

**What explains variation in the strength of behavioral responses to predation risk? A  
standardized test with large carnivore and ungulate guilds in three ecosystems.**

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*Word Count:* Total including abstract, references, tables and figures = 7957.

**Abstract.** If access to food is affected by the risk of predation, then the number of individuals killed by predators is an incomplete measure of the limiting effect of predation. Nonetheless, it is often assumed that the costs of antipredator responses (risk effects) are either small enough to be ignored or positively correlated with direct predation, and thus unlikely to alter inferences based on predation rates. These assumptions are rarely tested. Here we studied five large carnivores and ten prey species in three Zambian ecosystems to test relationships between direct predation, antipredator vigilance and trade-offs with foraging. The presence of a predator caused vigilance to increase by a factor of 2.4, with substantial variation among prey species in the strength of this response. This was associated with a 28% decrease in the proportion of individuals foraging, a trade-off that was consistent across species. We detected no correlation between direct predation and the strength of antipredator responses, which undermines the gambit of ignoring risk effects. The strength of antipredator responses was uncorrelated with broad attributes of predators and environments, but was correlated with attributes of prey. Responses were stronger for small species and for browsers/mixed feeders relative to grazers. It has previously been noted that small ungulates face higher rates of direct predation. Building on this inference, our results suggest that carnivore loss/restoration will also have stronger behaviorally-mediated effects on small ungulates, particularly browsers and mixed feeders. If such species increase their representation where carnivores are depleted, then cascading effects on vegetation would be expected.

*Keywords:* predation; risk effect; predator-prey dynamics; large carnivore; ungulate

Almost all species face some risk of predation, and almost all species react with some form of inducible defense. By varying the strength of their defenses, prey can reduce the likelihood of predation when risk is high, but also reduce the costs of defense when risk is low (Harvell & Tollrian 1999, Tollrian & Harvell 1999). Antipredator defenses can be behavioral, morphological, physiological or ecological (Agrawal & Fishbein 2006, Creel *et al.* 2005, Lima & Dill 1990, van Donk *et al.* 1999, Werner *et al.* 1983), and they are seen in taxa ranging from algae, protists, plants and invertebrates to all classes of vertebrates (Tollrian & Harvell 1999). The costs of defense can be manifest through reduced survival, growth or reproduction (Christianson & Creel 2014, Creel *et al.* 2007, Pangle *et al.* 2007, Peckarsky *et al.* 1993, Ruxton 1997, Zanette *et al.* 2011), and studies from a broad range of species have yielded a consensus that inducible defenses evolve when four conditions are met: (1) there are reliable cues about the level of risk, (2) antipredator responses reduce risk, (3) risk is variable but sometimes strong, and (4) antipredator responses carry costs (Harvell & Tollrian 1999, Tollrian & Harvell 1999). If risk does not vary or defenses are not costly, then constitutive (fixed) defenses are expected. Thus, for species with inducible defenses, the costs of defense are expected to partition the limiting effect of predation into two components, direct killing and risk effects. While the existence of risk effects is well-established by many experiments and some field studies, we still know very little about their importance for conservation and management (Creel *et al.* 2007, DeCesare *et al.* 2013, Madin *et al.* 2011, Muhly *et al.* 2010).

This situation has several origins. First, new ideas usually move from basic to applied fields of study, and this transition takes time. Second, most early studies of risk effects used experimental approaches with invertebrates and small vertebrates (Crowl & Covich 1990, Peckarsky *et al.* 1993, Ruxton 1997, Werner *et al.* 1983), and because conservation of the

species was not of immediate concern, implications of the results for conservation were not a focal point. Third, risk effects are difficult to measure in the wild, and it remains plausible that they are often ignored in conservation and management mainly because they are hard to measure and easily attributed to other causes (Creel & Christianson 2008). Most direct measurements of risk effects rely on experimental approaches that do not allow inference about their strength under natural conditions, a problem that is well-recognized (Christianson & Creel 2014, Peers *et al.* 2018). Conversely, many studies of predation in the context of conservation and management still do not consider the possibility of risk effects. If a linear model that does not include a term for risk effects is fit to data on the dynamics (or demography) of a species with antipredator defenses that vary and carry a fitness cost, its coefficients will be affected by omitted variable bias (Maddala & Lahiri 1992). Omitted variable bias has two consequences for inference: risk effects go un-measured because they were assumed not to exist, and the effects of risk are rolled into the estimated effects of food supply or direct predation, biasing inference about their strength. While it is widely recognized that risk effects are difficult to measure, this broader consequence of ignoring them is rarely addressed. To avoid inferential errors, analyses that guide conservation and management must recognize that when foraging success is affected by the risk of predation, then top-down and bottom-up limitation are not independent processes (Sinclair & Arcese 1995). Addressing this point requires an approach that allows one to either isolate risk effects (Creel *et al.* 2007, Nelson *et al.* 2004, Pangle *et al.* 2007, Peckarsky *et al.* 1993), or to partition the total effect of predation into direct and risk components while controlling for other limiting effects (Christianson & Creel 2014).

Two additional problems limit our understanding of the strength of risk effects in natural systems. The first is conceptually simple, though logistically difficult to address. Most prey

species are embedded in a guild of similar prey, and each member of the guild is exposed to predation by multiple predators. In many systems, the number of predator-prey dyads is so large that obtaining representative data is a formidable challenge. For each predator-prey dyad, data are required on the strength of antipredator response (which requires observation under conditions of known and variable risk), the intensity of direct predation, and prey population size (to convert direct predation to per-capita units). Each of these three variables requires considerable effort to measure in the wild for even a single predator-prey pair in a single ecosystem. Consequently, replication across multiple predators, prey and ecosystems is not common (Moll et al. 2017). Studies with such replication are needed to advance the field, because the variation observed across predator-prey-ecosystem combinations is large enough that inferences from one combination cannot be extrapolated with confidence (see Results).

The final problem was explained well by Lank & Ydenberg (2003), who noted that “the most straight-forward meaning and measure of predation risk could be the observed rate or probability of mortality due directly to predators”, but “a quite different meaning of predation risk is the inherent probability of becoming a prey item in any particular situation if no antipredator measures are taken.” The second measure drives selection for antipredator responses, but the first measure is what we observe in the field. As Figure 1 illustrates, it is not logically necessary that predator-prey dyads with low realized predation rates are also dyads with low inherent risk. Thus, it is also not logically necessary that predator-prey dyads with low realized predation will be associated with weak antipredator responses. Because antipredator responses affect direct predation rates before we measure them in the field, the (observed) correlation between direct predation and the strength of antipredator responses can be weak or

negative, even though the (unobserved) correlation between inherent risk and antipredator responses is expected to be positive (Creel & Christianson 2008).

Research to date has not established whether risk effects are typically strong or weak in comparison to direct predation. In some cases they are strong (Christianson & Creel 2014, Nelson *et al.* 2004, Pangle *et al.* 2007, Peckarsky *et al.* 1993, Schmitz 1998), but for the vast majority of systems we do not know (Peers *et al.* 2018). Existing theory suggests that the attributes of predators (Schmitz 2008), prey (Creel 2011) and environments (Heithaus *et al.* 2009) might predict the strength of risk effects, but we know almost nothing about the empirical relationship between antipredator responses and direct predation rates in the wild (Creel *et al.* 2017, LaManna & Martin 2016). We addressed this information gap by quantifying three variables in each of three Zambian ecosystems (Greater Liuwa, GLE, Luangwa Valley, LVE; and Greater Kafue GKE):

(1) Patterns of prey selection by the five members of the large carnivore guild (African wild dogs, *Lycaon pictus*; cheetahs, *Acinonyx jubatus*; leopards, *Panthera pardus*; spotted hyenas, *Crocuta crocuta*; and lions, *Panthera leo*).

(2) Levels of proactive and reactive antipredator vigilance for a set of 10 ungulate prey species that spanned representative ranges of body mass, herd size and foraging ecology, in response to the immediate presence of each predator species.

(3) The density of each prey species (accounting for variation in detectability), so that patterns of direct predation could be converted to per capita units.

We then used generalized linear models to test how variation in vigilance was related to direct predation risk, and to the ecological attributes of prey, predators and ecosystems. Our intent was

to apply a set of standardized methods to: (a) test the relationship between direct predation and antipredator responses across predator-prey-ecosystem combinations, (b) identify broad ecological correlates of the strength of antipredator responses, and (c) consider implications for the conservation and management of predator-prey systems.

## **Methods**

We collected the data described below between 1 January 2011 and 1 January 2017.

### *Ecosystems*

In LVE our 2,775 km<sup>2</sup> study area is located in the in the eastern portion of South Luangwa National Park and the adjacent Lupande and Lumimba Game Management Areas (GMAs). The area is a mosaic of deciduous and thorn woodlands with interspersed small grassland areas. Animal densities are highest near the Luangwa River, which flows through the study site from north to south. Human settlement is prohibited in the national park, where the main human land use is photo-tourism. The GMAs have mixed land uses including human settlements, photo-tourism, legal trophy hunting and illegal wire snaring. The most common prey were impala (*Aepyceros melampus*), puku (*Kobus vardonii*), warthog (*Phacochoerus africanus*), zebra (*Equus quagga*), buffalo (*Syncerus caffer*) and hippo (*Hippopotamus amphibious*), which comprised 85% of carnivore diets ( $N = 389$  kills). Our GLE study area of 4,800 km<sup>2</sup> includes most of Liuwa Plain National Park and the adjacent West Zambezi GMA. Data is focused on an intensive study area of 1,200 km<sup>2</sup> in the southern portion of the park where the majority of large carnivores are resident (Droge *et al.* 2016, M'soka *et al.* 2016a). The area is primarily open grassland with small isolated patches of open broadleaved forest. Limited human settlement is allowed both in the GMA and National Park. The LVE supports Africa's second largest wildebeest (*Connochaetes taurinus*) migration, and the ungulate community is dominated by

wildebeest, zebra and oribi (*Ourebia ourebi*) (M'soka *et al.* 2016b), which comprise >90% of carnivore diets ( $N = 670$  kills) (Creel *et al.* 2017, Droge *et al.* 2016). In GKE our 5,200 km<sup>2</sup> study area includes portions of Kafue National Park and adjacent West Mumba and Kasonso Busanga GMAs, with an intensive study site of 3,840 km<sup>2</sup> bounded on the south by the M9 road, on the north by papyrus swamps in the Busanga Plain, on the west by the park boundary and on the east by the Kafue and Lufupa Rivers. GKE is primarily miombo woodland with interspersed floodplains, and it supports a diverse (21 species) community of ungulates at low densities (Matandiko 2016). The primary human use of the park is photo-tourism, with trophy hunting, illegal snaring and human settlement in the GMAs. Depletion of large prey has altered large carnivore diets over the past half century, and the most common prey for large carnivores are now impala, puku and warthog, although hippo and buffalo remain important for lions (Creel *et al.* 2018).

#### *Predators*

We collected data on responses of prey to each of the five carnivores (wild dog, spotted hyena, lion, leopard and cheetah) in each of the three ecosystems (GLE, LVE and GKE) with the following exceptions. Cheetahs are absent from LVE, leopards are absent from GLE, and spotted hyenas have long been uncommon in GKE (Mitchell *et al.* 1965), so they were not included. Spotted hyena density in LVE is not known, but we detected few hyena kills and they were not included. Leopards are common in GKE and LVE (Rosenblatt *et al.* 2016) and we included them in our analysis of antipredator responses, but the three criteria for data quality described in the next paragraph excluded all predator-prey combinations involving leopards from analysis that tested the relationship between antipredator responses and per-capita predation rates.



## 161 *Prey*

162           We included 10 ungulate prey species in our analysis with representative ranges of body  
 163 mass, herd size and foraging ecology, because these attributes can affect the risk of predation, the  
 164 effectiveness of antipredator behavior, or its costs. From a potential set of more than 20 species,  
 165 we restricted our analysis to predator-prey-ecosystem combinations for which the following  
 166 criteria were met: (a) Predation by that predator on that prey was observed in that ecosystem (see  
 167 *Prey Selection* for details). (b) We obtained a minimum of 350 observations of prey behavior  
 168 from a minimum of 20 separate sampling occasions for that predator-prey-ecosystem  
 169 combination (see *Observation of Proactive and Reactive Vigilance* for details). (c) We obtained  
 170 an estimate of prey population density with a coefficient of variation below 0.2 for that prey-  
 171 ecosystem combination (see *Prey Density from Distance Sampling* for details). For analysis of  
 172 correlations between antipredator responses and the ecological attributes of predators, prey and  
 173 ecosystems these criteria yielded data for a set of 10 prey species (Table 1). Some prey in this  
 174 set were killed more often than expected on the basis of their relative abundance (maximum =  
 175 1.14), and some considerably less often (minimum = 0.12), providing good scope for analysis  
 176 (9.5-fold variation). Analysis of the correlation between antipredator responses and per-capita  
 177 direct predation (Table 2, Figure 3) also required accurate data on prey population density (see  
 178 *Prey Density from Distance Sampling*), which restricted this analysis to 15 predator-prey-  
 179 ecosystem combinations: GLE: wildebeest-cheetah, wildebeest-wild dog, wildebeest-lion,  
 180 wildebeest-spotted hyena, oribi-spotted hyena, zebra-spotted hyena LVE: impala-wild dog,  
 181 puku-wild dog, impala-lion, puku-lion, warthog-lion, zebra-lion; GKE: impala-lion, puku-wild  
 182 dog, puku-lion.

## 183 *Prey Density from Distance Sampling*

To convert patterns of prey selection to a measure of per-capita realized direct predation (Figs. 1 & 3), we estimated prey density (accounting for variation in detection) using distance sampling with methods we have described previously (Creel *et al.* 2018, M'soka *et al.* 2016b, Matandiko 2016). Briefly, at each study site we established a fixed grid of transects totaling ~125 kilometers, with 4 kilometer spacing between adjacent transects. Twice annually (in the dry and wet seasons), we drove transects at  $\leq 15$  km/h, with the driver using a GPS to maintain the track while two rooftop observers scanned for herbivores. When a herd (or single animal) was sighted we stopped the vehicle and recorded its position and the distance and bearing to the animal(s) using a GPS, laser rangefinder and compass. For each prey species, we fit a distance sampling model to these data with the `distsamp` or `gdistsamp` functions of the `unmarked` package in R (Chandler 2011, Fiske & Chandler 2011) to estimate density in units of herds/km<sup>2</sup>, with correction for the effects of distance and habitat type on the probability of detection. We converted density from herds/km<sup>2</sup> to individuals/km<sup>2</sup> using transect-specific mean herd size for each species, which we obtained from zero-truncated poisson models using the `vglm` function in the `VGAM` package in R (Zuur *et al.* 2009). We propagated the variance in herd size into estimates of density via bootstrapping in R.

Distance sampling models could not be fit for prey species that were uncommon, because they require a sufficient number of detections during the transect sampling to fit a detection function. Here, we restricted our analysis to prey-ecosystem combinations with a minimum of 40 detections within the transect sampling and estimates of density with a coefficient of variation below 0.2. These criteria provided estimates of population density for impala, puku, warthog and zebra in LVE, wildebeest, zebra and oribi in GLE, and impala, puku and warthog in GKE.

*Prey Selection*

We recorded the species of animals killed during ‘follows’ of radiocollared carnivores through complete hunting periods (74% of kills), and other sightings obtained with and without radiotelemetry (26%) (Creel *et al.* 2018, Droge *et al.* 2016). We restricted this analysis to 1,158 kills (452 in GLE, 317 in GKE, 389 in LVE) for which the predator was identified with high confidence (kills directly observed, or judged to be less than one hour old with only one carnivore species present and no sign of other species having been present). Preliminary analysis confirmed that patterns of prey selection were not affected by the method of detection within this data set.

We calculated the realized per capita rate of predation (Fig. 1) for each predator-prey pair as a selection ratio, with numerator equal to the proportion of kills that a prey species formed in a predator’s diet, and the denominator equal to the proportion that the same prey species formed in the ungulate community. This ratio is equal to one for prey that are killed in proportion to their abundance, greater than one for prey that are preferentially selected, and less than one for prey that are under-selected.

#### *Observation of Proactive and Reactive Vigilance*

We recorded the behavior of prey herds in 1,142 scan-sampling observation periods of 30-60 minutes (344 in GLE, 207 in GKE, 591 in LVE). For each herd observed, we recorded herd size, composition, and the proportion of adults that were vigilant, foraging, moving and running (a subset of moving). Before observations we recorded the distance to the nearest known predator, predator species, predator group size and composition, the presence/absence of a kill at the location of the predator, grass height class (0-10 cm, 10 cm – 1 m, >1m), grass color class (green, brown or mixed), and wind speed (using a Kestrel handheld anemometer held above the vehicle and rotated slowly to maximize the reading).

To efficiently obtain these data, we first located carnivores by radio-tracking, recorded their location using a GPS, and then searched for ungulate herds. We restricted observations to herds that were not being stalked or chased, and prioritized observations that were difficult to obtain to stratify the data over distances from 50 meters to two kilometers. We measured the straight-line distance between ungulate herds and predators using a GPS fix for each location. We did not collect data at distances greater than two kilometers because prior research showed that other, undetected predators can affect inferences for distances above two kilometers (Creel *et al.* 2014). We stopped the vehicle prior to causing disturbance or vigilance and waited several minutes before beginning data collection to avoid effects of our presence. In a preliminary analysis we tested whether anti-predator behavior was better explained by the distance to predators (treated as a continuous variable) or by a dichotomy between predators being ‘present’ at any distance below a threshold, and ‘absent’ beyond the threshold. We found that a threshold of 450 meters consistently revealed responses to predator presence (see Fig 2A), and we used this threshold to distinguish between ‘reactive’ vigilance in response to an immediate threat and ‘proactive’ vigilance to monitor diffuse threats. We confirmed that similar changes in vigilance were detected across a range of thresholds from 200 meters to 600 meters for the four best-sampled species (puku, impala, warthog and zebra). While differences in mean vigilance were consistent across this range, a threshold of 450 meters yielded the least variation among species, so we considered it the best ‘common currency’ for consistent comparison of a broad set of predators, prey and ecosystems.

We observed prey around dawn and dusk, when light conditions allowed behavioral observation but the risk of predation was still high. Adults and young of the year were distinguishable for all species, and our analysis here is restricted to the behavior of adults. A

herd was operationally defined as a set of individuals with low and relatively constant inter-individual distance (typically <10 body lengths) that were simultaneously moving in the same speed and direction, or simultaneously stationary. We recorded behavior by scan sampling at 5 minute intervals, using binoculars to scan the herd from one edge to the opposite edge and a digital recorder to record the age, sex and behavioral state of each individual. We recorded an animal as vigilant if it was stationary with its head held sharply above shoulder height with the eyes and ears simultaneously focused, not chewing or ruminating. Less-restrictive definitions of vigilance allow the possibility that an animal could simultaneously be vigilant and ruminating. Ruminating ungulates cannot listen effectively for predation cues (Lynch et al. 2015), and simultaneously focusing sight and hearing is characteristic of full anti-predator vigilance in these species ('intense' vigilance in the sense of Periquet *et al.* (2012), 'induced' vigilance in the sense of Blanchard & Fritz (2007). For grazers (Table 1), we defined foraging as remaining stationary with the head down taking bites or investigating the vegetation, alternating steps with bites/investigation, or ruminating. For browsers, we defined foraging as remaining stationary with the head directed into woody vegetation, alternating steps with bites/investigation, or ruminating. For mixed feeders we combined these definitions. Using these operational definitions, vigilance and foraging were easily and consistently classified for these species. Observers were trained by simultaneously and independently classifying individual behavior with an experienced observer to obtain  $\geq 95\%$  congruence.

For each observation period, we calculated the proportion of adults that were vigilant or foraging. Because we recorded other behaviors not analyzed here (moving, bedded, standing [not vigilant], and 'other' [grooming, mating]), the proportions of individuals vigilant and foraging do not sum to one (see Fig 2B).

## 276 *Statistical Procedures*

277       The dependent variable for our primary analyses is the proportion of adults that were  
 278 vigilant within a herd. Because this dependent variable is bounded between zero and one, we  
 279 modelled effects with beta regression models using the betareg package in R with values of  
 280 exactly 0 or 1 shifted by 0.00001 (Cribari-Neto & Zeileis 2010, Ferrari & Cribari-Neto 2004).  
 281 Because data on per-capita realized direct predation were available only for prey-ecosystem  
 282 combinations where distance sampling models could be fit, we fit one model to examine the  
 283 relationship of vigilance to direct predation (Table 2), and a second model to examine the  
 284 relationship of vigilance to the attributes of predators, prey and the environment (with all effects  
 285 estimated simultaneously, see Tables 1 and 3). To examine the trade-off between vigilance and  
 286 foraging, we fit a negative exponential model with an interaction term for species identity. We  
 287 confirmed good fit for all models with standard diagnostics obtained by applying the plot  
 288 function to model objects in R (Zuur *et al.* 2009). Finally, we controlled for collinearity by  
 289 adjusting coefficients from multiple regressions with variance inflation factors obtained by  
 290 comparison of multivariate and univariate models.

## 291 **Results**

### 292 *Broad Effects of Carnivore Presence on Vigilance*

293 Overall, ungulates responded to short-term risk by more than doubling their level of vigilance  
 294 (Fig. 2A). Averaged across all predator-prey-ecosystem combinations, the proportion of adults  
 295 vigilant increased from  $0.08 \pm 0.01$  (SE) with no carnivores immediately present to  $0.19 \pm 0.02$   
 296 with carnivores present ( $Z = 4.61$ ,  $P < 0.0001$ , beta regression). While this broad pattern of  
 297 response was clear, there was substantial variation among prey species in proactive vigilance,  
 298 reactive vigilance, and the magnitude of difference between the two (Fig. 2A). One strategy

(‘never drop your guard’) was employed by oribi, which maintained the highest levels of proactive vigilance but showed no increase in vigilance when a predator was immediately present. A more typical strategy (‘respond when you must’) was exemplified by zebra, which showed low levels of proactive vigilance but increased their vigilance substantially in response to short-term risk. Lechwe, warthog and wildebeest employed a third strategy (‘don’t freak out’), responding to risk but maintaining relatively low levels of both proactive and reactive vigilance. Below, we identify broad ecological factors that help to explain this variation.

### *The Trade-off between Vigilance and Foraging*

As the proportion of individuals vigilant increased, the proportion of individuals foraging decreased (Fig. 2B,  $b = 0.97 \pm 0.05$  SE,  $t = 18.16$ ,  $P < 0.0001$ ). While the strength of antipredator responses varied substantially (Fig. 2A), this trade-off was relatively consistent across species ( $P \geq 0.17$  for all levels of the interaction of prey species with slope). It is not logically necessary that an increase in vigilance would produce a decrease in foraging, because the sum of the two proportions is substantially less than one (mean proportion vigilant = 0.127, mean proportion foraging = 0.520, distributions shown in the margins of Fig 2B). Nonetheless, the regression of Fig 2B reveals that the absolute proportion of adults foraging decreased in a one-to-one fashion (from 0.54 to 0.44) as vigilance increased from the level with predators absent (0.08) to the level with predators present (0.18).

### *Antipredator Responses and Direct Predation*

Vigilance was negatively correlated with per-capita realized direct predation (Table 2), as is expected if induced defenses reduce direct predation. This result was driven by a negative relationship between proactive vigilance and direct predation; reactive vigilance showed no correlation with direct predation (Fig. 3). The negative correlation was also almost entirely

driven by one outlier with high leverage (warthog/lion/LVE). Dropping this one combination, there was no detectable correlation between antipredator responses and direct predation (Table 2, Fig. 3), as expected if stronger defenses are induced by higher inherent risk but induced defenses reduce direct predation prior to measurement (Fig.1). In contrast, dropping this combination caused almost no change in the estimated effect of carnivore presence on vigilance (Table 2).

#### *Antipredator Responses and Attributes of Predators, Prey and the Environment*

Both proactive and reactive vigilance levels were correlated with several aspects of prey ecology (Table 3). Browsers and mixed feeders had higher levels of vigilance than grazers (Fig. 4), small species had higher levels of vigilance than large ones (Fig 5), and herds of intermediate size had higher levels of vigilance than small or large herds (Fig. 6), though this last effect was not as well-supported as the other two.

In contrast to attributes of prey, the strength of vigilance was only weakly related to predator identity (Table 3), which spanned a gradient of hunting tactics from the wild dog (which is the most highly cursorial predator known), through the hyena, cheetah and lion to the leopard (which epitomizes reliance on stalking with a short final rush). The strength of vigilance was also only weakly related to the presence of a kill.

Environmental effects were also weak, in comparison to prey attributes. Differences among ecosystems and the effects of grass height, grass color and wind speed were all weak (Table 3).

#### *Direct Predation and Attributes of Prey*

While prey attributes correlated with antipredator behavior, these same variables were not good predictors of per-capita direct predation (body mass,  $b = 0.01 \pm 0.01$ ,  $t = 1.01$ ,  $P = 0.34$ ; foraging type (mixed feeders/browsers relative to grazers)  $b = -0.32 \pm 0.87$ ,  $t = -0.37$ ,  $P = 0.72$ ;



herd size,  $b = -0.40 \pm 1.02$ ,  $t = -0.39$ ,  $P = 0.71$ ; quadratic effect of herd size  $b = -0.84 \pm 1.24$ ,  $t = -0.68$ ,  $P = 0.52$ ; all continuous variables centered and scaled). This lack of correlation reinforces the importance of recognizing that realized direct predation does not necessarily reflect inherent risk (Fig. 1).

## Discussion

Across 10 ungulate prey species, vigilance increased by a factor of 2.4 when a carnivore was immediately present. In absolute terms, increased vigilance produced an almost one-to-one decrease in foraging that was consistent across prey species. This trade-off between vigilance and foraging probably arises because large carnivores often hunt ungulates when they are foraging. Ungulates respond to risk by simultaneously looking and listening (and probably smelling) for threats. An ungulate that is foraging can neither scan well (because of directing their vision to the process of selecting bites) nor listen well (because of laterally grinding vegetation with their molars). Selection has made carnivores sensitive to this vulnerability, so they often hunt ungulates when they are foraging. This pattern causes antipredator vigilance to trade off with foraging, as is expected from theory (Abrams 1993) and confirmed by observations and experiments with many species (Verdolin 2006).

Empirically, this trade-off did not detectably differ among the 10 prey species we examined, suggesting that variation in vigilance is propagated into variation in its costs. One of the biggest challenges in the study of risk effects is measuring how changes in behavior translate into effects on fitness or population dynamics. Our data do not allow direct inference about fitness or population dynamics, but with the vigilance induced by predator presence, the proportion of individuals foraging dropped to 72.1% of the foraging effort in herds with no vigilant animals (averaged across all predator-prey-ecosystem combinations). It seems unlikely

that this response is without cost, because that conclusion would seem to require an assumption that ungulates do not forage as effectively as possible unless forced to by risk.

Analyses that disregard risk effects rely on the implicit assumption that they are either small enough to ignore or positively correlated with direct predation. As we noted in the introduction, this assumption remains almost completely untested (Christianson & Creel 2014, Peckarsky *et al.* 2008, Peckarsky & McIntosh 1998, Peers *et al.* 2018). In our data, the correlation between direct predation and the strength of antipredator response was clearly not positive. Using standardized data from multiple predator-prey-ecosystem combinations, the relationship was either negative (using all the data) or flat (excluding one high-leverage outlier for warthogs and lions in Luangwa).

While direct predation did not predict the strength of antipredator responses, other variables did (Lima & Dill 1990), suggesting that they may be good empirical predictors of risk effects. The attributes of predators (Preisser *et al.* 2007, Schmitz 2008), prey (Creel 2011, Heithaus *et al.* 2009) and landscapes (Heithaus *et al.* 2009) have all been hypothesized to modulate the strength of risk effects. In our data, the body mass and foraging ecology of prey were the best predictors, with a weaker effect of prey herd size and little evidence for effects of predator hunting mode or environmental variables, when tested across a broad set of prey species. Heithaus *et al.* (2009) emphasized the probable importance of interactions between the attributes of predators, prey and environments. We agree that such interactions are likely, and could explain the relatively weak main effects of predator type and environmental variables that we detected here. Collecting data that allow estimation of interaction terms remains a difficult challenge for future studies of multiple predators and multiple prey in multiple ecosystems. In our results, such interactions might help to explain why grazers had lower vigilance levels than

browsers, because browsers might require more frequent scanning in environments with shorter lines of sight.

Controlling other effects, large species had lower levels of proactive and reactive vigilance than small ones. This result parallels the observation that large species are vulnerable to a smaller set of predators (Sinclair *et al.* 2003), and together these results suggest that body mass might be a particularly good predictor of the total limiting effect of predation. However, realized per capita predation was not detectably correlated with body size in our data, which weakens this inference.

Vigilance levels were greatest in herds of intermediate size, suggesting that there is a balance of other benefits that accrue to small herds (reduced detection by predators) and large herds (improved defense and dilution of risk), as noted by Heithaus *et al.* (2009), among others.

An important limitation of this analysis is that it considers only responses to short-term variation in risk. Ungulates can also detect and respond to long-term variation in risk. Interactions between the effects of long-term and short-term risk are expected from theory (Lima & Bednekoff 1999) and have been detected for African ungulates (Droge *et al.* 2017). An extension for future studies would be to examine multi-predator-multi-prey interactions in multiple ecosystems, considering risk at multiple scales. Another limitation is that ungulates can respond to risk in ways other than increasing vigilance, and other antipredator responses could either strengthen or offset the patterns we found. We focused this analysis on vigilance because it is a central element of antipredator response for these species and it trades off with foraging, so the interpretation of an increase in vigilance is clear. Other responses (such as changes in habitat selection or herd size) can vary in their direction and interpretation. For example, high risk can provoke aggregation to improve detection of predators and dilute risk, or disaggregation to

reduce detection by predators. High risk can provoke movement to closed habitats to reduce detection by predators, or to open habitats to improve detection of predators at a distance. These complications reduce the coherence of inferences about broad patterns of antipredator response and its associated costs across multiple species and ecosystems. Finally, while we restricted observations to periods when the risk of predation was high (Droge et al. 2016), we did not include behavioral observations at night, and it is possible that these would modify the patterns we observed.

## **Implications for Conservation and Management**

1. More than 30 years ago, McNamara & Houston (1987) examined trade-offs between predation and access to food, and showed why “the number of animals that die from starvation may not provide a reliable indication of the importance of food”. For the same reasons, the existence of this trade-off implies that the number of animals that are killed may not provide a reliable indication of the importance of predation (Creel & Christianson 2008). As Peers et al. (2018) recently noted, we do not know whether risk effects are important for most species. While this is true, it is also true that we do not know that they are unimportant. A decade ago, we noted that “ecologists often measure the direct rate of predation and ignore risk effects when assessing the impact of predators on prey. This traditional approach implicitly assumes that direct effects are larger than risk effects, or that risk effects (typically unmeasured) correlate positively with direct effects” (Creel & Christianson 2008). Tests of this correlation remain rare. Our results do not support the hypothesis that risk effects correlate positively with direct predation, which undermines the gambit of assuming that risk effects can be ignored. As noted in the introduction, this gambit not only leaves risk effects unmeasured (and thus propagates

uncertainty about their strength), it opens the door for omitted variable bias to produce misleading inferences about the strength of direct predation and food limitation.

2. Effective conservation of endangered species often depends on understanding the drivers of population dynamics. If we do not understand the effects of predation and food supply on population dynamics, guidance for conservation and management will often be compromised.

3. Many experimental studies of risk effects use predator cues with little explicit consideration of the range of cue intensities and modalities that prey experience in the wild (Peers *et al.* 2018), and how these variables could affect the strength of response (but for examples that carefully address this problem, see Pangle *et al.* [2007] and Peckarsky *et al.* [1993]). Field studies have the inherent advantage of examining responses to the risks that nature presents, but commonly squander this advantage by substituting environmental attributes as a proxy for direct data on the presence of predators. While environmental attributes can affect predation risk (Creel *et al.* 2005) and the strength of antipredator behavior (Moll *et al.* 2017), we believe that this approach is unlikely to advance our understanding of risk effects in a generalizable way. To understand the non-consumptive effects of predators on prey dynamics in a manner that can readily be applied to conservation and management, it will ultimately be necessary to observe responses to predators and measure their costs in context.

4. Finally, prey body mass and foraging ecology were the best general predictors of risk effects in the large-carnivore ungulate systems we examined, in the sense of explaining the most variation in the strength of responses by a broad set of prey to a broad set of predators in several ecosystems. Building on similar conclusions about the factors that affect direct predation (Sinclair *et al.* 2003), our results suggest that the total limiting effect of predation is stronger for small ungulates, particularly browsers and mixed feeders. This inference can be used to guide

expectations about the consequences of large carnivore extirpation or restoration for ungulate community composition. In particular, it predicts that small browsers/mixed feeders will have increased representation in ungulate communities where carnivores are depleted or extirpated. In turn, this may lead to cascading effects on vegetation through a shift in browsing intensity relative to grazing intensity.

## Acknowledgements

Our thanks to the Zambia Department of National Parks and Wildlife for permission to conduct this research, and for collaborative efforts to monitor and conserve these carnivore and ungulate populations. Funding: this research was supported by the World Wildlife Fund– Netherlands; Knut och Alice Wallenbergs Stiftelse; Worldwide Fund for Nature – Netherlands; National Science Foundation (IOS-1145749 ); National Geographic Society Big Cats Initiative; National Geographic Committee for Research and Exploration; Vulcan Inc.; and Gemfields Inc.

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Table 1. Properties of prey species included in the analyses.

<b>Prey Species</b>	<b>Ecosystems</b>	<b>Observed Predation by<sup>A</sup></b>	<b>Body mass (kg)<sup>B</sup></b>	<b>Herd Size <math>\bar{X}</math> (SE)<sup>C</sup></b>	<b>Foraging type<sup>D</sup></b>
Oribi	GLE	WD,CH,SH	14.4	2.5 (0.09)	M-B
Impala	GKE, LVE	LI,WD,LE	51.8	9.1 (0.54)	M-B
Warthog	GKE, LVE	LI,WD,CH,LE	59.1	2.8 (0.23)	G
Puku	GKE, LVE	LI,WD,CH,LE	68.1	7.2 (0.37)	G
Lechwe	GKE, GLE	LI,WD,CH,LE	75.9	19.1 (4.64)	G
Hartebeest	GKE	LI	148.8	6.8 (0.85)	G
Wildebeest	GLE	LI,WD, CH, SH	180.0	7.9 (1.35)	G
Waterbuck	GKE,LVE	WD,CH	232.1	5.3 (0.81)	M-B
Zebra	GKE, GLE, LVE	LI,SH	296.1	10.1 (1.26)	G
Giraffe	LVE	LI	824.0	3.4 (0.41)	M-B

Notes:

*A*: LI = lion, WD = African wild dog, CH = cheetah, SH = spotted hyena, LE = leopard

*B*: mean of published adult male and female mass (Dorst & Dandelot 1972, Gittleman 1986, Mills & Hes 1997)

*C*: mean and standard error for herds from which behavioral data were collected in this study

*D*: G = grazer, M-B = mixed feeder or browser.

Table 2. Results from a beta-regression to test the relationship between vigilance and the per-capita realized rate of predation (also see Fig. 3) for 35 combinations of predator species, prey species, ecosystem and short-term carnivore presence. **(A)** Including an outlier with high leverage (warthogs reacting to lions in Luangwa). **(B)** Excluding this outlier. Coefficients (*b*) are on the logit scale (*i.e.*, units are log-odds of vigilance vs. non-vigilance), with back-transformed values (*italics*) and 95% confidence intervals (parentheses) below.

<b>Effect</b>	<b><i>b</i></b>	<b>SE</b>	<b><i>z</i></b>	<b><i>P</i></b>
<i>A. Full Data</i>				
Carnivore presence	0.917 <i>0.115</i> (0.044, 0.227)	0.194	4.717	<0.0001
Per-capita risk of predation	-0.319 <i>-0.025</i> (-0.031, -0.003)	0.151	-2.11	0.035
<i>B. Drop High Leverage Outlier</i>				
Carnivore presence	0.862 <i>0.105</i> (0.041, 0.222)	0.146	5.928	<0.0001
Per-capita risk of predation	-0.124 <i>-0.015</i> (-0.031, 0.041)	0.188	-0.659	0.510

Table 3. Results from a beta-regression to test for effects of predator, prey and environmental attributes on vigilance. Coefficients (*b*) are on the logit scale (*i.e.*, units are log-odds of vigilance vs. nonvigilance).

<b>Effect<sup>(1)</sup></b>	<b><i>b</i></b>	<b>SE</b>	<b><i>z</i></b>	<b><i>P</i></b>
Carnivore Present <sup>(2)</sup>	0.332	0.067	4.950	<0.0001
<b>Predator Attributes</b>				
Carnivore Species <sup>(3)</sup>				
<i>Spotted Hyena</i>	0.044	0.137	0.319	0.750
<i>Leopard</i>	0.451	0.305	1.478	0.139
<i>Lion</i>	0.190	0.127	1.494	0.135
<i>Wild Dog</i>	0.218	0.155	1.816	0.069
Kill Present	0.121	0.087	1.516	0.131
<b>Prey Attributes</b>				
Scale(Mass) <sup>(4)</sup>	-0.087	0.033	-2.625	0.009
Mixed/Browser <sup>(5)</sup>	0.184	0.072	2.564	0.010
Scale(Herd Size) <sup>(4)</sup>	0.213	0.117	1.820	0.069
-Quadratic	-0.177	0.114	-1.551	0.121
<b>Ecosystem Differences<sup>(6)</sup></b>				
Kafue	0.039	0.097	0.400	0.689
Liuwa	-0.143	0.132	-1.083	0.279

1: Effects dropped from the model – *herd composition* (proportion female, proportion calves & subadults), *grass height* (0-10 cm, 10 cm – 1 m, >1m), *grass color* (brown, mixed, green) and *wind speed* (m/s). Criterion for exclusion was  $P > 0.20$ ; or  $P > 0.20$  for all factor levels.

2: Reference level is carnivore absent

3: Reference level is cheetah

4: Continuous predictors mass and herd size were centered and scaled to allow direct comparison of effect sizes.

5: Reference level is grazer.

6: Reference level is Luangwa.

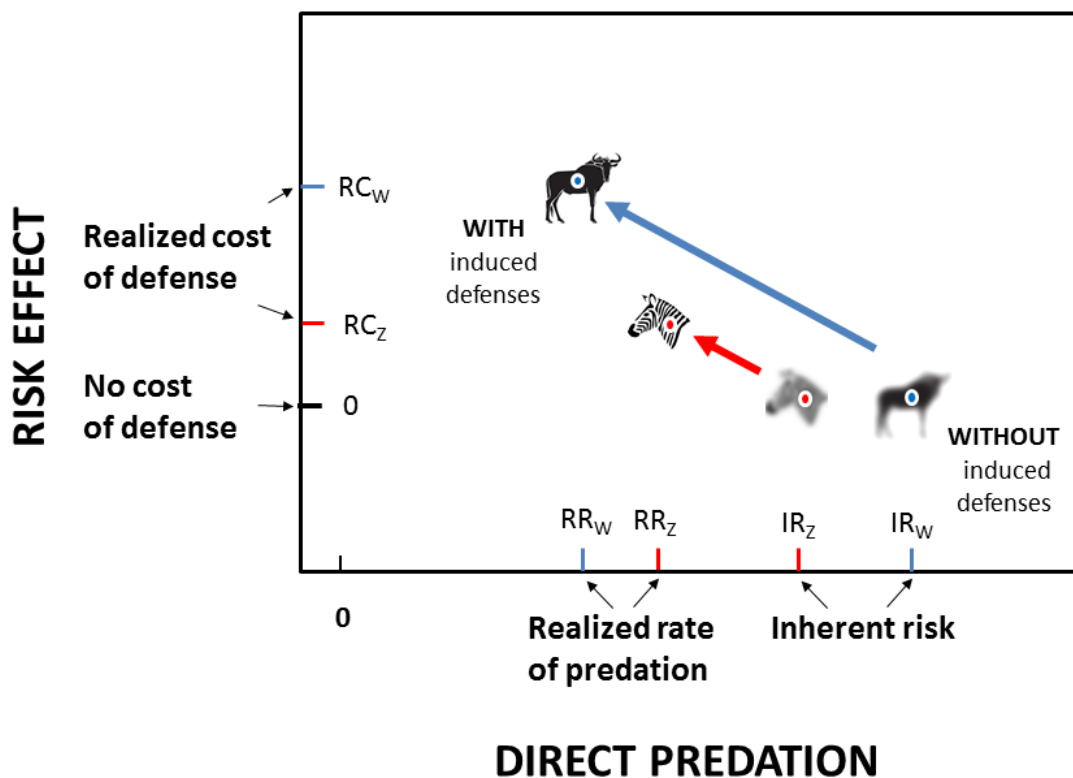


Figure 1. When considering the expected relationship between risk effects and the rate of direct predation, it is critical to recognize that the realized rate of predation is not equivalent to the inherent risk of predation that would exist without induced defenses. The total cost of predation is the sum of direct predation and risk effects, which are plotted here with equivalent units of fitness cost, so that selection favors any response that moves total costs closer to the origin (which represents the ideal of no predation with no cost of defense). The wildebeest (blue) and zebra (red) employ equally efficient behavioral defenses, yielding parallel shifts (arrows) in the phase-plane. For both species, the cost of direct predation decreases by more than the cost of defense, so selection favors both responses. If neither species employed behavioral defenses, the zebra would experience less predation, i.e., it faces lower inherent risk. Nonetheless, because its behavioral response is smaller in magnitude (shorter arrow) though equal in efficiency (identical slope), the zebra experiences a higher realized rate of predation. For species with induced defenses, inherent risk is virtually impossible to measure in the wild, and as this example shows, differences between species in realized predation rates ( $RR$ ) do not necessarily reflect differences in the inherent risk of predation ( $IR$ ), even in their direction ( $RR_Z > RR_W$  but  $IR_Z < IR_W$ ). While inherent risk cannot be measured, the problem can be resolved by recognizing the need to measure the costs of antipredator responses ( $RC_W$  and  $RC_Z$ ) and include them in the total limiting effect of predation.

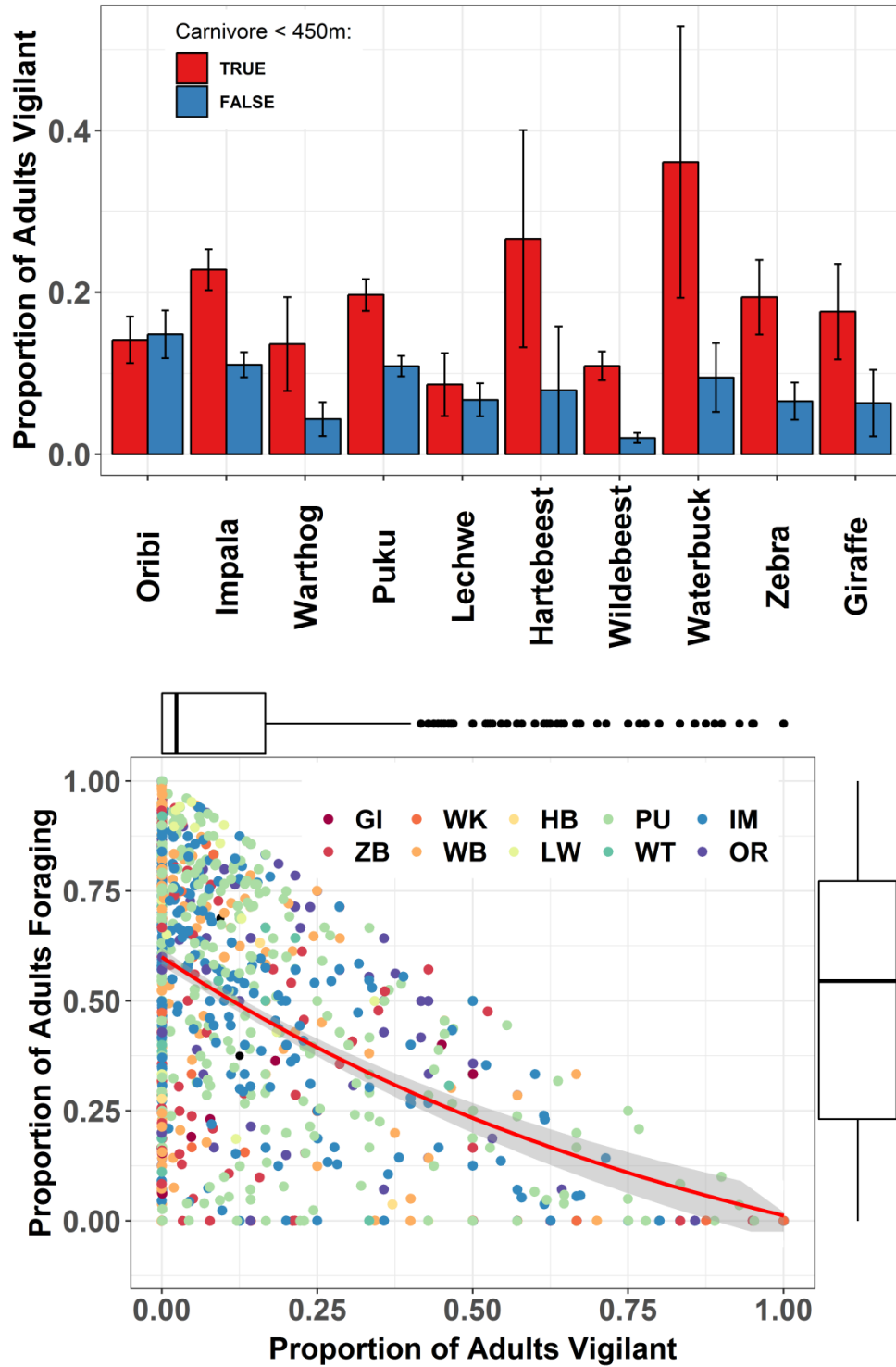


Figure 2 (**A**) Mean reactive (red) and proactive (blue) vigilance for each ungulate species. Whiskers show normal approximation 95% confidence limits. (**B**) Increases in vigilance are associated with decreases in foraging. Marginal boxplots show median, interquartile range, non-outlier range and outliers for each variable. Species codes in **B** are ordered by size, as in **A**.

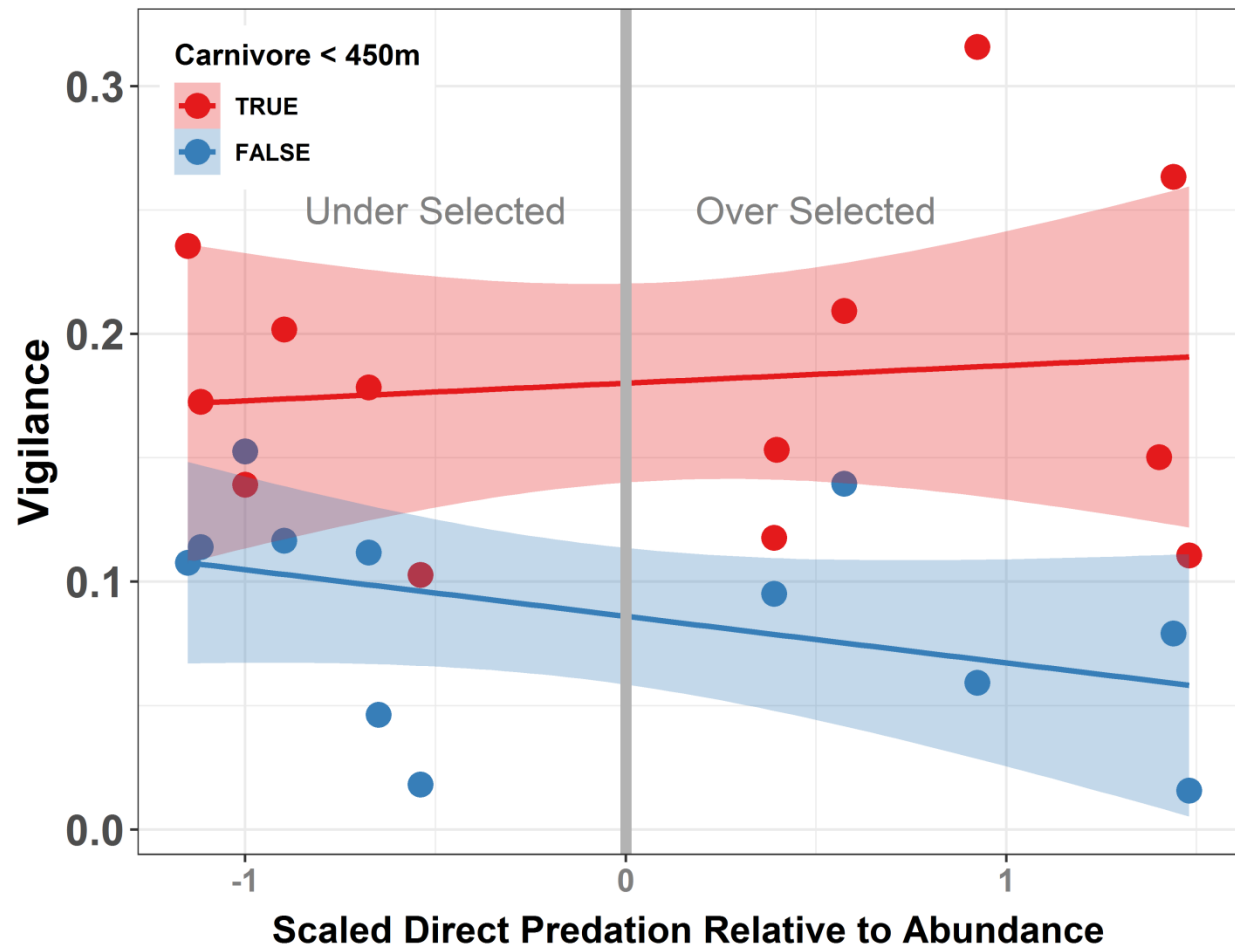


Figure 3. The relationship between reactive (red) and proactive (blue) vigilance and per-capita realized direct predation for 35 combinations of predator species, prey species, ecosystem and predator presence. Data from warthogs reacting to lions in Luangwa (an outlier with high leverage) are excluded in this plot.



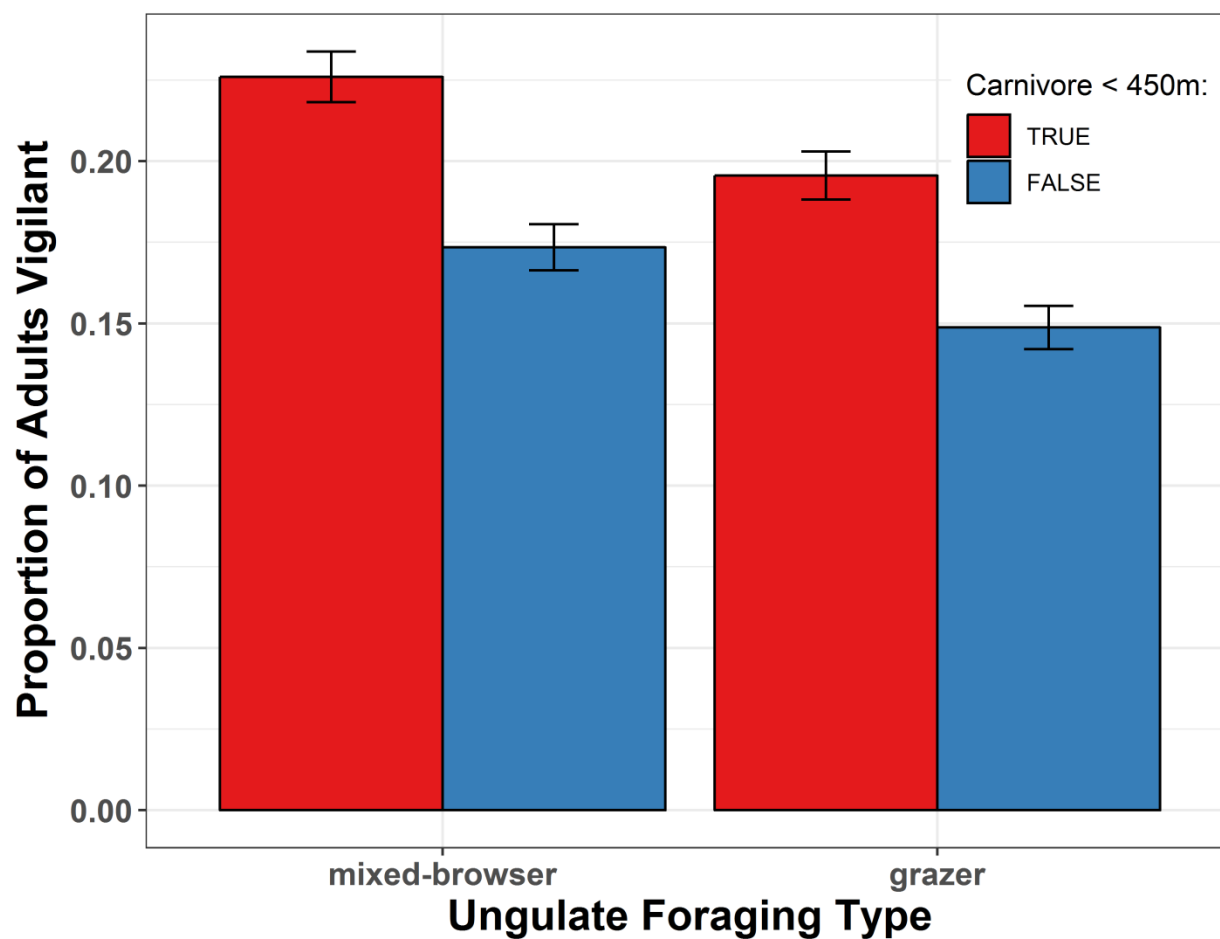


Figure 4. Effect of ungulate foraging type on vigilance. Bars show reactive (red) and proactive (blue) vigilance from the beta-regression model, averaged across the observed range of values other predictors. Whiskers show normal approximation 95% confidence limits on model estimates.

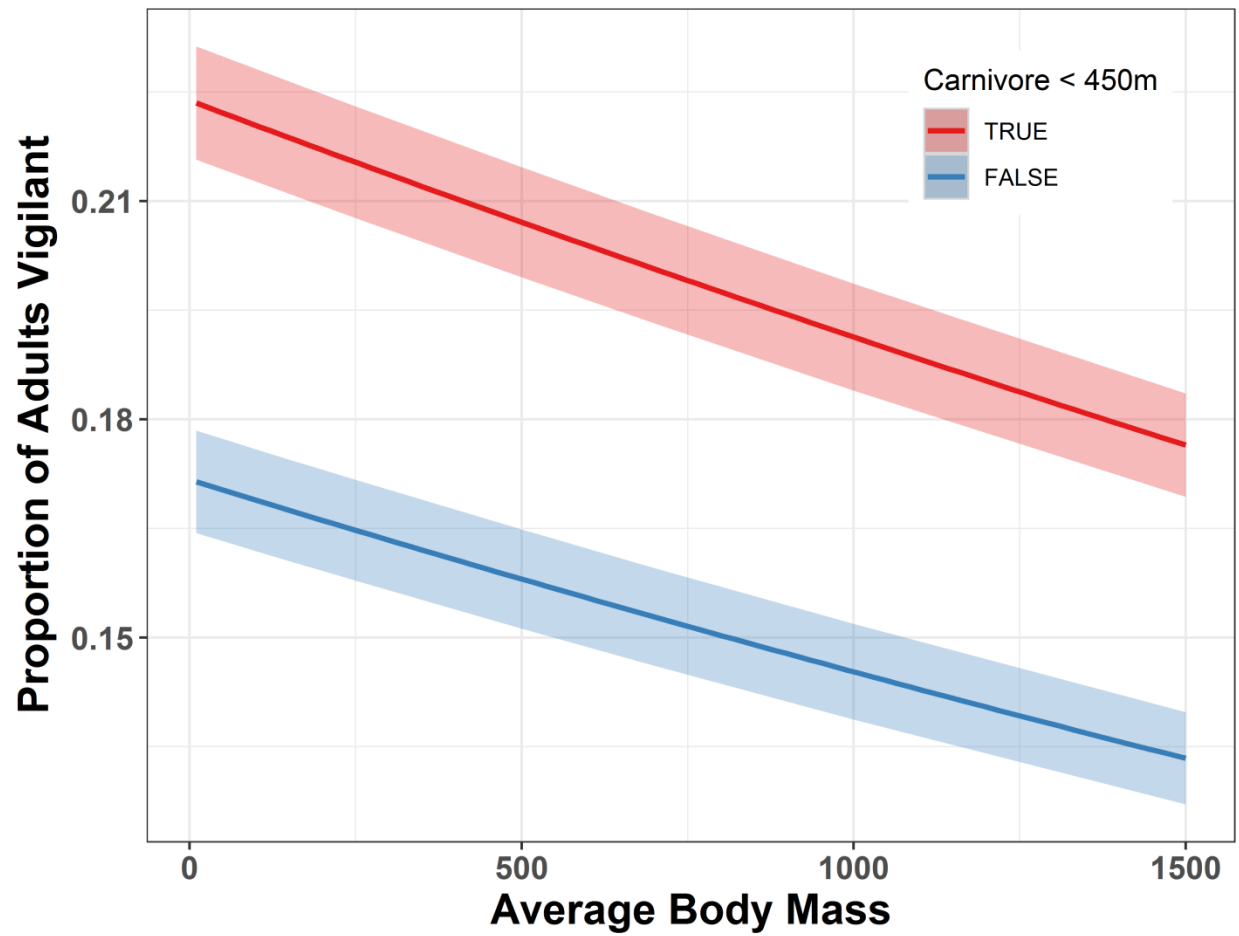


Figure 5. Effect of ungulate body mass on vigilance. Lines show reactive (red) and proactive (blue) vigilance from the beta regression model, averaged across the observed range of values other predictors. Bands show normal approximation 95% confidence limits on model estimates.

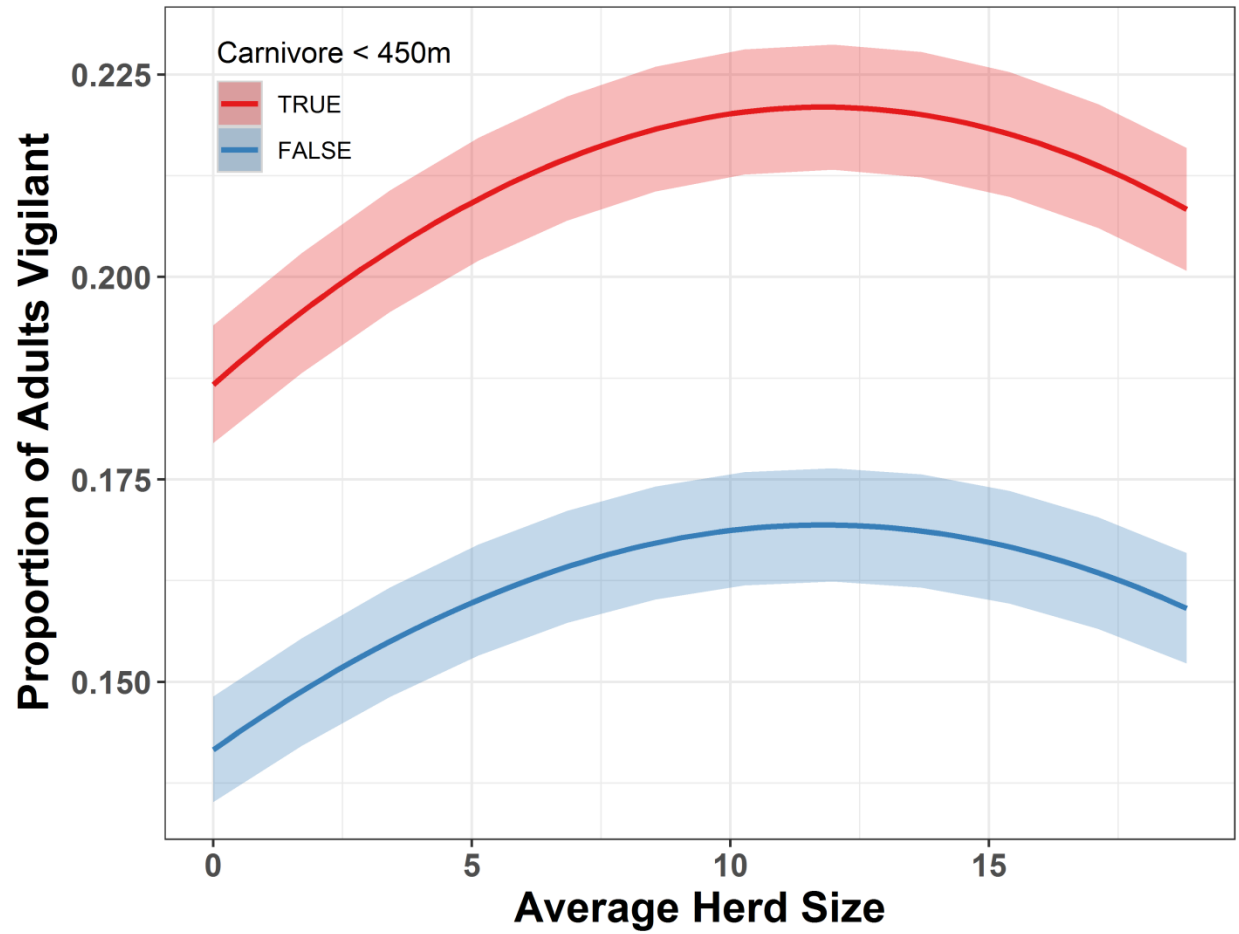


Figure 6. Effect of ungulate herd size on vigilance. Lines show reactive (red) and proactive (blue) vigilance from the beta regression model, averaged across the observed range of values for other predictors. Bands show normal approximation 95% confidence limits on model estimates.