

## Original Article

## Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community

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Predators alter prey dynamics by direct killing and through the costs of antipredator responses or risk effects. Antipredator behavior includes proactive responses to long-term variation in risk (e.g., grouping patterns) and reactive responses to short-term variation in risk (e.g., intense vigilance). In a 3-year field study, we measured variation in antipredator responses and the foraging costs of these responses for 5 ungulates (zebra, wildebeest, Grant's gazelle, impala, and giraffe) that comprised more than 90% of the prey community available to the 2 locally dominant predators, lions and spotted hyenas. Using a model-selection approach, we examined how vigilance and group size responded to attributes of the predator, prey, and environment. We found that 1) the strength of antipredator responses was affected by attributes of the predator, prey, and environment in which they met; 2) grouping and vigilance were complementary responses; 3) grouping was a proactive response to the use of dangerous habitats, whereas vigilance was a reactive response to finer cues about predation risk; 4) increased vigilance caused a large reduction in foraging for some species (but not all); and 5) there was no clear relationship between direct predation rates and the foraging costs of antipredator responses. Broadly, our results show that antipredator responses and their costs vary in a complex manner among prey species, the predators they face, and the environment in which they meet.

**Key words:** antipredator response, foraging, group size, risk effects, vigilance.

## INTRODUCTION

Even the simplest prey species alter their behavior in response to predation risk (Turchin and Kareiva 1989) by retreating to safe habitats (Kotler et al. 1991; Sih 1997), altering group size (Caro 2005; Creel and Winnie 2005), or increasing vigilance (Brown and Kotler 2004). In many cases, these antipredator responses are known to carry costs by decreasing feeding rates (Kotler et al. 1991; Brown and Kotler 2004), altering diets (Christianson and Creel 2010), or provoking physiological stress responses (Clinchy et al. 2004, 2013). Experimental studies have repeatedly shown that the costs of antipredator responses can reduce prey growth and reproduction (Werner et al. 1983; Peckarsky et al. 1993; Relyea and Werner 1999; Zanette et al. 2011) and that these “risk effects” can comprise a substantial fraction of the total effect of predators on prey dynamics. Although experiments have unambiguously demonstrated that risk effects can be strong, field studies are needed to

identify factors that modify the strength of antipredator responses, measure their costs, and understand relationships between direct predation and risk effects in the wild (Heithaus and Dill 2006; Creel and Christianson 2008; Schmitz 2008; Creel 2011).

Experimental data from a broad range of taxa show that risk effects are often due to reduced foraging success (Werner et al. 1983; Relyea and Werner 1999; Pangle et al. 2007), driven by trade-offs between vigilance and foraging behavior (Brown and Kotler 2004) or habitat shifts that increase safety but constrain foraging (Werner et al. 1983; Sih and McCarthy 2002), and in at least 1 case by altering the metabolic rate of prey (Hawlena and Schmitz 2010). To illustrate, juvenile Coho salmon (*Oncorhynchus kisutch*), waterfleas (*Daphnia* spp.), and larval backswimmers (*Notonecta hoffmanni*) exposed to simulated risk all employed antipredator responses that decreased their rate of energy intake (Milinski and Heller 1978; Sih 1982; Dill and Fraser 1984). Bluegill sunfish (*Lepomis macrochirus*) selected safer habitats in response to experimentally controlled predation risk from largemouth bass (*Micropterus salmoides*), which altered their diets and reduced their growth rates (Werner et al. 1983). Song sparrows (*Melospiza melodia*) exposed to simulated

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predation risk altered patterns of nest site selection, flight distance, and provisioning behavior, which reduced the number of eggs they laid and fledging success (Zanette 2003; Zanette et al. 2011). Two species of gerbils (*Gerbillus allenbyi* and *Gerbillus pyramidum*) shifted into safer habitats and spent less time foraging in response to predation risk from owls (Kotler et al. 1991). Similar experiments with many invertebrates and small vertebrates show that antipredator responses can carry foraging costs that affect fitness (Peckarsky et al. 1993; Relyea and Werner 1999; Brown and Kotler 2004).

### Antipredator responses to large carnivores and the costs of response

Until very recently, most discussions of predation in the context of ungulate population dynamics focused solely on direct mortality, but if predation risk affects the demography and dynamics of ungulates as it does other species (Creel et al. 2007), this approach is unlikely to measure the limiting effect of predation correctly. With many common study designs for research on ungulate dynamics, risk effects are likely to be mistaken for simple bottom-up limitation by access to food (Creel and Christianson 2008). Studies are needed to measure the costs of antipredator responses, which will allow us to test the relative importance of direct mortality and risk effects and to identify the factors that affect their relative importance.

Ungulates often respond to predation risk with increased vigilance and altered patterns of aggregation (Prins and Iason 1989; Hunter and Skinner 1998; Caro 2005; Creel and Winnie 2005), but we know relatively little about the factors that cause variation in the strength of antipredator responses within and among species. Recent studies have begun to address this question. Two of 5 ungulate species in Hwange National Park altered their group sizes in response to the presence of lions (Valeix et al. 2009), and all 5 approached waterholes more slowly when the risk of predation by lions was high (Valeix et al. 2009). Zebras increased vigilance levels in response to the immediate presence of lions, whereas wildebeest increased vigilance levels in response to variation in habitat type (Periquet et al. 2012). These results suggest that the cues used to assess predation risk vary among prey species (and in response to different predators: Thaker et al. 2011).

Within a species, it is possible that an entire set of antipredator responses is triggered by 1 general assessment of the current level of risk, but it is also possible that different antipredator behaviors are triggered by different risk factors. To evaluate these hypotheses, it is useful to distinguish between antipredator responses that are proactive (and thus respond mainly to cues about “risky places” or long-term variation in risk) and responses that are reactive (and thus respond mainly to cues about “risky times” or short-term variation in risk) (Creel et al. 2008; Broekhuis et al. 2013). Several studies have shown that the spatial distribution of ungulates is dependent on both habitat type (risky places) and the presence of predators within a habitat (risky times). For example, a set of 7 ungulates in Karongwe Game Reserve selected habitats in which the likelihood of encounter with lions and leopards (*Panthera pardus*) was low and selected areas within those habitats that were less commonly used by predators (Thaker et al. 2011). The local densities of 11 ungulate species in Hwange National Park were sensitive to both the long-term use of an area by lions and to the immediate presence of lions within 2 km (Valeix et al. 2009). In Hwange, local long-term predation risk had stronger effects on the distributions of browsers than on grazers (Valeix et al. 2009), suggesting that foraging strategies may constrain antipredator responses (Creel 2011). All of the ungulate species in the study of Valeix et al. (2009) in Hwange increased

their use of open grassland areas when lions were within 2 km. In contrast, elk (*Cervus elaphus*) shifted out of preferred grazing sites in open meadows into the cover of coniferous woodland in response to the immediate presence of wolves (*Canis lupus*) (Creel et al. 2005). Together, these studies suggest that prey select habitats partly on the basis of structural features that modulate risk and that prey respond to coursing and stalking predators in different ways. Open habitats may reduce the risk of predation by stalkers, whose hunting success is dependent on undetected approach (Schaller 1972; Stander 1991; Caro 1994), whereas closed habitats may reduce the likelihood of being detected or attacked by coursers, for whom prey encounter rates are a strong determinant of prey selection (Creel and Creel 2002) and whose hunting success is better when prey flee than when they stand their ground (Kruuk 1972; Mills 1990; Creel and Creel 2002).

Substantial data show that ungulate antipredator responses have consequences for fitness and population dynamics. For example, the presence of wolves caused elk to alter patterns of aggregation (Creel and Winnie 2005), vigilance (Winnie and Creel 2007; Creel et al. 2008), foraging behavior (Winnie and Creel 2007), habitat selection (Creel et al. 2005), and diet selection (Christianson and Creel 2008, 2010). These antipredator responses correlated with a decline in elk nutritional condition, including a decrease in energy intake equivalent to 27% of maintenance requirements and an increase in endogenous protein catabolism (Christianson and Creel 2010). Pregnancy rates decreased by 24–43% following wolf recolonization in 10 populations, whereas reproduction generally remained unchanged in nearby populations that were not colonized by wolves (Zager et al. 2005; Creel et al. 2007, 2011; Garrott et al. 2009; Stephenson 2010; White et al. 2011). Collectively, these studies suggest that risk effects can alter the dynamics of ungulates (Creel et al. 2013), as has been shown experimentally with many other taxa (Peckarsky et al. 1993; Zanette et al. 2011).

### Context dependency: what factors affect the strength of antipredator responses?

Prior studies suggest that the strength of antipredator responses is affected by attributes of the prey, predator, and environment in which they meet (Liley and Creel 2008; Valeix et al. 2009; Periquet et al. 2012). Here, we used formal model selection to determine what factors best predict the strength of antipredator responses for a set of 5 ungulates (zebra, *Equus quagga*; Grant’s gazelle, *Nanger granti*; wildebeest, *Connochaetes taurinus*; impala, *Aepyceros melampus*; and giraffe, *Giraffa camelopardalis*) exposed to variation in the risk of predation by lions and spotted hyenas. The data were collected for all species with standardized methods in 1 ecosystem over the same period of study, to avoid methodological confounding and uncontrolled ecological differences between sites. In particular, we tested how group size and vigilance levels differed in the immediate presence/absence of predators and how these responses were modified by 1) prey species identity (with variation among species in grazing/browsing/mixed feeding), 2) predator species identity (with 1 stalking and 1 coursing predator), 3) habitat type and structure, 4) distance to protective cover, 5) distance between predator and prey, 6) herd type (mixed or single species), and 7) interactions among these variables. Models of vigilance also tested for effects of group size. The set of models that we compared was selected to broadly test the relative importance of attributes of the predators, prey, and environment in determining the strength of antipredator responses (Preisser et al. 2007; Liley and Creel 2008; Schmitz 2008; Heithaus

et al. 2009; Creel 2011). We then examined the foraging costs of antipredator responses using a combination of model selection (as just described) and a direct test for trade-offs between foraging and vigilance.

Our model sets provide tests of 7 hypotheses about the strength and contingency of antipredator responses, with the following specific predictions:

1. Within a prey species, group size is primarily a proactive response to “risky places” (Creel et al. 2008). Consequently, group size will be more strongly affected by habitat type than by more immediate measures of predator presence.
2. Within a prey species, vigilance is primarily a reactive response to “risky times” (Creel et al. 2008). Consequently, vigilance will be more strongly affected by the immediate presence of predators than by habitat type and will be sensitive to more detailed cues such as the species of carnivore and its distance.
3. (A) Species with strong proactive responses by changing group size will have weak reactive responses through increased vigilance. (B) Species with large mean group sizes will show weak responses of group size to immediate risk because dilution of risk is asymptotically related to group size.
4. Predator identity will affect the strength of antipredator responses due to differences in functional traits of the predators: lions are ambush predators, whereas spotted hyenas are coursers (Preisser et al. 2007; Schmitz 2008; Creel et al. 2013).
5. (A) The presence of other prey species in mixed herds will reduce vigilance, through dilution of risk. (B) This effect will be stronger for species that are unlikely to be attacked in mixed herds (Fitzgibbon 1990a, 1990b).
6. Effects of risk on foraging behavior will be more strongly associated with increased vigilance than with changes in group size (Creel 2011), so species with the strongest vigilance responses will experience the greatest reductions in feeding.
7. Across the set of 5 prey species facing the same set of predators in the same ecosystem, there will be a negative relationship between direct predation and risk effects (as measured by a decrease in foraging behavior) (Creel and Christianson 2008).

## METHODS

### Study site

We gathered data from 2008 to 2010 on a study site of 350 km<sup>2</sup> in the Olkirimatian–Shompole Community Conservation Area in the South Rift Valley of Kenya. The site is a conservancy at the northeastern edge of the Serengeti–Mara ecosystem, with a mosaic of savanna and open woodland bounded on the west by the Rift Escarpment and bisected from north to south by the Ewaso Nyiro river. The site held resident populations of all large herbivores typical of the region except rhinoceros (*Diceros bicornis*). Based on ground transects using distance sampling to account for variation in detectability (see below), the 5 most common large herbivores were zebra, Grant’s gazelle, wildebeest, impala, and giraffe. We focused our data collection on these 5 species because they comprised more than 90% of the ungulate community, whether measured by the number of individuals or by biomass. Based on 396 days and nights of field observation and 43 318 photographs from motion sensitive cameras deployed on a grid system, the dominant large carnivores on the site were lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*)

(Schuette et al. 2013). Lion density, based on individual recognition of lions in radiocollared prides using photographic records, was  $\geq 0.136$  individuals/km<sup>2</sup> (excluding cubs less than 1-year old) (Schuette et al. 2013). On the basis of data from an extensive grid of motion sensitive cameras, raw detections of hyenas outnumbered detections of lions by a factor of 3.3. Leopards (*P. pardus*) were present, particularly in riverine areas of the study site, at an unknown but low density (detected only 14 times in 3 years of camera trapping). Cheetahs (*Acinonyx jubatus*) and wild dogs (*Lycan pictus*) were present intermittently at very low densities.

### Distance sampling with ground transects to estimate ungulate population densities

To measure variation among prey species in the per-capita risk of predation, we required estimates of population size for each species. We estimated population densities by driving a systematic transect grid on 21 occasions, sampling each transect both day and night on each occasion for a total of 2898 km (Schuette et al. 2013). On each occasion, we sampled the same 16 fixed transects, which totaled 69 km. Transects were aligned east–west, not on roads or tracks, systematically spaced at 2-km intervals across the entire site. Surveys were conducted by 3 trained observers, with 1 individual responsible for driving and maintaining the route via Global Positioning System (GPS) with a moving map. Two observers using a roof hatch recorded the species, group size, distance, and bearing to all detected animals, with 1 observer responsible for each side of the vehicle. We stopped the vehicle as needed to count herds with binoculars. At night, the vehicle headlights were red filtered, which was effective at avoiding disturbance, particularly because the vehicle was moving slowly. The observers used handheld 12-V spotlights to detect animals at night. We estimated population densities using the unmarked package in R with species-specific detection probabilities and species-specific covariates for detection probability and density (Schuette et al. 2013). We truncated the transect data at a maximum distance of 400 m for impala and Grant’s gazelle and 500 m for giraffe, wildebeest, and zebra because a low probability of detection beyond these thresholds decreased the precision of density estimates. Estimated densities from the night were slightly higher than daytime estimates; the densities that we report here are pooled.

### Behavioral observations of prey species

We used 494 scan-sample observation periods of 30–60 min to record herd size, composition, and the proportion of adults that were vigilant or foraging. We also recorded other behaviors not discussed here: the mean proportion of adults that were vigilant was 0.10 and the mean proportion of foraging adults was 0.36. For each herd that we observed, we recorded the distance to the nearest known predator, predator species, predator group size and composition, and the presence/absence of a kill at the time of observation. To efficiently obtain these data, we first located lions or spotted hyenas by radio tracking, recorded their location using a GPS, then searched for ungulate herds by driving a spiral pattern. We selected ungulate herds for observation to stratify the data over the 5 focal prey species, to stratify over distances from 50 m to 2 km, and to sample habitat types representatively. We measured the straight-line distance between ungulate herds and predators using a GPS fix for each location. Based on initial observations, we attempted to gather roughly half of the data within 1 km of a predator group and half between 1 and 2 km. The original data included a small

proportion of observations with predators beyond 2 km to examine the potential for reactions to predators at greater-than-anticipated distance: these data were not included in the final analysis because increasing variance of responses suggested that other, undetected predators produced misleading results at distances above 2 km. In our analysis, we tested whether antipredator behavior was affected 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. In the results reported here, we used this single threshold of 400 m for each species in analyses of the responses of group size, vigilance, and foraging, but the results changed little when we used species-specific thresholds identified by inspection of group size plotted as a function of distance. It is possible that on some occasions a predator that we failed to detect was closer to the observed prey herd than the closest predator that we did detect, causing observations to be classified as “predator absent” when an undetected predator was actually present (false negatives). If this problem was common in our data, it would be expected to mask antipredator responses but would not be expected to create apparent responses where none existed (Creel et al. 2013). Because we detected strong antipredator responses, such false negatives are not a serious concern for our inferences (following the same logic that Type II statistical errors are not a concern when strong effects are detected).

We observed prey around dawn and dusk, when conditions allowed accurate behavioral observation, but the risk of predation was still high. We recorded the date, time, location, weather, habitat type, distance to nearest woodland edge (in 4 categories), and the data described above on short-term predation risk. We recorded prey herd size, species composition, and age–sex composition. Adults and young of the year were distinguishable for all species. We recorded behavior using scan sampling at 5-min intervals, for 30–60 min, using binoculars or a spotting scope to scan the herd from one edge to another, using a digital recorder to record a 3-part observation for each individual (“adult male, peripheral, grazing”). We recorded an animal as vigilant if it was stationary with its head held above shoulder height with the eyes and ears simultaneously focused, not chewing or ruminating. For ungulates, less-restrictive definitions of vigilance allow the possibility that an animal is simultaneously vigilant and ruminating; we used a stringent definition of vigilance for 2 reasons. First, ruminating individuals are not fully vigilant because ruminating individuals cannot listen for predation cues, and simultaneous focus of sight and hearing is diagnostic of full antipredator vigilance in ungulates (“intense” vigilance in the sense of Periquet et al. 2012 and “induced” vigilance in the sense of Blanchard and Fritz 2007). Second, it is logical to test the foraging costs of vigilance using a definition that is sufficiently narrow to exclude both active foraging and rumination (Blanchard and Fritz 2007). Less complete vigilance (“routine” vigilance in the sense of Blanchard and Fritz 2007) may be compatible with rumination, but data from other ungulates (e.g., bison [*Bison bison*] and elk [*C. elaphus*]) have shown that foraging rates are reduced even by “routine” vigilance (Fortin et al. 2004; Blanchard and Fritz 2007) and that rumination increases predation risk (Molinari-Jobin et al. 2004; Blanchard and Fritz 2007).

### Direct predation risk

To measure variation among species in the risk of predation, we required data on the relative frequency of each prey species in kills made by lions and spotted hyenas. We recorded the species of 101 kills located primarily by 396 follows of radiocollared lions and

hyenas. Both lions and hyenas were fit with Telonics MOD-400 transmitters and butyl belting collars, and both species were immobilized with a medetomidine/ketamine combination reversed with atipamezole. We did not conduct behavioral observations of ungulate herds while following carnivores but did record the species, age-class, and sex of all prey that they killed. We conducted follows at night from a Toyota Land Cruiser with red-filtered headlights, following at a distance that did not detectably disturb the predators or prey herds, usually around 100 m. We made observations using night vision goggles and binoculars, sometimes assisted with intermittent use of handheld red-filtered spotlight.

### Statistical analysis

We examined the factors affecting 3 dependent variables: group size, the proportion of adults that were vigilant, and the proportion of adults that were foraging. For each of these response variables, we used model selection via Akaike’s information criterion (corrected for sample size,  $AIC_c$ ) to compare a set of generalized linear models (GLMs) that were identified a priori (Tables 1, 3, and 5). The models in each set included variables associated with short-term variation in risk (e.g., the presence of a predator) and variables associated with long-term variation in risk (e.g., habitat type). The models in each set ranged in complexity, with as few as 2 predictors and as many as 7. All models included prey species and either predator presence (categorical) or distance to the nearest predator (continuous). Broadly, some predictors described attributes of the predator (predator species, presence, and distance), prey (prey species, herd type [mixed or single species], and herd size for models of vigilance and foraging), and environment (habitat type [woodland, grassland, and bushland], habitat structure [open and closed], and distance to cover [with 5 levels]).

No single model included 2 predictors that were intended to describe the same ecological effect in different ways, so predator presence was never in the same model as distance to predator, and habitat type was never in the same model as habitat structure. Because we were particularly interested in responses of prey to immediate predation risk, we considered 2 functional forms for the relationship of antipredator responses to the distance to predators and considered interactions between prey species and predator presence. To keep the a priori model sets reasonably small, we did not consider any other interactions.

We used model averaging to obtain unconditional estimates of each regression coefficient and its confidence limits, using the MUMIN package in R (Tables 2, 4, and 6). For models of group size, we fit GLMs with a Poisson distribution and log link, using the glm function of the base stats package in R. In goodness-of-fit testing, we compared the Poisson GLM to a negative binomial GLM fit with the glm.nb function from the MASS package. For models of the proportion of individuals that were vigilant or foraging within a herd, we fit linear models with a logit link using the lm function of the base STATS package. For all models, we assessed goodness of fit by examining Q–Q and scale–location plots and by examining the distribution of residuals as functions of fitted values, leverage, and each of the independent variables (including independent variables not in the best-supported model). For the ordinary linear models of vigilance and foraging, we assessed goodness of fit using  $R^2$  values. For the GLMs of group size, we calculated pseudo- $R^2$  using the “brute force” method of Zuur et al. (2009). For the Poisson GLM, we also tested for lack of fit by comparison to a quasi-Poisson model that included an overdispersion parameter ( $\hat{c}$ , estimated as deviance/degrees of freedom [dff]). Based on this

test, we applied  $\hat{c}$  as a variance inflation factor before testing the significance of coefficients or determining confidence intervals (CIs).

Finally, for each of the dependent variables, we used forward and backward stepwise regression to test whether the best-supported model in our a priori set was outperformed by other combinations of the independent variables. For these tests, we used the `drop1`, `add1`, and `anova` functions in the base STATS package of R to implement sequential *F*-tests using analysis of deviance. In each case, this procedure confirmed that the best-supported model was in the a priori set, so we did not conduct post hoc analyses.

## RESULTS

### Group size

Group size was dependent on a broad set of variables. One of the most complex models received 99% of the model-selection weight, with an  $AIC_c$  score 9.7 units better than the second best-supported model (Table 1). Group size varied among species (Figure 1 and Table 2), with the largest herds for obligate grazers (wildebeest and zebra), intermediate herd sizes for mixed feeders (impala and Grant's gazelle), and the smallest herds for obligate browsers (the giraffe). For all species, mixed herds were significantly larger than single-species herds (Table 2). For variables that prey might use to assess predation risk (or to make decisions about their response to risk), group size was affected by predator presence, the species of predator, an interaction between predator presence and the species of prey, and habitat type (Tables 1 and 2). Zebra and impala both aggregated into larger groups when predators were present, whereas wildebeest disaggregated into smaller groups, and Grant's gazelle and giraffe showed weak responses (Figure 1). Although 5 prey species provide limited scope to examine interspecific variation, these differences in aggregation/disaggregation were not clearly related to mean group size (Figure 1), foraging strategy, or body size. Prey groups were larger in open habitats and far from protective cover (Table 1), and group size responded more strongly to spotted hyenas than to lions. Group size models with a simple dichotomy between predators “present” versus “absent” had better  $\Delta AIC_c$  scores than

models that replaced this dichotomy with a continuous measure of distance to the nearest predator (but were otherwise identical).

### Vigilance

Two models of vigilance received a total 99% of the model weight (Tables 3 and 4), with relatively equal strength of support ( $\Delta AIC_c = 0.46$ ). These models had very similar structures, differing only by the inclusion of group size in the best-supported model (Table 3). The proportion of individuals that were vigilant was higher in single-species herds than in mixed herds. Vigilance was sensitive to the presence of predators and was better explained by the distance to predators than by a dichotomy between predators present/absent. A logarithmic function of distance to predators fit substantially better than a linear function (the second and third best-supported models were separated by 8.33  $AIC_c$  units, entirely due to different functions for the relationship between vigilance and distance to the predator [compare Models 2 and 3 in Table 3]). These results show that vigilance levels were sensitive to the immediacy of risk in a manner that is not well described by dichotomizing risk with a distance threshold.

Vigilance varied among prey species (Tables 3 and 4) in a manner that was inversely related to herd size, as expected through dilution of risk (compare Figures 1 and 2). Thus, vigilance levels were lowest in obligate grazers that formed the largest herds (wildebeest and zebra), intermediate among mixed feeders with intermediate group sizes (impala and Grant's gazelle), and highest for the obligately browsing giraffe, which formed the smallest groups. Vigilance levels were also lower for prey species that had strong changes in group size when predators were present, whether by aggregating or disaggregating (compare Figures 1 and 2), suggesting that vigilance and aggregation patterns are complementary components of an integrated response to risk.

### Foraging

Four models of foraging received similar support from the data, with model weights of 18–35% and  $\Delta AIC_c$  scores  $\leq 1.28$ . All of these models had similar structures (Table 5). The proportion of foraging adults increased when herds were near protective cover, in

**Table 1**

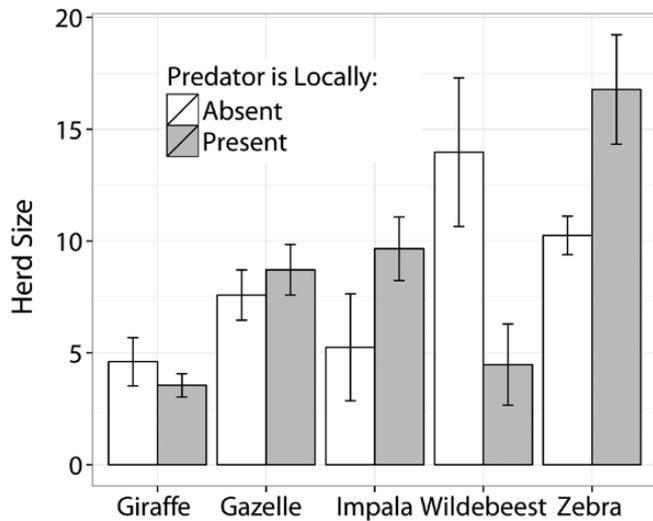
**The response of ungulate group size to the immediate presence of a predator and other factors that can affect the risk of predation, using AIC ( $\Delta AIC_c$  scores) and model weights ( $\omega_i$ ) to identify models with most support from the data**

Model <sup>a,c</sup>	df	$\Delta AIC_c$	$\omega_i$
GroupSize ~ Habitat + HerdType+ PredatorSpecies + Species × PredatorPresence	14	0	0.99
GroupSize ~ Habitat + PredatorSpecies + Species × PredatorPresence	13	9.71	0.01
GroupSize ~ Habitat + Species × PredatorPresence	12	19.3	<0.01
GroupSize ~ Habitat + Species × PredatorDistance	12	67.3	<0.01
GroupSize ~ OpenClosed+ PredatorSpecies + HerdType + CoverDistance + Species × PredatorPresence	17	156.1	<0.01
GroupSize ~ CoverDistance + Species × PredatorPresence	14	189.4	<0.01
GroupSize ~ OpenClosed + Species × PredatorPresence	11	259.1	<0.01
GroupSize ~ HerdType + Species × PredatorPresence	11	271.7	<0.01
GroupSize ~ PredatorSpecies + Species × PredatorPresence	11	276.0	<0.01
GroupSize ~ Species × PredatorPresence	10	281.1	<0.01

<sup>a</sup>All group size models were fit as GLMs with a log link and Poisson distribution.

<sup>b</sup>Variables within model statements for this and subsequent tables—GroupSize: number of individuals of a species within a herd, including individuals of all ages and sexes (also see HerdType and Species below); Habitat: dominant local habitat type, categorical with 3 levels (bushland, woodland, and grassland); Species: identity of prey species, categorical with 5 levels (giraffe, gazelle, impala, wildebeest, and zebra); PredatorPresence: presence of predator within species-specific threshold distance (defined in text), categorical with 2 levels (present and absent); PredatorDistance: distance (m) between prey herd observed and nearest predator, continuous (not in any models with PredatorPresence); OpenClosed: dominant local habitat type, categorical with 2 levels (open and closed) (not in any models with Habitat); PredatorSpecies: identity of nearest predator, categorical with 2 levels (lion and spotted hyena); HerdType: categorical variable with 2 levels, indicating whether a prey group was single species or part of a mixed herd; CoverDistance: distance (m) to nearest woodland edge (protective cover), categorical with 5 levels (0 m [within cover], 1–30 m [edge], 31–100 m [near], 101–300 m [far], and >300 m [very far]).

<sup>c</sup>Pseudo- $R^2 = 0.29$  for the most complete model.



**Figure 1**  
The relationship of herd size to the presence of predators for 5 ungulate species. Predators were classified as present at a distance of 400 m or less for this figure, but similar patterns are seen if species-specific thresholds are used. The effects of variables other than predator presence were controlled in statistical analysis, but simple means and 95% confidence limits are shown here.

**Table 2**  
**Model-averaged coefficients for the effect on group size of short-term predator presence and other factors that may affect predation risk**

Effect: level	$\hat{\beta}$	SE( $\hat{\beta}$ )	$\zeta$	P	$\alpha$
Habitat: grass <sup>a</sup>	0.025791	0.001707	15.036	<0.000001	***
Habitat: woodland <sup>a</sup>	0.010405	0.001888	5.483	<0.000001	***
Species: Grant's gazelle <sup>b</sup>	0.009825	0.007300	1.339	0.180	
Species: impala <sup>b</sup>	0.004091	0.006927	0.588	0.557	
Species: wildebeest <sup>b</sup>	0.022254	0.006171	3.589	0.0003	***
Species: zebra <sup>b</sup>	0.015446	0.008372	1.836	0.066	+
Predator: present <sup>c</sup>	-0.018111	0.007831	2.301	0.021	*
Predator: present × species: Grant's gazelle <sup>d</sup>	0.017153	0.007295	2.340	0.019	*
Predator: present × species: impala <sup>d</sup>	0.019027	0.007124	2.658	0.007	**
Predator: present × species: wildebeest <sup>d</sup>	-0.010590	0.005015	2.101	0.035	*
Predator: present × species: zebra <sup>d</sup>	0.034829	0.009073	3.820	0.0001	***
Distance to predator (m)	0.007560	0.008765	0.863	0.388	
Distance to predator × species: Grant's gazelle <sup>e</sup>	-0.004097	0.008175	0.499	0.618	
Distance to predator × species: impala <sup>e</sup>	-0.018012	0.006559	2.733	0.00628	**
Distance to predator × species: wildebeest <sup>e</sup>	0.012963	0.006832	1.888	0.0590	+
Distance to predator × species: zebra <sup>e</sup>	-0.005050	0.007504	0.670	0.503	
Habitat structure: open <sup>f</sup>	0.008357	0.001660	5.008	<0.000001	***
Predator species: lion <sup>g</sup>	-0.004882	0.001414	3.430	0.00050	***
Herd type: single species <sup>h</sup>	-0.004892	0.001446	3.367	0.00076	***
Distance to cover: 1–30 m <sup>i</sup>	0.001358	0.001719	0.786	0.432	
Distance to cover: 31–100 m <sup>i</sup>	-0.008565	0.001995	4.272	0.000002	***
Distance to cover: 101–300 m <sup>i</sup>	0.007545	0.001806	4.156	0.000003	***
Distance to cover: >300 m <sup>i</sup>	0.004076	0.001432	2.831	0.00463	**

<sup>a</sup>Habitat reference level is bushland.  
<sup>b</sup>Species reference level is giraffe.  
<sup>c</sup>Predator reference level is absent.  
<sup>d</sup>Interaction reference level is giraffe.  
<sup>e</sup>Interaction reference level is giraffe.  
<sup>f</sup>Habitat structure reference level is closed.  
<sup>g</sup>Predator species reference level is spotted hyena.  
<sup>h</sup>Herd type reference level is mixed species.  
<sup>i</sup>Distance to cover reference level is 0 m (within cover).  
 Significance codes: \*\*\* <0.001, \*\* <0.01, \* <0.05, + <0.10.

mixed herds, and far from predators (Tables 5 and 6). The proportion of foraging adults varied weakly among species and decreased in mixed habitats relative to pure grassland or pure woodland. Finally, foraging was more strongly affected by the presence of spotted hyenas, relative to the effect of lions.

The proportion of foraging adults did not show a strong relationship to predator presence (Figure 3 and Table 6). This is perhaps not surprising because foraging can be reduced by a trade-off with vigilance, but it is not directly a type of antipredator behavior. A stronger test for foraging costs is to examine the relationship between foraging and vigilance (Figure 4), which shows that foraging decreased as vigilance increased (Wald statistic = 31.89,  $P < 0.001$ ). Because the mean proportion of adults that were vigilant was 0.10 and the mean proportion of foraging adults was 0.36, there was considerable scope for vigilance to increase without a reduction in foraging. Despite this, the negative slopes in Figure 4 reveal foraging costs, which varied among species (Figure 4A: Wald statistic for species × vigilance effect on foraging = 7.04,  $P = 0.133$ ). To illustrate this variation, the trade-off curve was steeper for gazelles (Figure 4B: foraging =  $0.39 \times e^{-2.70 \times \text{proportion vigilant}}$ ) than for giraffes (Figure 4C: proportion foraging =  $0.36 \times e^{-1.71 \times \text{proportion vigilant}}$ ), particularly within the typical range of vigilance levels (e.g., see Figure 1 for mean vigilance levels). We consider the relationship between these foraging costs and direct predation rates in Discussion.

**Table 3**

**Evaluation of response of ungulate vigilance to the immediate presence of a predator and other factors that can affect the risk of predation, using AIC ( $\Delta AIC_c$  scores), and model weights ( $\omega_i$ ) to identify models with most support from the data**

Model <sup>a-c</sup>	df	$\Delta AIC_c$	$\omega_i$
Vigilance ~ GroupSize + HerdType + Species + ln(PredatorDistance)	9	0.00	0.55
Vigilance ~ HerdType + Species + ln(PredatorDistance)	8	0.46	0.44
Vigilance ~ HerdType + Species + PredatorDistance	8	8.79	0.01
Vigilance ~ Species + PredatorDistance	7	9.58	<0.01
Vigilance ~ HerdType + Species × PredatorDistance	12	13.59	<0.01
Vigilance ~ HerdType + Species + PredatorPresence	8	14.05	<0.01
Vigilance ~ Species + PredatorPresence	7	15.39	<0.01
Vigilance ~ OpenClosed + Species + PredatorPresence	8	17.27	<0.01
Vigilance ~ PredatorSpecies + Species + PredatorPresence	8	17.49	<0.01
Vigilance ~ Habitat + Species + PredatorPresence	9	18.18	<0.01
Vigilance ~ HerdType + Species × PredatorPresence	12	19.24	<0.01
Vigilance ~ Species × PredatorPresence	11	12.14	<0.01
Vigilance ~ CoverDistance + Species + PredatorPresence	11	21.35	<0.01
Vigilance ~ OpenClosed + PredatorSpecies + HerdType + CoverDistance + Species + PredatorPresence	14	21.60	<0.01

<sup>a</sup>Vigilance: the proportion of adults with their heads above shoulder level with eyes and ears focused in the same direction, not chewing or ruminating. The proportion (+0.001 to allow transformation of zeros) of individuals that were vigilant was logit transformed prior to analysis.

<sup>b</sup>Following logit transformation of the dependent variable, all models were fit as ordinary linear models assuming a Gaussian distribution.

<sup>c</sup>For most complete model,  $F = 3.56$ ,  $R_{adj}^2 = 0.15$ ,  $P = 0.00007$ .

**Table 4**

**Model-averaged coefficients for the effect on vigilance of short-term predator presence and other factors that may affect predation risk**

Effect: level	$\hat{\beta}$	SE( $\hat{\beta}$ )	$z$	$P$	$\alpha_i$
Group size	0.095991	0.060214	1.586	0.112677	
HerdType: single species <sup>a</sup>	0.100587	0.058212	1.719	0.085542	+
Species: Grant's gazelle <sup>b</sup>	-0.068671	0.100042	0.683	0.494576	
Species: impala <sup>b</sup>	-0.100120	0.081648	1.220	0.222392	
Species: wildebeest <sup>b</sup>	-0.354533	0.092734	3.804	0.000142	***
Species: zebra <sup>b</sup>	-0.312833	0.100785	3.089	0.002007	**
ln(distance to predator)	-0.243523	0.058226	4.162	0.000034	***
Distance to predator	-0.191306	0.092416	2.063	0.039080	*
Distance to predator × species: Grant's gazelle <sup>c</sup>	0.260172	0.206108	1.256	0.209126	
Distance to predator × species: impala <sup>c</sup>	0.037540	0.179896	0.208	0.835518	
Distance to predator × species: wildebeest <sup>c</sup>	0.247937	0.187259	1.317	0.187709	
Distance to predator × species: zebra <sup>c</sup>	0.264329	0.198917	1.322	0.186113	
Predator: present <sup>d</sup>	0.135927	0.089188	1.518	0.129064	
Habitat structure: open <sup>e</sup>	-0.031090	0.060842	0.508	0.611118	
Predator species: lion <sup>f</sup>	-0.011993	0.062956	0.190	0.849652	
Habitat type: grassland <sup>g</sup>	-0.068422	0.071907	0.947	0.343736	
Habitat type: woodland <sup>g</sup>	-0.081542	0.071520	1.134	0.256600	
Predator: present × species: Grant's gazelle <sup>h</sup>	-0.189053	0.212338	0.886	0.375683	
Predator: present × species: impala <sup>h</sup>	0.021690	0.207877	0.104	0.917314	
Predator: present × species: wildebeest <sup>h</sup>	-0.169265	0.141767	1.188	0.234836	
Predator: present × species: Grant's gazelle <sup>h</sup>	0.004316	0.297178	0.014	0.988471	
Distance to cover: 1–30 m <sup>i</sup>	0.027474	0.068020	0.402	0.687754	
Distance to cover: 31–100 m <sup>i</sup>	0.052058	0.073283	0.707	0.479688	
Distance to cover: 101–300 m <sup>i</sup>	0.108612	0.076777	1.408	0.159254	
Distance to cover: >300 m <sup>i</sup>	-0.015019	0.065601	0.228	0.819809	

<sup>a</sup>Herd type reference level is mixed species.

<sup>b</sup>Species reference level is giraffe.

<sup>c</sup>Interaction reference level is giraffe.

<sup>d</sup>Predator reference level is absent.

<sup>e</sup>Habitat structure reference level is closed.

<sup>f</sup>Predator species reference level is spotted hyena.

<sup>g</sup>Habitat reference level is bushland.

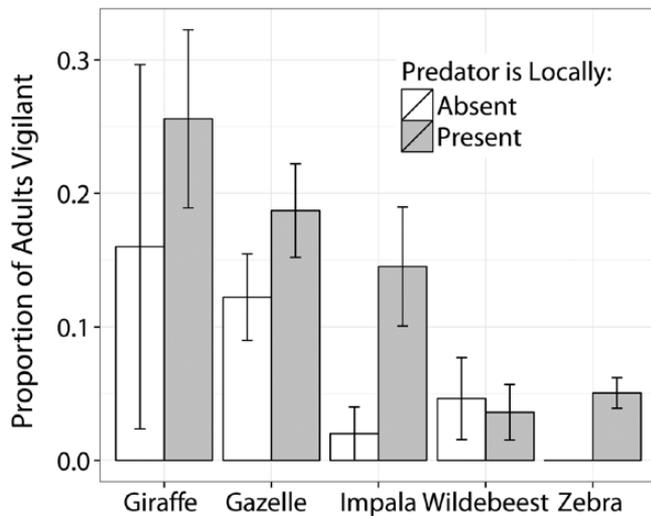
<sup>h</sup>Interaction reference level is giraffe.

<sup>i</sup>Distance to cover reference level is 0 m (within cover).

Significance codes: \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ , + $P < 0.10$ .

## Direct predation relative to abundance

The per-capita risk of predation varied among prey species by a factor of approximately 5 (Figure 5). The most abundant prey species, zebra ( $0.34 \pm 0.14$  standard error [SE] of the prey community), was also the most commonly killed ( $0.59 \pm 0.10$  SE of kills). Zebras were overselected by a factor of 1.7, consistent with a common pattern that large carnivores tend to overselect the most available prey. In contrast, Grant's gazelles were significantly underselected ( $0.08 \pm 0.04$  of kills) although they were the second most common prey species ( $0.27 \pm 0.07$  of the prey community). Other species



**Figure 2**

The relationship between the proportion of adults that were vigilant and the presence of predators. Vigilance was defined in a narrow manner that excluded “routine” vigilance (see Methods). Predators were classified as present at a distance of 400 m or less for this figure, but similar patterns are seen if species-specific thresholds are used. The effects of group size and other variables on vigilance were controlled in statistical analysis, but simple means and 95% confidence limits are shown here.

**Table 5**

**Evaluation of response of ungulate foraging to the immediate presence of a predator and other factors that can affect the risk of predation, using AIC ( $\Delta AIC_c$  scores) and model weights ( $\omega_i$ ) to identify models with most support from the data**

Model <sup>a-c</sup>	df	$\Delta AIC_c$	$\omega_i$
Foraging ~ GroupSize + Habitat + PredatorSpecies + HerdType + CoverDistance + Species + ln(PredatorDistance)	16	0.00	0.35
Foraging ~ Habitat + PredatorSpecies + HerdType + CoverDistance + Species + ln(PredatorDistance)	15	0.52	0.27
Foraging ~ Habitat + PredatorSpecies + HerdType + CoverDistance + Species + PredatorDistance	15	1.22	0.19
Foraging ~ Habitat + PredatorSpecies + HerdType + CoverDistance + Species + PredatorPresence	15	1.28	0.18
Foraging ~ Habitat + PredatorSpecies + HerdType + CoverDistance + Species × PredatorDistance	19	6.63	0.01
Foraging ~ PredatorSpecies + Species + PredatorPresence	8	13.52	<0.01
Foraging ~ HerdType + Species + PredatorPresence	8	20.08	<0.01
Foraging ~ Habitat + Species + PredatorPresence	9	20.09	<0.01
Foraging ~ Species + ln(PredatorDistance)	7	21.93	<0.01
Foraging ~ CoverDistance + Species + PredatorPresence	11	22.19	<0.01
Foraging ~ HerdType + Species × ln(PredatorDistance) <sup>d</sup>	12	23.08	<0.01
Foraging ~ Species + PredatorPresence	7	25.16	<0.01
Foraging ~ Habitat + Species + PredatorPresence	8	26.88	<0.01
Foraging ~ Species × PredatorPresence	11	30.78	<0.01

<sup>a</sup>Foraging: the proportion of adults that were browsing, grazing, or ruminating. The proportion (+0.001 to allow transformation of zeros) of foraging adults was logit transformed prior to analysis.

<sup>b</sup>Following logit transformation of the dependent variable, all models were fit as ordinary linear models assuming a Gaussian distribution.

<sup>c</sup>For most complete model,  $F = 4.14$ ,  $R_{adj}^2 = 0.19$ ,  $P < 0.000001$ .

<sup>d</sup>Model added for exploratory analysis.

were not significantly over- or underselected, but point estimates of per-capita risk were relatively high (but imprecise) for giraffe and relatively low for wildebeest and impala (Figures 5 and 6).

## DISCUSSION

### Proactive and reactive responses to risk: modulation by attributes of predators, prey, and the environment

Our results support the hypothesis that grouping patterns are a proactive response to the use of dangerous habitats, whereas vigilance is a reactive response to finer cues about predation risk (Tables 1 and 3). The results also support the hypothesis that these 2 responses are complementary. First, high levels of vigilance were seen in the species with the smallest groups, as revealed neatly by the mirror imagery of Figures 1 and 2. Species with strong changes in aggregation when predators were present (e.g., wildebeest and zebra: Figure 1) also had relatively low levels of vigilance, and species that had strong changes in vigilance when predators were present had smaller group sizes. Collectively, these results support the conclusion that grouping and vigilance are complementary responses to risk. The data did not support the hypothesis that species with the largest groups would show weak responses of group size to risk.

Considering all prey species, groups were larger in open habitats. If this aggregation is an antipredator response, then the result parallels data from ungulates in Hwange, where responses to predation risk from lions were stronger in open habitats (Valeix et al. 2009; Periquet et al. 2012). However, our data do not cleanly support the inference that aggregation in open habitats is antipredator response (Figure 1) because some species aggregated when predators were present (e.g., zebra) but others disaggregated (e.g., wildebeest), and some showed no response (e.g., Grant's gazelle). Prior research with elk has showed that aggregation in open habitats was a foraging response that occurred at time of low risk rather than an antipredator response that occurred at times of high risk (Creel and Winnie 2005).

In this study, interspecific variation in herd size was clearly related to foraging strategy, with obligate grazers forming the largest groups.

**Table 6**

**Model-averaged coefficients for the effect on foraging of short-term predator presence and other factors that may affect predation risk**

Effect: level	$\hat{\beta}$	SE( $\hat{\beta}$ )	$z$	$P$	$\alpha$
Group size	0.10314	0.06338	1.619	0.10548	
Habitat type: grassland <sup>a</sup>	0.21160	0.07297	2.886	0.00391	**
Habitat type: woodland <sup>a</sup>	0.08853	0.07111	1.239	0.21550	
Predator species: lion <sup>b</sup>	-0.19071	0.06465	2.935	0.00333	**
Herd type: single species <sup>c</sup>	-0.16933	0.05946	2.833	0.00461	**
Distance to cover: >300 m <sup>d</sup>	-0.02500	0.06713	0.370	0.71105	
Distance to cover: 1–30 m <sup>d</sup>	0.15925	0.06707	2.362	0.01816	*
Distance to cover: 101–300 m <sup>d</sup>	0.05555	0.07724	0.716	0.47429	
Distance to cover: 31–100 m <sup>d</sup>	-0.06122	0.07308	0.833	0.40463	
Species: Grant’s gazelle <sup>e</sup>	-0.03286	0.10250	0.319	0.74975	
Species: impala <sup>e</sup>	0.05411	0.08575	0.628	0.53012	
Species: wildebeest <sup>e</sup>	-0.05363	0.09552	0.559	0.57639	
Species: zebra <sup>e</sup>	0.16507	0.10300	1.595	0.11075	
ln(distance to predator)	0.06092	0.06966	0.871	0.38402	
Distance to predator	0.02572	0.06381	0.401	0.68847	
ln(distance to predator) × species: Grant’s gazelle <sup>f</sup>	-0.11421	0.11159	1.018	0.30859	
ln(distance to predator) × species: impala <sup>f</sup>	-0.01134	0.08678	0.130	0.89654	
ln(distance to predator) × species: wildebeest <sup>f</sup>	-0.12228	0.09230	1.318	0.18753	
ln(distance to predator) × species: zebra <sup>f</sup>	-0.13827	0.11330	1.214	0.22474	
Predator: present × species: Grant’s gazelle <sup>g</sup>	0.20780	0.22237	0.930	0.35248	
Predator: present × species: impala <sup>g</sup>	0.27865	0.21772	1.273	0.20285	
Predator: present × species: wildebeest <sup>g</sup>	0.07672	0.14814	0.515	0.60632	
Predator: present × species: zebra <sup>g</sup>	-0.03937	0.31132	0.126	0.89987	
Habitat structure: open <sup>h</sup>	0.03974	0.06313	0.626	0.53104	
Predator: present <sup>i</sup>	0.02355	0.06919	0.339	0.73485	

<sup>a</sup>Habitat reference level is bushland.

<sup>b</sup>Predator species reference level is spotted hyena.

<sup>c</sup>Herd type reference level is mixed species.

<sup>d</sup>Distance to cover reference level is 0 m (within cover).

<sup>e</sup>Species reference level is giraffe.

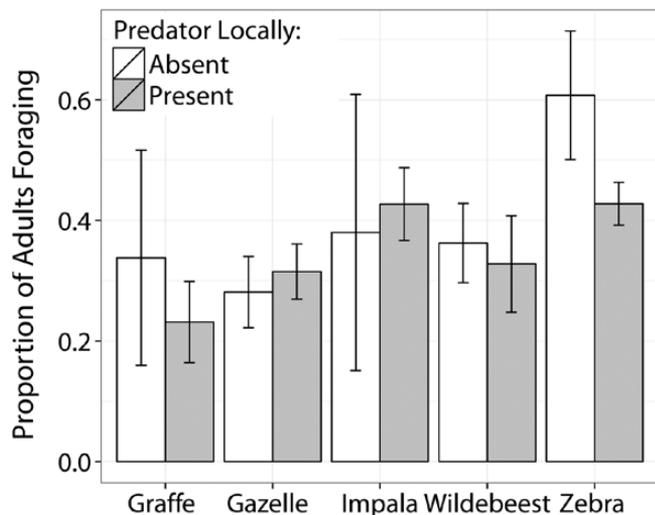
<sup>f</sup>Interaction reference level is giraffe.

<sup>g</sup>Interaction reference level is giraffe.

<sup>h</sup>Habitat structure reference level is closed.

<sup>i</sup>Predator reference level is absent.

Significance codes: \*\*\* <0.001, \*\* <0.01, \* <0.05, + <0.10.

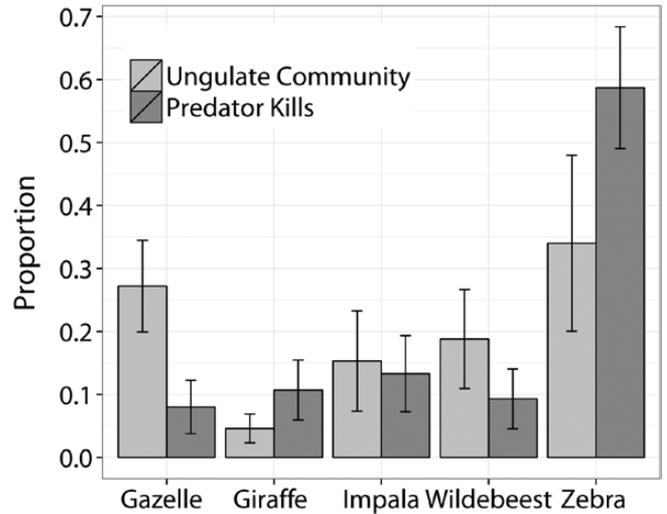
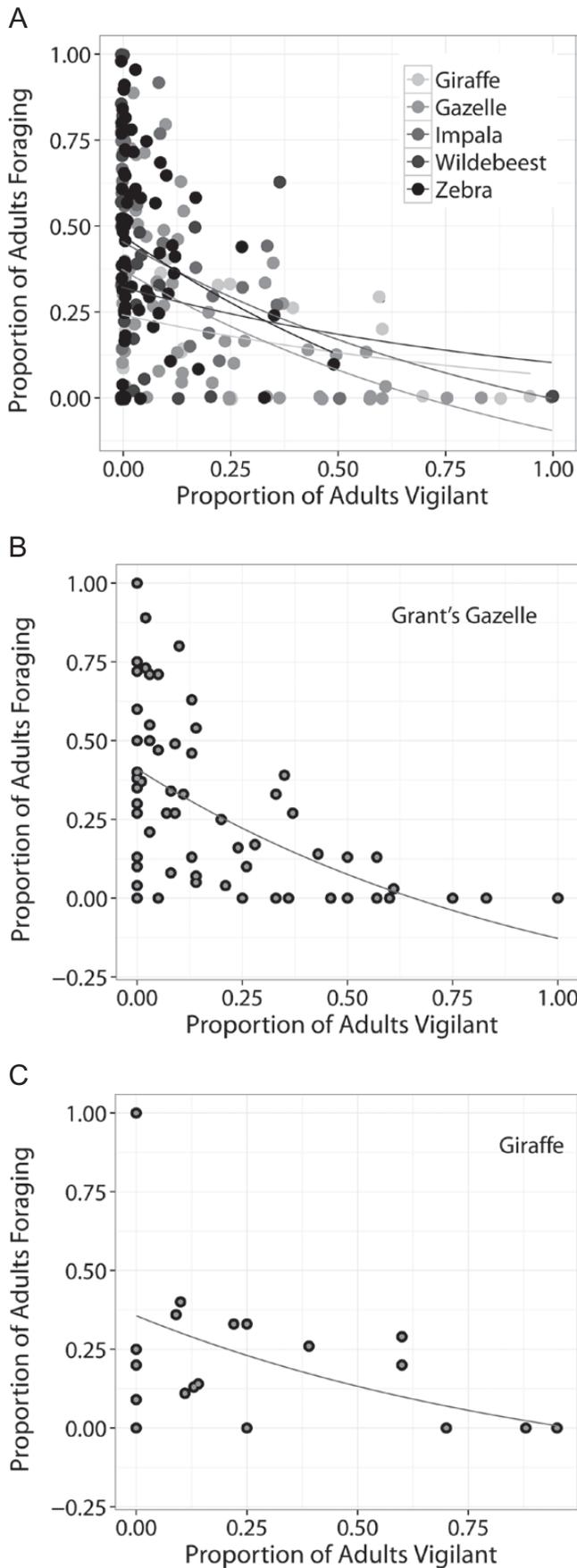


**Figure 3**

The relationship between the proportion of foraging adults and the presence of predators. Predators were classified as present at a distance of 400 m or less for this figure, but similar patterns are seen if species-specific thresholds are used. The effects of group size and other variables on vigilance were controlled in statistical analysis, but simple means and 95% confidence limits are shown here.

Interspecific variation in herd size may also be related to variation among species in the importance of passive dilution of risk, relative to active antipredator responses such as active defense or vigilance (Creel 2011). Vigilance levels were lowest in obligate grazers that formed the largest herds (wildebeest and zebra), intermediate among mixed feeders with intermediate group sizes (impala and Grant’s gazelle), and highest for the obligately browsing giraffe, which formed the smallest groups. Vigilance levels were also lower for prey species that had strong responses of grouping patterns to the presence of predators, whether that response was to aggregate or to disaggregate. Collectively, these results support 2 closely related hypotheses: First, dilution of risk reduces the need for (and benefit of) individual vigilance (Elgar 1989; Caro 2005). Second, species with weaker proactive responses (habitat-sensitive aggregation patterns) engage in stronger reactive responses (vigilance).

Variation in group size was better explained by a simple dichotomy between predators “present” versus “absent” than by continuous functions of the distance to the nearest predator. In contrast, variation in vigilance was better explained by the log of distance to the nearest predator. Variation in group size was affected by habitat type (a correlate of long-term risk: Valeix et al. 2009; Thaker et al. 2011), but vigilance was not. Collectively, these differences support the hypothesis that proactive antipredator behaviors such as grouping respond to coarse, long-term cues about risk, whereas reactive



**Figure 5**

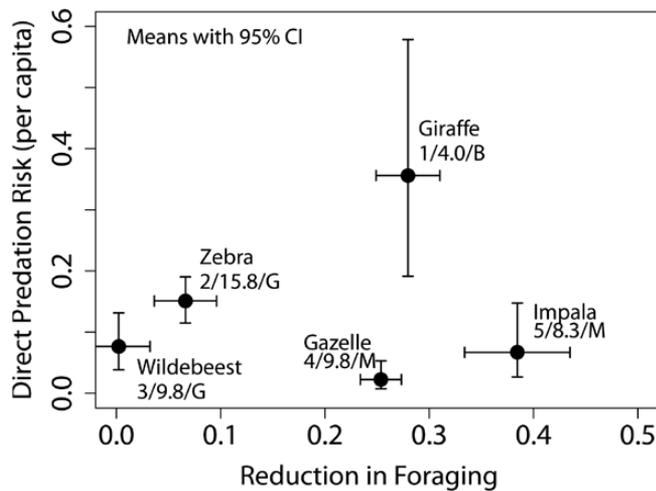
The proportion of the ungulate community composed of each species, and the proportion of kills composed of each species. Bars show 95% CIs. Some species were overselected by predators (notably zebra), whereas others were killed less often than expected if predation was random (notably Grant's gazelle).

responses such as increased vigilance are sensitive to finer, short-term cues, including current group size and composition (mixed or single species) and the immediacy of predation risk (as described by decelerating, logarithmic function of distance).

Changes in group size and the proportion of foraging individuals were both stronger in response to spotted hyenas (courseurs) than to lions (ambush predators), although the species of predator did not detectably alter vigilance responses. This result contrasts with recent data from invertebrate predators and prey, where sit-and-wait ambush predators induced stronger responses than more mobile predators that actively pursued their prey (Preisser et al. 2007; Schmitz 2008). For invertebrate predators, one hypothesized explanation for this difference is that the location of ambush predators is more predictable. This logic may generalize to large carnivores but produce a different result, so that ambush predators induce weaker risk effects. Among large carnivores, the hunting success of ambush predators relies heavily on surprise (Schaller 1972), which should cause strong selection against predictability. In contrast, courseurs do not rely on surprise and are often more successful when prey flee than when they do not (Mills 1990; Creel and Creel 2002), yielding weaker selection against predictability. This line of reasoning does raise the question of why sit-and-wait predators can succeed among invertebrates, if their locations are indeed predictable for prey. Finally, courseurs have exceptionally large energetic costs of hunting (Gorman et al. 1998), and it is reasonable to hypothesize that the energetic costs of avoiding such predators are also large (Creel et al. 2013).

**Figure 4**

(A) There was a significant trade-off between increased vigilance and decreased foraging. Each point plots the mean for 1 independent observation period. The strength of this trade-off varied among species, as illustrated by the comparison of (B) Grant's gazelles (for whom foraging behavior decreased strongly with increased vigilance) and (C) giraffes (for whom foraging was only weakly related to vigilance). Shaded area shows the 95% CI for the GLM.



**Figure 6**

The relationship between per-capita direct predation and the reduction in foraging when predators were present (a central component of risk effects in ungulates). Point labels: body mass rank/mean herd size/foraging strategy (G = grazing, B = browsing, and M = mixed).

### Trade-offs between direct predation and foraging costs

In some prior studies, the strength of antipredator responses was more closely related to the rate of attack than to the rate of mortality due to predation (Fernandez-Juricic et al. 2004). This pattern is expected if the rate of direct predation is jointly determined by exposure to predation risk and by the strength of behavioral responses to that exposure (Creel and Christianson 2008). Consequently, when direct predation rates and risk effects are measured across a set of prey species exposed to the same risks, variation in the strength of antipredator responses is expected to produce a negative relationship between risk effects and direct predation (Creel and Christianson 2008). For ungulate prey, this prediction is supported by several studies that have found low vigilance among individuals (Fitzgibbon 1990a, 1990b) or species (Scheel 1993) with high predation risk. This relationship is important for predator-prey dynamics because it implies that the total effect of a predator on prey dynamics may be poorly described by the rate of direct predation alone (Creel and Christianson 2008).

In this study, prey species differed in the degree to which they increased vigilance under conditions of high risk (Figure 2) and in the strength of trade-offs between vigilance and foraging (Figure 4). It is possible to take both of these effects into account when calculating the costs of antipredator responses, as illustrated by the following example. In response to the presence of a predator, the proportion of individuals that were vigilant increased by a larger amount in impala (from 0.09 to 0.27, or 3-fold) than in gazelle (from 0.14 to 0.25, or 1.8-fold) (Figure 2). The slope of the relationship between foraging and vigilance was also steeper for impala (proportion foraging =  $0.59 \times e^{-2.74 \times \text{proportion vigilant}}$ ) than for gazelle (proportion foraging =  $0.39 \times e^{-2.70 \times \text{proportion vigilant}}$ ), particularly within the relevant range of vigilance levels (Figure 4). Together, these effects led to a 38.4% reduction in foraging efficiency for impala and a 25.4% reduction in foraging efficiency for gazelle (Figure 6). Repeating this calculation for all prey species, 4 species had significantly lower foraging efficiency when predators were present, but the strength of this effect varied substantially (impala  $38.4 \pm 5.0\%$ , giraffe  $28.0 \pm 3.1\%$ , gazelle  $25.4 \pm 2.0\%$ , zebra  $6.6 \pm 3.0\%$ , mean  $\pm$

SE) and wildebeest showed no detectable foraging cost ( $0.2 \pm 3.0\%$ ). We used a set of behavioral criteria that focused on high-intensity “induced” vigilance, and our results confirm the conclusion that intense vigilance typically carries foraging costs, although low-intensity “routine” vigilance may not (Blanchard and Fritz 2007). We emphasize that prey species may also vary in exposure to predators through time, the proportion of time spent foraging might not capture all foraging costs, and costs of responses unrelated to foraging may be important (Creel et al. 2009; Clinchy et al. 2013).

We combined these estimates of foraging costs with our estimates of direct predation rates to examine variation among species in the limiting effect of predation. Figure 6 is a phase plane in which the ordinate measures direct predation rates and the abscissa measures reduced foraging as one aspect of risk effects. Predation has no limiting effect at the origin, and limiting effects increase with distance from the origin along either axis. To fully understand the relative importance of direct predation and risk effects, there is an unresolved issue of the relationship between a unit cost on each axis—we would ideally like to know how, for example, a 10% increase in direct predation or a 10% decrease in foraging efficiency affect population growth or individual fitness. Other costs of antipredator behavior could be examined and plotted along additional dimensions for a more comprehensive assessment of relationships between direct predation and risk effects, and we suggest that this approach will be broadly useful to quantify the importance of risk effects as a component of the total limiting effect of predation.

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