 2009). In a small reserve with multiple predators, we found that ungulates distinguished among potential predators and showed a distribution pattern that simultaneously minimized predation risk from at least some of the predators. Ungulate species reduced their probability of being killed by avoiding risky habitats and selecting safer habitats. Of the hypothesized strategies to reduce predator encounters, we found that ungulates generally utilized one of two strategies. Most of the smaller bodied ungulate species (impala, warthog, waterbuck, kudu) avoided the space use of all predators, while the larger bodied ungulate species (wildebeest, zebra, giraffe) were less likely to occur in areas where the UDs of lion and leopard were high. Notably, the strength of avoidance for the space use of

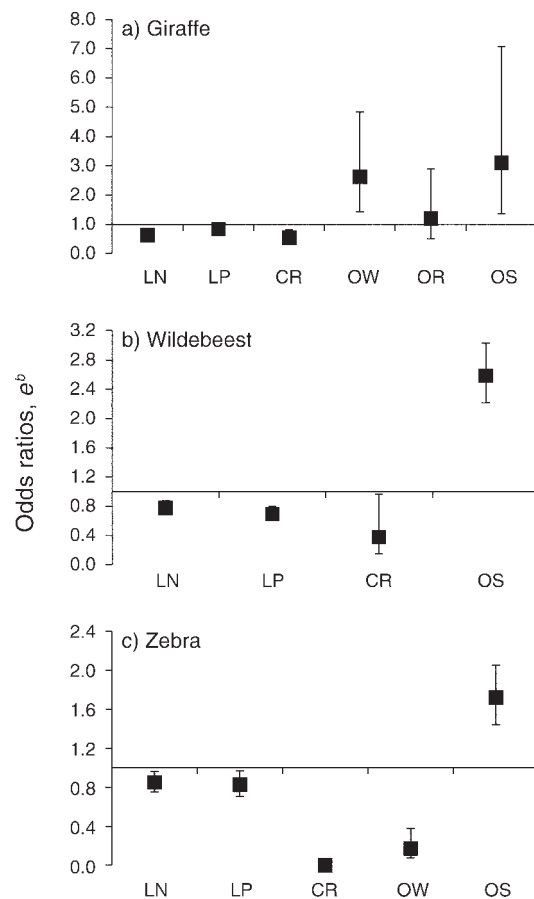


FIG. 5. Odds ratios ( $e^b$ ) and 95% confidence intervals for the model-averaged parameters in the highest ranked models predicting the presence of (a) giraffe, (b) wildebeest, and (c) zebra in KGR. Parameters are utilization distributions of lion (LN) and leopard (LP), and closed riverine (CR), open riverine (OR), open woodland (OW), and open scrub (OS) habitats.



predators generally did not correspond to the relative predation threat from those predators.

Support for the threat-sensitive predator avoidance hypothesis has been found for a range of taxa when tested in controlled conditions at the local scale (e.g., Persons and Rypstra 2001, Mathot et al. 2009, Thaker et al. 2010). We failed to find support for this hypothesis at the landscape level. Warthog was the only species that showed spatial avoidance of predators based on their level of threat, but we are cautious in concluding that warthog had complete information on relative predation threat from the four main carnivores. In general, the response of all ungulates was strongest for the sit-and-pursue predators, thereby supporting the hypothesis that the hunting mode of the predator affects the antipredator strategy of the prey (Preisser et al. 2007). In particular, we found strong negative responses to lion, even if lion was not the main predator. This was expected given that lion are the largest and most dominant predator in most African landscapes (Creel et al. 2001) and have been shown to affect the habitat use (Valeix et al. 2009) and population dynamics (Owen-Smith et al. 2005) of ungulates in other, larger, reserves.

As predicted, no ungulate species avoided areas of high utilization of the cursorial predators, African wild dog and cheetah, as their only predator avoidance strategy. African wild dog were the second most important predator in KGR (based on number of prey killed; Fig. 1), and had a narrow territorial range (Fig. 3), possibly to avoid interference competition from lion (Creel et al. 2001). These factors may have allowed some prey (impala, warthog, waterbuck, and kudu) to also avoid areas of high African wild dog activity, despite the less predictable hunting strategy of this predator. Interference competition between lion and other predators may explain the positive association between the presence of kudu and the space use of lion (Creel et al. 2001), as kudu were avoiding areas of their main predators, African wild dog and cheetah. Interference competition between lion and cheetah (Durant 1998) may explain why the space use of cheetah was a weaker predictor for other ungulate species (warthog and impala) that strongly avoided areas of high lion activity.

Prey also can avoid predation risk by seeking refuge in safer areas or avoiding high-risk habitats (Orrock et al. 2004, Kittle et al. 2008). Ungulate distributions in KGR indicate that habitat avoidance and selection not only were common strategies, but often were stronger than avoidance of the predator activity areas. Sinclair et al. (2003) suggest that adult mortality of smaller ungulates (<150 kg) in the northern Serengeti is regulated by predation pressure, while that of larger species are driven by bottom-up processes (but see Owen-Smith and Mills 2008). We found that, in the relatively small reserve of KGR, giraffe and waterbuck (both above the threshold body size of 150 kg) selected more than one habitat type, which may reflect their resource selection as well as a strategy to select safer habitats. This

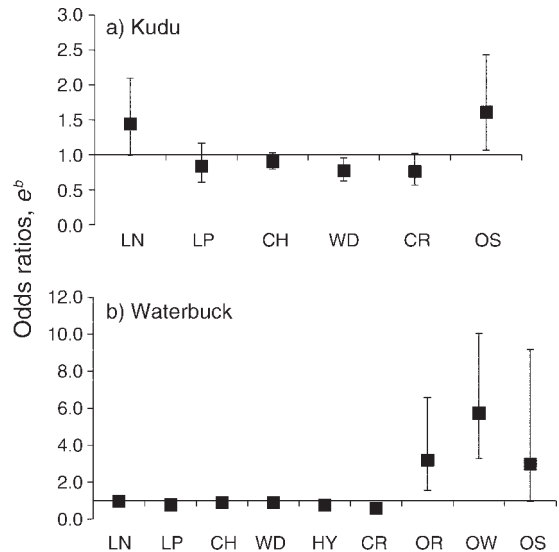


FIG. 6. Odds ratios ( $e^b$ ) and 95% confidence intervals for the model-averaged parameters in the highest ranked models predicting the presence of (a) kudu and (b) waterbuck in KGR. Parameters are utilization distributions of lion (LN), leopard (LP), cheetah (CH), African wild dog (WD), and spotted hyena (HY), and closed riverine (CR), open riverine (OR), open woodland (OW), and open scrub (OS) habitats.

behavioral strategy is particularly likely for waterbuck, which are strongly limited by surface water availability (Redfern et al. 2003), as we found a higher odds of occurrence in open riverine habitat (Fig. 6b), despite the greater predation risk (Fig. 2).

We would like to note here that these antipredator-based spatial distributions of ungulates are unlikely to be an artifact of the small size of KGR (85 km<sup>2</sup>). Mean carnivore densities in KGR (0.05 individuals/km<sup>2</sup>) are intermediate to those in the Serengeti (0.07 individuals/km<sup>2</sup>) and Kruger National Park (0.04 individuals/km<sup>2</sup>) (Hayward et al. 2007). Furthermore, for a similar suite of predators and prey species, the predator to prey ratio in KGR was also intermediate (1:53) to that of the Serengeti (1:82) and the Kruger National Park (1:27) (derived from Hayward et al. 2007). Therefore, we feel that the decision rules driving the distribution pattern of ungulates in KGR are relevant to other African savannas and even to other multi-predator systems where predators differ in their hunting strategies.

Studies that focus on the interactions between a single predator and prey in a multi-predator system can be inadequate for understanding antipredator responses (Caro 2005). The importance of incorporating multiple predators in studies of ecosystem functioning is widely recognized (see reviews in Ives et al. 2005, Schmitz 2007). But there is still a general lack of information on the behavioral strategies, such as vigilance tactics (Lima 1992) and activity patterns (Krupa and Sih 1998), that prey can use to minimize predation risk from multiple predators. At the land-

scape level, we found that prey position themselves to simultaneously minimize the probability of encountering predators and the probability of being killed. The strength of these antipredator strategies was also species specific, depending mainly on the relative predation risk in different habitats and the hunting mode of predators. In general, ungulates did not show threat-sensitive antipredator responses at the landscape level, but used a simpler behavioral rule of avoiding the activity areas of sit-and-pursue predators instead. Antipredator decision rules, however, are likely to change at different spatial scales (e.g., Hebblewhite and Merrill 2009), and we see this as an important avenue for future research, especially when predation risk from multiple predators becomes more variable and when resource requirements become more constrained.

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#### LITERATURE CITED

- Allison, P. D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute, Cary, North Carolina, USA.
- Andruskiw, M., J. M. Fryxell, I. D. Thompson, and J. A. Baker. 2008. Habitat-mediated variation in predation risk by the American marten. *Ecology* 89:2273–2280.
- Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2009. Spatial partitioning of predation risk in a multiple predator-multiple prey system. *Journal of Wildlife Management* 73:876–884.
- Boyce, M., P. Vernier, S. Nielsen, and F. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Caro, T. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, Illinois, USA.
- Compton, B. W., J. M. Rhymer, and M. McCollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. *Ecology* 83:833–843.
- Creel, S., G. Spong, and N. M. Creel. 2001. Interspecific competition and the population biology of extinction-prone carnivores. Pages 35–60 in D. Macdonald, J. Gittleman, R. Wayne, and S. Funk, editors. *Carnivore conservation*. Cambridge University Press, Cambridge, UK.
- Creel, S., J. Winnie, Jr., B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86:3387–3397.
- Durant, S. M. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. *Journal of Animal Ecology* 67:370–386.
- Environmental Systems Research Institute. 2008. ArcGIS. Version 9.3. Environmental Systems Research Institute, Redlands, California, USA.
- Garton, E. O., M. J. Wisdom, F. A. Leban, and B. K. Johnson. 2001. Experimental design for radiotelemetry studies. Pages 16–42 in J. J. Millsaugh, editor. *Radio tracking and animal populations*. Academic Press, San Diego, California, USA.
- Gitzen, R. A., J. J. Millsaugh, and B. J. Kernohan. 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *The Journal of Wildlife Management* 70:1334–1344.
- Hayward, M., J. O'Brien, and G. Kerley. 2007. Carrying capacity of large African predators: predictions and tests. *Biological Conservation* 139:219–229.
- Hebblewhite, M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 90:3445–3454.
- Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. *Oikos* 111:101–111.
- Hirst, S. M. 1969. Road-strip census techniques for wild ungulates in African woodland. *Journal of Wildlife Management* 33:40–48.
- Hosmer, D., and S. Lemeshow. 2000. *Applied logistic regression*. Wiley-Interscience, New York, New York, USA.
- Ives, A. R., B. J. Cardinale, and W. E. Snyder. 2005. A synthesis of subdisciplines: predator–prey interactions, and biodiversity and ecosystem functioning. *Ecology Letters* 8: 102–116.
- Kauffman, M., N. Varley, D. Smith, D. Stahler, D. MacNulty, and M. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecology Letters* 10:690–700.
- Kittle, A. M., J. M. Fryxell, G. E. Desy, and J. Hamr. 2008. The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia* 157:163–175.
- Krupa, J. J., and A. Sih. 1998. Fishing spiders, green sunfish, and a stream-dwelling water strider: male-female conflict and prey responses to single versus multiple predator environments. *Oecologia* 117:258–265.
- Laundré, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: re-establishing the “landscape of fear” in Yellowstone National Park, USA. *Canadian Journal of Zoology* 79:1401–1409.
- Lehmann, M. B., P. J. Funston, C. R. Owen, and R. Slotow. 2008. Feeding behaviour of lions (*Panthera leo*) on a small reserve. *South African Journal of Wildlife Research* 38:66–78.
- Lima, S. L. 1992. Life in a multi-predator environment: some considerations for antipredatory vigilance. *Annales Zoologici Fennici* 29:217–226.
- Lima, S. L. 1998. Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behaviour* 27:215–290.
- Lima, S. L. 2002. Putting predators back into behavioral predator-prey interactions. *Trends in Ecology and Evolution* 17:70–75.
- Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *The American Naturalist* 153:649–659.
- Mathot, K. J., P. J. van den Hout, and T. Piersma. 2009. Differential responses of red knots, *Calidris canutus*, to perching and flying sparrowhawk, *Accipiter nisus*, models. *Animal Behaviour* 77:1179–1185.
- Millsaugh, J. J., R. M. Nielson, L. McDonald, J. M. Marzluff, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. *The Journal of Wildlife Management* 70:384–395.
- Morosinotto, C., R. Thomson, and E. Korpimäki. 2009. Habitat selection as an antipredator behaviour in a multi-

- predator landscape: all enemies are not equal. *Journal of Animal Ecology* 79:327–333.
- Mucina, L., and M. C. Rutherford. 2006. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria, South Africa.
- Niemann, S. M. 2010. Feeding ecology and carrying capacity of a reintroduced pack of African wild dogs in a relatively small, fenced reserve. Thesis. University of KwaZulu-Natal, Durban, South Africa.
- Orrock, J., B. Danielson, and R. Brinkerhoff. 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behavioral Ecology* 15:433–437.
- Owen-Smith, N., D. Mason, and J. Ogutu. 2005. Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. *Journal of Animal Ecology* 74:774–788.
- Owen-Smith, N., and M. G. L. Mills. 2008. Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology* 77:173–183.
- Persons, M., and A. Rypstra. 2001. Wolf spiders show graded antipredator behavior in the presence of chemical cues from different sized predators. *Journal of Chemical Ecology* 27: 2493–2504.
- Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86:501–509.
- Preisser, E. L., J. L. Orrock, and O. J. Schmitz. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. *Ecology* 88:2744–2751.
- Redfern, J. V., R. Grant, H. Biggs, and W. M. Getz. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* 84:2092–2107.
- Schmitz, O. J. 2005. Behavior of predators and prey and links with population-level processes. Pages 256–278 in P. Barbosa and I. Castellanos, editors. *Ecology of predator–prey interactions*. Oxford University Press, Oxford, UK.
- Schmitz, O. J. 2007. Predator diversity and trophic interactions. *Ecology* 88:2415–2426.
- Searle, K. R., C. J. Stokes, and I. J. Gordon. 2008. When foraging and fear meet: using foraging hierarchies to inform assessments of landscapes of fear. *Behavioral Ecology* 19: 475.
- Sih, A. 2005. Predator-prey space use as an emergent outcome of a behavioral response race. Pages 241–255 in P. Barbosa and I. Castellanos, editors. *Ecology of predator–prey interactions*. Oxford University Press, London, UK.
- Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* 13:350–355.
- Sinclair, A., S. Mduma, and J. Brashares. 2003. Patterns of predation in a diverse predator–prey system. *Nature* 425: 288–290.
- SPSS. 2006. SPSS, Version 15.0. SPSS, Inc., Chicago, Illinois, USA.
- Thaker, M., A. Vanak, S. Lima, and D. Hews. 2010. Stress and aversive learning in a wild vertebrate: the role of corticosterone in mediating escape from a novel stressor. *The American Naturalist* 175:40–50.
- Thomson, R. L., J. T. Forsman, F. Sarda-Palomera, and M. Monkkonen. 2006. Fear factor: prey habitat selection and its consequences in a predation risk landscape. *Ecography* 29: 507–514.
- Valeix, M., A. J. Loveridge, S. Chamaille-Jammes, Z. Davidson, F. Murindagomo, H. Fritz, and D. W. Macdonald. 2009. Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology* 90:23–30.
- Willems, E. P., and R. A. Hill. 2009. Predator-specific landscapes of fear and resource distribution: effects on spatial range use. *Ecology* 90:546–555.

#### APPENDIX A

Subset of a priori hypotheses used to predict the presence of each ungulate species on the landscape at Karongwe Game Reserve, South Africa (*Ecological Archives* E092-035-A1).

#### APPENDIX B

Model-averaged parameter estimates for top AIC-ranked models predicting ungulate distribution on the landscape in Karongwe Game Reserve, South Africa (*Ecological Archives* E092-035-A2).

#### APPENDIX C

Mean cross-validated Spearman-rank correlations ( $r_s$ ) between the probability of occurrence and bin ranks for each species across sub-samples ( $n = 5$ ) (*Ecological Archives* E092-035-A3).