

Risky times and risky places interact to affect prey behavior

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Abstract

Both short-term and long-term variation in predation risk can affect the behavior of prey, thus affecting growth, reproduction, survival, and population dynamics. Inferences about the strength of such ‘risk effects’ in the wild have been limited by a lack of studies that (i) relate antipredator responses to the magnitude of direct predation, (ii) measure responses of prey to risk from complete predator guilds, and (iii) quantify risk in more than one way. Here, we quantified behavioral responses of a complete ungulate prey guild to long-term and short-term variation in risks from all of the large predators in Liuwa Plain National Park, with known patterns of direct predation. Our analysis allowed the first direct test for interaction between responses to long-term and short-term risk in the wild, and revealed that prey vigilance responded strongly to locations with high long-term risk when short-term risk was high, but not when short-term risk was low. This result has broad ramifications for the design and interpretation of field studies of antipredator behavior, its costs, and its consequences for population dynamics.

Introduction

Experiments with many species have shown that exposure to predation risk induces responses by prey that can carry costs affecting growth, reproduction, survival, and population dynamics¹⁻⁶. Despite this, we have a very limited understanding of the magnitude of these ‘risk effects’ in the wild, in part because field studies are rarely designed in a manner that allows risk effects to be disentangled from simple bottom-up limitation by food^{7,8}. Our understanding has also been limited by a lack of studies that (i) measure responses of prey to risk from complete predator guilds, (ii) relate the intensity of antipredator responses to the magnitude of direct predation, and (iii) employ methods that quantify risk at more than one spatiotemporal scale.

The first point is conceptually obvious: different predators typically create risks at different places and times⁹⁻¹¹. We have learned a great deal by quantifying the responses of prey to a single predator, particularly in cases where one predator is the dominant threat to a given prey species^{12,13}, but in many systems this approach is likely to provide an incomplete assessment of the constraints imposed by predation risk¹⁴. Despite this, studies of responses by prey to the risks presented by complete predator guilds remain uncommon¹⁵.

The second point is also conceptually simple, but surprisingly few studies have tested how the strength of antipredator response relates to the magnitude of direct predation¹⁴, particularly under natural circumstances^{4,15,16}. While it is logical to hypothesize that prey will respond most strongly to the predators that kill them most often^{15,17}, it is also logical to hypothesize that a low level of direct predation might be the consequence of effective responses by the prey, rather than low ‘risk’^{18,19}. Clearly, describing this relationship is necessary to understand the relative importance of direct predation and risk effects as determinants of the total limiting effect of predators on prey⁷.

The third point is conceptually more subtle: selection should favor prey that assess and respond to risk at more than one scale, but most field studies (including our own¹²) have quantified risk in just one way. In studies of ungulate prey responding to risk from large predators, prior studies have used GPS radiocollars to describe long-term variation in risk as peaks and valleys in the distribution of predator locations¹³ or kill sites²⁰, or as habitat types that vary in use by predators¹⁵. Responses to long-term variation in risk have also been assessed by comparison of study sites with variation in predator presence or density¹² or by comparing sites before and after predator colonization²¹. Other studies have used direct observations to measure short-term variation in risk as the immediate presence/absence or proximity of predators or kills^{16,22}, and some have used data from GPS collars to determine responses to short-term risk^{13,23}. From such studies, it is clear that prey can respond to both short term variation in risk (the ‘risky times’ hypothesis) and spatial variation in the long term risks associated with a site (the ‘risky places’ hypothesis). Behavioral studies have focused mainly on risky times, while ecological research has focused mainly on risky places²⁴. Surprisingly, the hypothesis that these two aspects of risk have interactive effects on prey behavior remains untested in the wild.

Here, we used a combination of data from GPS collars on predators and direct observation of prey under conditions of known immediate risk to examine the behavioral responses of a complete ungulate guild comprised of wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*) and oribi (*Ourebia oribi*) to both long-term and short-term variation in risk from all of the large predators in Zambia’s Liuwa Plains ecosystem (African wild dogs, *Lycaon pictus*, spotted hyaenas, *Crocuta crocuta*, lions, *Panthera leo*, and cheetahs, *Acinonyx jubatus*; leopards, *Panthera pardus*, are not found in Liuwa). We quantified short term variation in risk using the distance to the nearest predator at the time of observation, the predator’s species, and whether a

kill was present at the predator's location. We quantified long term variation in risk by determining the location's year-round intensity of use by predators. We used AIC scores to test whether the model's explanatory power was improved by replacing use by all predators with use by each of the predator species, use by each predator functional group (stalkers and coursers), or use by the predator that was immediately closest at the time of observation. We also tested whether the model was improved by restricting these measures of long term risk to kill sites (rather than all predator locations). Because long term risk is often described indirectly through habitat variables^{28,29}, we tested whether measures of vegetation structure improved the model's description of prey behavior. Finally, we used direct observation of each predator species to quantify patterns of direct predation on each of the ungulate species. These data allowed the first test (to our knowledge) for interaction between antipredator responses to long-term (LT) and short-term (ST) variation in risk under natural conditions, as predicted by Lima & Bednekoff in 1999²⁵, and as detected in laboratory settings^{26,27} and field experiments²⁶.

Results

To identify the parameters that affected prey vigilance, we began with a quasi-binomial generalized linear model that included effects of prey species, the predator species that was nearest at the time of observation, the distance between the two (a measure of short term risk), the presence or absence of a recent kill at the predator's location (another possible measure of short term risk) and three measures of long term risk at the location of the prey: (1) the utilization distribution (UD) of predators (all species), (2) the UD of kill sites (all species), and (3) the proportion of kills that the observed prey species constituted for the nearest predator (Table 1). We included three two-way interactions that we hypothesized (*a priori*) to be important: prey

species x predator species, distance to the nearest predator x predator species, and an interaction between long and short term risk (UD of predators x distance to the nearest predator).

From the initial model of prey vigilance, likelihood ratio tests eliminated weak effects of the proportion of kills of the observed prey species by the predator that was present ($df=1$, $F = 0.003$, p -value 0.96), the presence or absence of a fresh kill at the predator's location ($df = 1$, $F = 0.6407$, p -value 0.42), the utilization distribution of kill sites ($df = 1$, $F = 0.0003$, p -value = 0.98) and the interaction between the predator species and distance ($df = 3$, $F = 1.2963$, p -value = 0.28). The resulting model (Table 2) included effects of prey identity, predator identity, interaction between predator and prey identity, ST risk (distance between the predator and the prey), LT risk (the UD of the predator that was present: see next paragraph), and interaction between ST risk and LT risk (see Table 2 for coefficients and their standard errors). As we have previously reported (Creel et al., in press) vigilance in LPNP was not detectably related to variation in herd size ($b = -0.014 \pm 0.001$ SE, $t = 1.41$, $P = 0.16$), or composition [proportion females] $b = 0.004 \pm 0.006$ SE, $t = 0.68$, $P = 0.49$), probably because herd sizes are small in comparison to many savanna ecosystems ($\bar{X} \pm SE$: oribi 2.47 ± 0.09 , zebra 13.03 ± 2.80 , wildebeest 6.46 ± 1.42), so that LPNP ungulates cannot depend on strong dilution of risk to provide safety.

Controlling for differences among predator and prey species, vigilance levels were much higher in locations of high LT risk, increasing by 139% with an increase of one standard deviation in LT risk (Fig 2, right panel, $b = 1.39$, $S.E.M. = 0.39$, $t = 3.55$, $P < 0.001$). LT risk was best described by the local intensity of use by the predator that was immediately closest at the time of observation rather than other measures of LT risk. As expected, vigilance tended to decrease as the distance to the nearest predator increased (i.e., as ST risk decreased), but the

main effect of ST risk on vigilance was weaker than that of LT risk (Fig 2, left panel, $b = -0.27$, S.E.M. = 0.245, $t = -1.13$, $P = 0.26$), and the effect of ST risk was manifest primarily through a strong interaction with LT risk (Fig 2, middle panels, $b = -0.66$, S.E.M. = 0.33, $t = -2.02$, $P = 0.04$). When a predator was close (< 250 m), vigilance increased strongly and consistently in locations with high LT risk, but responses to LT risk were weak and variable when no predators were immediately nearby.

Substituting alternative measures of LT risk into the final model, AIC scores revealed that prey responded most strongly to the UD of the predator species that was immediately present. The next best model was the UD of all predators combined ($\Delta AIC = 0.93$), with considerably weaker support for models with the UDs of stalkers, coursers or individual species.

The addition of grass height did not improve the model's explanatory power. Confidence intervals for the effect of grass height on vigilance greatly overlapped zero (grass 10 cm – 1 m: $b = -0.14 \pm 1.01$ S.E., $t = -0.14$, $P = 0.89$; grass > 1 m: $b = -0.40 \pm 0.69$ S.E., $t = -0.59$, $P = 0.56$; reference level was grass < 10 cm), and confidence intervals overlapped zero for all but one of the interactions between grass height, predator species and prey species.

Discussion

As expected, ungulates were more vigilant in places that were heavily used by predators over the long term. Contrary to expectation, there was little evidence that ungulates were more vigilant if they were closer to the nearest predator at the time of observation. This result came, however, from a model that allowed for interaction between LT and ST risk, and variation in ST risk did affect vigilance in a manner that depended on the LT risk of the location. Controlling for differences in mean vigilance among prey species and differences in their responses to the four

predators, vigilance was greatest when high levels of ST risk (a predator immediately nearby) occurred in locations with high LT risk (heavy use by that predator species). It is striking that the best measure of LT risk to describe this interaction was the UD of the predator that was immediately present, indicating a fine-tuned assessment by prey of the relationship between ST and LT risk, rather than a consistently stronger response to specific predator species or functional types (stalker vs. courser). To summarize, prey responded most strongly when they encountered immediate risk in a place where they could have anticipated that very risk.

The result that prey responded more strongly to times of high ST risk in places with high LT risk has a parallel in the theory of Lima & Bednekoff²⁵, who emphasized that “antipredator behavior depends on both the immediate and the background level of predation risk”. Although Lima & Bednekoff²⁵ focused entirely on temporal variation in risk, while we quantified spatial and temporal variation in risk, both bodies of work suggest that responses to ST risk depend on associated patterns of LT risk. It has also been shown that the strength (and retention) of learned responses to risk are affected by past exposure to risk in laboratory studies with fish^{26,27}, and tadpoles²⁶ and in a field experiment with fish²⁶. Our results confirm that both the *risky places hypothesis* (LT risk) and the *risky times hypothesis* (ST risk) are important²⁴ and that they do not act independently in their effects on the strength of antipredator responses. This interaction presents serious challenges for the design of research on risk effects. A real effect of ST risk could easily be masked by unmeasured variation in LT risk (or vice versa), and an apparent effect of ST risk might actually be caused by unmeasured variation in LT risk (or vice versa). Few (if any) prior field studies have employed a design that addresses these complications, so our results have broad implications for the design and interpretation of studies of antipredator behavior, its costs, and its consequences for population and community dynamics.

Vegetation structure is often used as a proxy for LT risk^{28,29}. Because the vegetation on our study site was highly homogeneous open grassland, we did not include vegetation type in our original model, but we did test *post-hoc* if vegetation structure (grass height) improved the model appreciably, and it did not. With the accumulation of studies collecting location data over long periods from GPS collars, it will be an interesting question for further research (at sites with more complex structure) whether vegetation structure or predator utilization itself is a better predictor of risk effects³⁰. We suggest that variables such as vegetation structure and topography should be tested in addition to data on the predators themselves, and not as a proxy for such data.

Our analysis found that responses varied among predator-prey pairs, but not as expected if the strength of response was positively correlated to direct predation rates¹⁷. The strength of responses (Table 2) did align with the predictions of Preisser, Orrock & Schmitz³¹ who predicted that stalking predators, like lions and cheetahs, should have stronger effects on prey behavior than coursing predators, like wild dogs and hyenas. It is notable, however, that the effect of interactions between predator and prey identity offset this difference (e.g. wildebeest responded very strongly to wild dogs: Table 2), so that models including LT risk from wild dogs, hyenas or both coursers performed better (AIC 1797.329-1799.028) than models including LT risk from lions, cheetahs or both stalkers (AIC 1799.77-1800.70). Neither the immediate presence of a kill nor the long term distribution of kill sites had any detectable effect on vigilance, suggesting that kill locations³² are a weak proxy for data on the predators themselves when seeking to understand risk effects. In the short term, the presence of a kill could be an indicator of risk in systems where many individuals might be killed (e.g. some invertebrate

systems³³), but for ungulate-large carnivore systems, a kill decreases the short-term likelihood of a hunt and may be interpreted as a cue of safety.

Conclusion

It is becoming increasingly clear that predators can have strong effects on prey demography and dynamics through the costs of antipredator behavior, and that these effects might cascade to affect community structure and function. For a more complete understanding of the strength of these risk effects, we still require studies that measure responses of prey to risk from complete predator guilds, relate the intensity of antipredator responses to the magnitude of direct predation, quantify risk at more than one spatiotemporal scale, and test for interactions in these effects. Several field studies have simultaneously examined the effects on prey behavior of both short term and long term variation in predation risk^{24, 34, 35}, but data from the wild do not yet provide an empirical basis to assess whether the interaction between short term and long term risk that we observed will prove to be a general pattern, as theory suggests it should be²⁵. If so, then studies capable of describing this interaction will be critical for a proper understanding of risk effects.

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Methods

Study Area and Populations

Our data were gathered in a 1200 km² study area in the southern part of the 3660 km² Liuwa Plain National Park (LPNP) in Zambia. The area has little topography (no rivers flow within the study site) and the vegetation is dominated by uniform short and intermediate grasslands with occasional tree islands (Fig. 1). The ungulate community is dominated by migratory wildebeest (*Connochaetes taurinus*) at densities ranging from 6.2 – 60.8 individuals/km², migratory zebra (*Equus quagga*) at densities ranging from 1.8 – 8.1 individuals/km², and non-migratory oribi (*Ourebia ourebi*) at densities ranging from 1.1 – 14.5 individuals/km². These densities were estimated from distance sampling (which allowed correction for each species' probability of detection) on a systematic transect grid, several times in each year of the study³⁶. Hyenas greatly outnumbered other predators within the study area, with 151 hyenas in four clans³⁷, 6 lions in one pride, 22 wild dogs in two packs and 17 known cheetahs. Leopards are not present in LPNP, nor is there any record of their presence in recent times³⁷.

Predator Follows to Quantify Magnitude of Direct Predation

Patterns of prey selection by the four predators and the methods used to obtain these data have been described in detail elsewhere¹¹. Briefly, radio-collared predators were followed for complete hunting periods (from when they became active until they became inactive), typically for several consecutive hunting periods. During these follows, we recorded the species (and when possible the age and sex) of prey that were encountered, hunted and killed. These follows, combined with opportunistic observations, yielded a sample of 453 kills where the identity of the predator was directly observed ($N = 351$) or inferred with high confidence ($N = 102$). High confidence was assigned to kills that were not directly observed but were very fresh, with only

one predator species present, no other predators detected nearby, and no signs of attendance by other predators. Patterns of prey selection did not differ detectably between the complete data set and the subset of kills that were directly observed.

Location Data from Predators

Locations of African wild dogs, hyenas and lions were collected between June 24, 2010 and December 23, 2015 using GPS and VHF radio collars fit to individuals in all but one predator group known to reside wholly or largely within the study site (details below). All immobilization procedures to fit animals with collars were conducted with permission of the Department of National Parks and Wildlife (DNPW, formerly ZAWA), following animal welfare standards and protocols required by the Zambia Department of Veterinary and Livestock Services and the DNPW. From January 07, 2012 to April 13, 2013 the alpha female of a resident African wild dog pack was fitted with a GPS collar taking a location every 5 hours for a total of 1354 locations. A second resident pack was fitted with VHF collars and was monitored from June 25, 2010 to May 30, 2014, when the pack dissolved into multiple dispersal groups following the death of the alpha male; a total of 359 locations from this pack were used. From October 24, 2010 to May 13, 2012 5 hyenas (in three of the four resident clans) were fitted with GPS collars (recording a location every 2 or 3 hours for a total of 187, 725 and 3,493 locations for each clan). During the course of the study one of these clans split into two, but frequent re-sightings of known individuals confirmed that the two newly-formed clans remained largely within the source clan's area. The remaining clan was monitored with VHF collars on five clan members, which provided a total of 318 locations (two hyenas in this clan were fitted with GPS collars but the GPS function failed in both). The lion population in Liuwa consisted of 1 coalition of 2 males, and 1 pride of females and cubs that formed a cohesive social group totaling six individuals. Between June 24, 2010 and

May 28, 2015 at least one male and one female lion was fitted with a GPS satellite collar (recording a location every 3 or 4 hours for a total of 11,018 locations) and one additional female was fitted with a VHF collar for the duration of the study. Cheetah locations came from observations of 7 cheetahs fitted with VHF collars (and their associates) between June 30, 2010 and December 23, 2015, with one collar in each group known to use the site. These included single locations from opportunistic observations, and multiple locations from hunt follows in which cheetahs were observed continuously through at least one complete period of hunting activity (and up to 7 days) on 50 occasions between November 11, 2012 and December 23, 2015. When moving, a GPS location was recorded at 15 minute intervals, and while stationary a single location was recorded; a total of 2,000 locations from cheetahs were used. Although the locations from cheetahs were not collected with GPS collars, this sampling provided representative data for cheetah movements within the study site.

For each of the four species, these locations were used to fit a utilization distribution that was resampled in an identical manner for each species to compare space use (as described below). The location data for the four species come from overlapping periods from 2010 to 2015, but the interval sampled was not identical for all species. However, data from GPS collars showed that the ranging patterns of lions and hyenas changed little year to year, sampling of wild dogs was intensive for the entire period during which they used the site, and the locations of cheetahs showed no evidence of territorial partitioning of the study area, suggesting that the sampling provided representative data¹¹.

Utilization Distributions Fit to Location Data to Quantify Spatial Variation in Long-term Risk

From the locations described above we calculated a utilization distribution (UD) for each species^{38,39} using the adehabitatHR package⁴⁰ in R⁴¹, with a grid cell size of 500 meters. This spatial

scale was fine enough to provide a meaningful description of variation in space use, and the data for each species allowed us to fit UD_s (shown in ref 11) at this scale. Randomly thinning the data for lions (with the most locations) to equal the sample size for wild dogs (with the fewest locations) yielded very little change in the estimated UD. Standard methods for selection of bandwidth as a smoothing parameter, e.g. least squares cross validation³⁹, did not always converge, and the standard reference bandwidth (h_{ref}) yielded rather discontinuous utilization distributions. In such cases, several authors^{42,43} recommend using a subjective visually chosen bandwidth. We adopted a more objective version of this approach, by calculating the daily distance moved for each individual animal (by summing the distances between consecutive locations within a day for individuals fitted with GPS collars or observed during continuous hunt follows, which are described below). We then selected the 90th percentile of the frequency distribution of daily distances (95th for cheetahs, with sparser data) as the smoothing parameter. This procedure yielded largely continuous UD_s, occasionally keeping densely clustered locations separate in a reasonable manner. Because the home ranges of the two wild dog packs and the four hyena clans had little overlap, UD_s were calculated separately for each group, then combined and rescaled to result in a total utilization of 1 for the combined UD. This process properly resolved areas of low use between home ranges. For cheetahs and lions, individual ranges overlapped very substantially, so we calculated a single UD for each species.

It is possible that prey respond primarily to predators on the basis of functional groups (e.g., stalkers vs. coursers) rather than species^{15,44}, though tests of this hypothesis have shown variable results^{15,16,20}. To test this possibility we combined the UD_s of the coursing predators, hyenas and wild dogs, and those of stalking predators, cheetahs and lions, and again rescaled

them to a total utilization of 1. Finally, to calculate the utilization of the study area by all of the predators, we combined the UD's of all four species and again rescaled to a total utilization of 1.

To more completely examine what factors drive variation in antipredator response, we also fit each of the UD's just described to a subset of the data restricted to kill sites, to test whether long term risk is better described by the locations at which predators made kills rather than the locations that predators used for all purposes.

Ungulate Observations to Quantify Responses to Risk

To measure the behavioral response of prey to short-term and long-term variation in risk, we used 348 scan-sample observations of ungulate herds. For each observation we recorded the location, distance to the nearest known predator, predator species, presence/absence of a kill, and the date and time. We then recorded the species, number of animals in the herd, sex and age class (adult, sub-adult, juvenile), and its behavior at the moment of the observation. For this analysis, our primary response variable was the proportion of adults vigilant ($\bar{X} = 0.09$), operationally defined as an ungulate being stationary and holding its head above shoulder height with the ears and eyes focused simultaneously, while not chewing (neither taking bites nor ruminating). This definition focuses on clear-cut attentiveness to the surroundings and excludes more ambiguous 'routine' vigilance^{16,45,46}. We focused on vigilance because it is the most common antipredator behavior for all three of these species⁴⁷ and increased vigilance causes reduced feeding in these species⁴⁷. We did not use data from herds that directed vigilance at the observer. To sample behavior representatively, each of the 348 observations consisted of an average of 7 scans, performed at intervals of 2-10 minutes (depending on herd size, which determined the time required to scan the herd). To avoid pseudoreplication, the unit of analysis was the observation period, rather than scans within observation periods (i.e., we tested for effects on the mean

proportion of adults vigilant, with one mean per observation period). Herds were observed from a stationary vehicle, with either binoculars or a spotting scope. Scans were conducted primarily around dusk and dawn when predators were still active but observation conditions were good. While we do not focus on group size in this analysis, we confirmed that the inferences reported here for the effects of long-term and short-term risk on vigilance were not altered by the inclusion of group size as a predictor.

To collect these data efficiently, we began by locating a predator, recording its location and searching for nearby ungulates. We recorded the location of the prey herd and determined the straight-line distance (in meters) between the predator and prey. We aimed to stratify observations across prey species and distance to the nearest predator, so that half ($N = 176$) of the ungulate scans were within 500 meters of a predator and half ($N = 172$) were at longer distances (of which 99 observations were for distances between 500 m and 1 km, and 73 were for distances between 1 km and 2 km). We also distributed ungulate observations across the entire study area, though ungulate observations were unavoidably more concentrated in areas with higher long-term use by predators (because predators were not often found within 2 km of prey in areas of low use). It is possible that another undetected predator was sometimes closer to the observed herd, but due to the openness of the terrain this was probably uncommon. This inference was reinforced by taking care that no vigilance was observed towards unmonitored predators during the scans.

Measures of Short Term and Long Term Variation in Predation Risk

We measured the risk of predation in two basic ways. *Short term* variation in the risk of predation ('ST risk') was measured by recording the distance to the nearest predator at the time of observation, and whether a kill was present at the predator's location. As described above,

observations were made at dawn and dusk when predation risk remained high, but observations were linked to the presence of predators that were not actively hunting or moving, so that distance could be measured accurately. *Long term* variation in risk ('LT risk') was measured by determining the intensity of use by each predator (i.e., the height of its UD) at the location of the observation. We further tested whether antipredator behavior was related to the species of predator, the species of prey, and the frequency of predation on each prey species by each predator. Models that substituted predator functional type (stalker vs courser) for predator species were compared, and models that described long term risk by fitting UDs only to kill sites, rather than fitting UDs to all predator locations. Finally, we tested whether measures of short-term and long-term risk interacted in their effects on vigilance.

We used 453 kills for which the predator and prey species could be assigned with confidence to measure the proportion of predation by each of the four predators on each of the three prey species (Table 1). These same data were used to create an overall UD of all kill sites, of kill sites for each species except for zebra (which were killed too infrequently to create a distribution of kill sites), of kill sites for each predator species, of kill sites for each predator functional type (stalker and courser), of kill sites for each predator-prey pair (restricted to those for which there were enough data: wild dog – wildebeest, wild dog – oribi, cheetah – wildebeest, cheetah – oribi, hyena – wildebeest, lion – wildebeest) and of kill sites for each predator functional type – prey species pair (stalker – wildebeest, stalker – oribi, courser – wildebeest, courser – oribi).

At the location of each ungulate observation, we extracted the value for each of the UDs just described as alternative measures of long term variation in risk, and then (as described below) identified which measures of LT and ST risk best predicted vigilance by prey.

Model Identification

To identify the parameters that affected vigilance, we began with a quasibinomial generalized linear model that included effects of prey species, predator species (i.e., the species that was immediately nearest), the distance between the two (a measure of immediate, short term risk), the presence or absence of a recent kill at the predator's location (another possible measure of short term risk) and three measures of long term risk at the location of observation: 1.) The UD of predators (all species), 2.) The UD of carcasses (all species), and 3.) The proportion of kills that the observed prey species constituted for the nearest predator. We included three two-way interactions that we hypothesized (*a priori*) to be important: prey species x predator species, distance to the nearest predator x predator species, and an interaction between long and short term risk (UD of all predators x distance to the nearest predator). We used all of the data to estimate the main effects of ST risk and LT risk, but it was not possible to collect a large sample of observations with high ST risk (i.e., a carnivore nearby) in areas with very low LT risk (i.e., where carnivores rarely go). In addition, for observations with low ST risk (i.e. the nearest carnivore was quite distance from the location of the prey), it is not clear that measures of LT and ST risk based on widely separated locations for the predator and prey would be meaningful. To address these issues when testing for an interaction between LT and ST risk, we assigned a value of 0 for LT risk to observations with the nearest predator more than 450m away, thus restricting the test for interaction between the effects of LT risk and ST risk to situations in which ST risk was appreciable (i.e., we tested whether LT risk interacted with ST risk when ST risk was known to be present).

We then used likelihood ratio tests for sequential deletion of weak effects from this model, but retained main effects that were part of strong interactions. As described previously,

long term risk was measured in more than one way, and we used AIC scores to test whether the model's explanatory power was improved by replacing the UD of all predators with the UD for each of the predator species, the UD of each predator functional group (stalker and courser), or the UD for the predator that was immediately present. Similarly, we used AIC scores to test if explanatory power was increased by replacing the UD of kill sites for all prey species with the UD of kills sites only for the prey species observed. Lastly, we used AIC scores to check whether the distance between predator and prey had better explanatory power than a simple factorial presence/absence parameter, where presence was defined as the predator being less than 450m from the prey based on the results of prior research¹⁶.

With the quasibinomial GLM identified by these steps, we tested whether the addition of a vegetation structure parameter improved the explanatory power of the model, to test whether prey used attributes of the environment itself to assess risk, beyond assessments of the long and short term presence of predators. There was little variation in vegetation structure on our study site, which was > 90% open grassland, so we tested instead for effects of grass height, with three levels (<10 cm, 10 cm – 1 m, >1 m). We tested the addition of this effect to the model as a single parameter, as an interaction with ungulate species, as an interaction with predator species and as a three-way interaction with both ungulate species and predator species. This test was conducted as a final step because measurements of grass height were available only for a subset of the data (N = 334 observations).

Continuous predictor variables were centered and scaled prior to analysis so that effects could be compared directly.

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

490 **Data availability**

491 An MOU on data ownership exists between the authors and African Parks, but within the
492 constraints of that agreement, data will be shared upon reasonable request.

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528 **Author contributions**

529 S.C. developed the methods of data collection. S.C., M.S.B., E.D. and J.M. designed the study in
530 Liuwa Plain NP while E.D., J.M. and M.S.B. collected the data. E.D. performed the data analysis
531 with assistance of S.C.. E.D., with assistance of S.C. wrote the manuscript while the other
532 authors provided input on all earlier versions of the manuscript.

533

Table 1. The proportion of kills made by each predator species that were comprised of each prey species. 95% binomial confidence interval in parentheses.

	Wildebeest	Oribi	Zebra
Wild Dog	0.76 (0.69 – 0.82)	0.23 (0.17 – 0.30)	--
Cheetah	0.22 (0.13 – 0.35)	0.64 (0.50 – 0.76)	--
Hyena	0.95 (0.87 – 0.98)	0.01 (0.00 – 0.07)	0.04 (0.01 – 0.07)
Lion	0.96 (0.88 – 0.99)	--	0.04 (0.01 – 0.12)

Table 2. Effects on prey vigilance levels from the final generalized linear model. Short term risk was described by the distance to the nearest predator at the time of observation. Long term risk was described by a kernel utilization distribution fit to carnivore locations for the complete study period.

Effect ³	Estimate	SE	t	P
<i>Intercept</i>	-3.49137	1.275	-2.738	0.007
<i>Risk</i>				
Short Term Risk (Distance)	-0.277	0.245	-1.129	0.26
Long Term Risk	1.389	0.391	3.554	<0.001
ST X LT interaction	-0.663	0.327	-2.025	0.044
<i>Predator Species¹</i>				
Spotted hyena	-1.549	1.32	-1.173	0.241
Lion	2.844	2.032	1.399	0.163
African wild dog	-6.216	2.021	-3.076	0.002
<i>Prey Species²</i>				
Wildebeest	-4.015	1.426	-2.813	0.005
Zebra	3.004	3.377	0.89	0.374
<i>Species Interaction</i>				
Wildebeest X Hyena	1.654	1.49	1.11	0.268
Zebra X Hyena	-1.494	3.43	-0.436	0.663
Wildebeest X Lion	-1.619	2.223	-0.728	0.467
Zebra X Lion	-4.342	4.031	-1.077	0.282
Wildebeest X Wild Dog	9.352	2.255	4.147	<0.001
Zebra X Wild Dog	0.669	4.338	0.154	0.877

1: Reference level is cheetah.

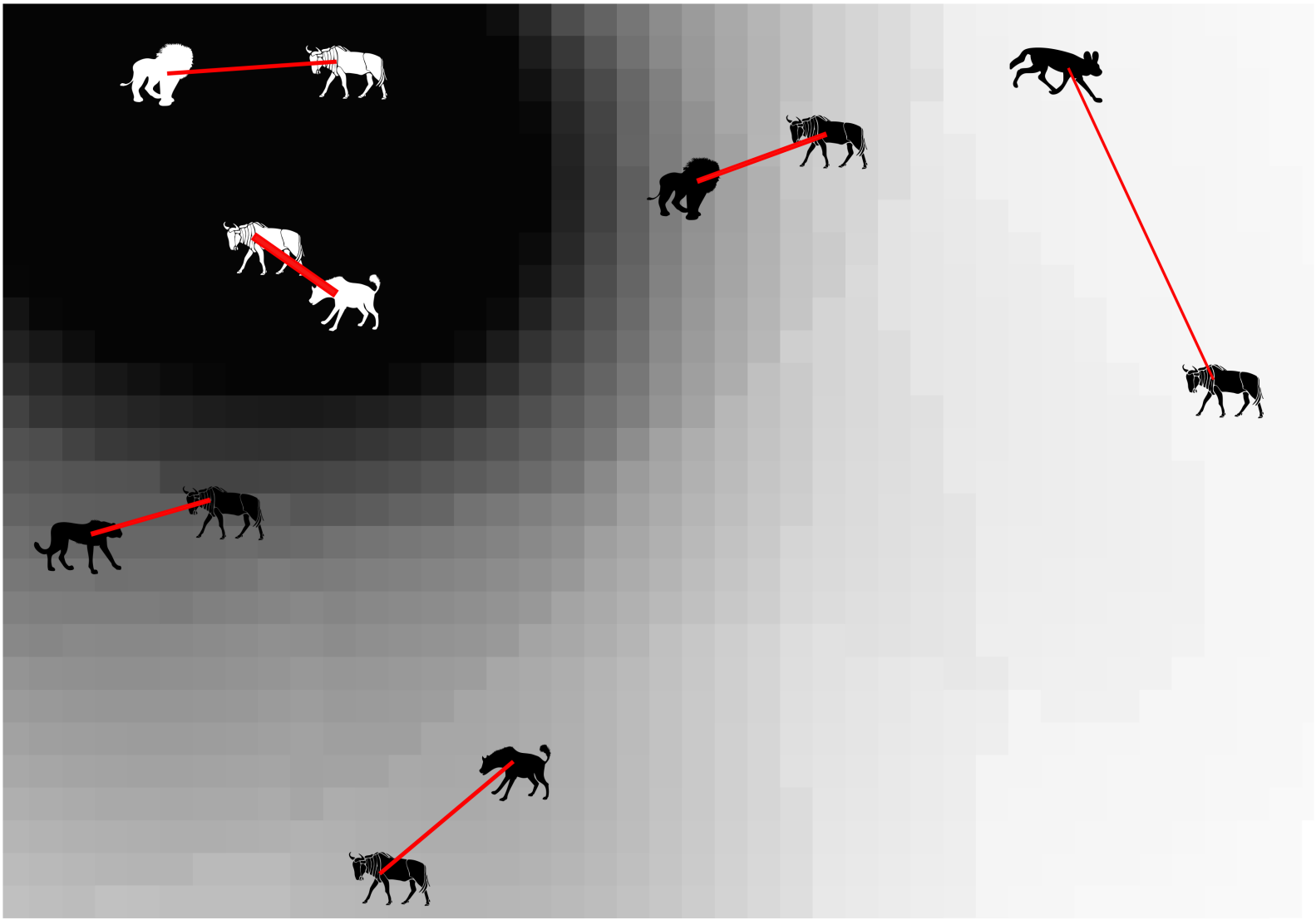
2: Reference level is oribi.

3: Multiplicative effects, with all continuous variables centered and scaled for direct comparison.

Figure Legends

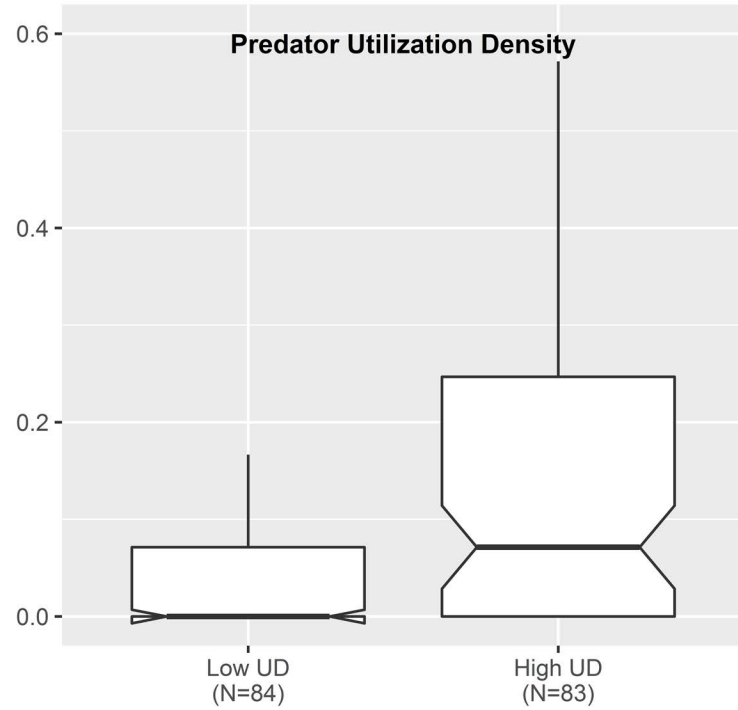
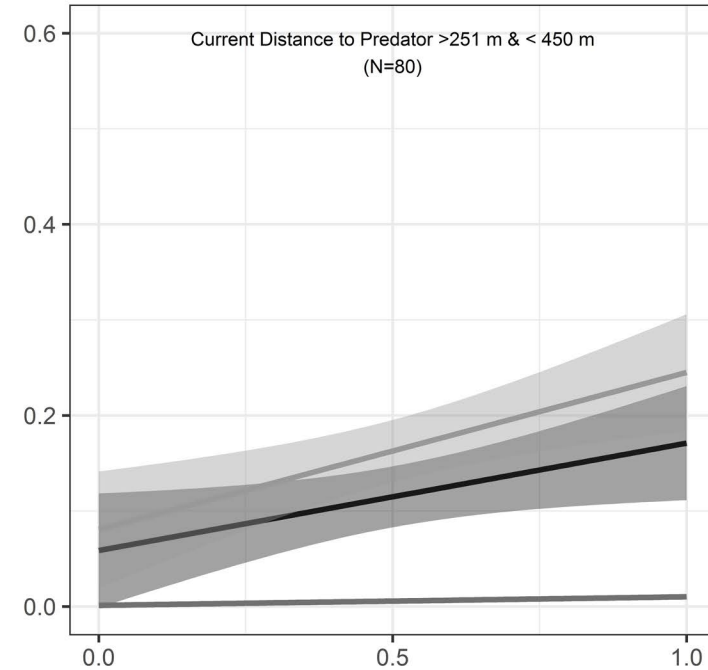
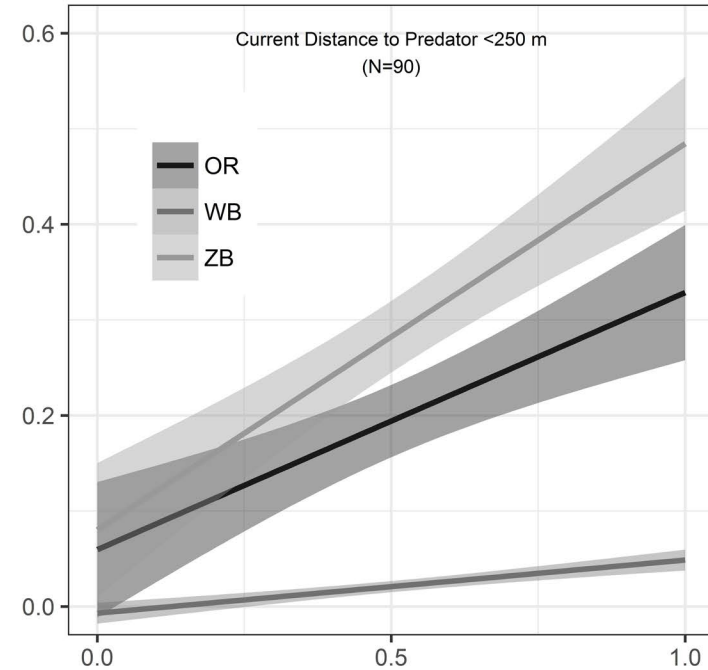
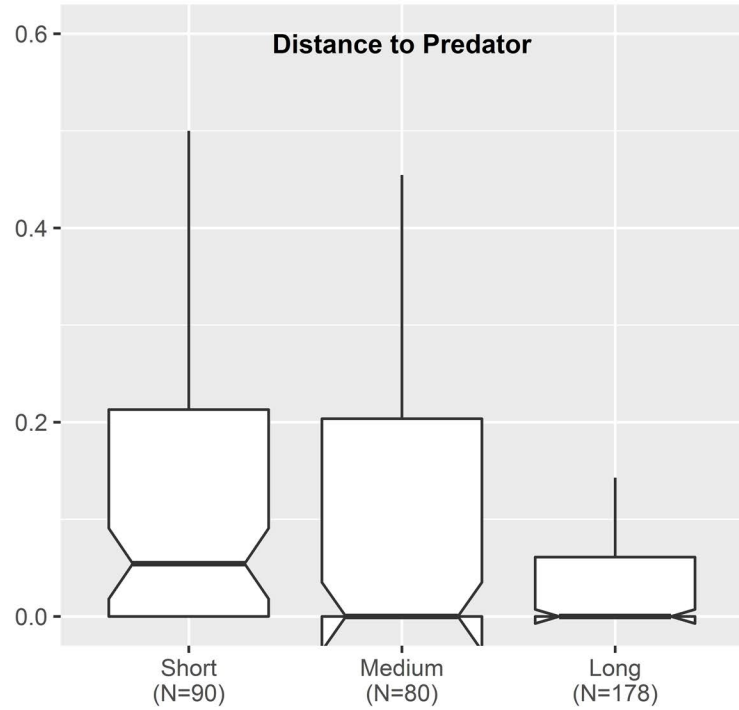
Figure 1. Schematic diagram for methods relating prey behavior to variation in short term and long term risk. (*Top*) A schematic diagram using wildebeest as an example to illustrate how the behavior of prey was related to short-term and long-term variation in risk. Background shading indicates long term risk, with darker areas indicating greater intensity of use by predators, as described by a kernel utilization distribution fit to predator locations for the entire study period. Comparison of models with prey utilization distributions fit to different subsets of data allowed us to test whether long term risks from all predators, from specific predators, from specific predator functional groups (stalker & courser) or from kill sites yielded more power to explain variation in prey behavior. Red lines indicate immediate short term risk, assessed by the distance to the nearest predator at the time of observation, its species, and whether a kill was present. We attempted to balance the data for all combinations of ST and LT risk, though some combinations (predator close in area of very low predator use) are not common. (*Bottom*) The uniformly open vegetation structure and lack of topographic variation within the study site simplified interpretation of prey responses to the patterns just described.

Figure 2. Interaction in the effects of short term and long term risk on prey behavior. The vigilance of prey was affected by short term risk (*left panel*, relating vigilance to the distance to the nearest predator at the time of observation), long term risk (*right panel*, relating vigilance to the long term intensity of predator use at that location) and an interaction between the two (*middle panels*). Controlling for differences among prey species, vigilance increased strongly in response to long term risk under circumstances of high short term risk, but not under circumstances of low short term risk. (*Left and right panels*) Bars show median, interquartile range and range. Pairs of bars with non-overlapping notches identify medians that differ with 95% confidence. (*Middle panels*) Back-transformed predictions and their 95% confidence limits from the best generalized linear model (Table 2), holding the effects of variation in response to different carnivores at their means.





Proportion of adults vigilant



Predator Utilization Density