Original Article

Influence of immediate predation risk by lions on the vigilance of prey of different body size

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The effects on vigilance behavior of environmental cues that affect perceived risk of predation have been widely measured in gregarious herbivores. How extrinsic (e.g., predator activity within certain habitats) and intrinsic (e.g., within-group competition) cues interact depends on the biology of the prey species. However, very little is known about the impact of the actual presence of the predator in the vicinity on fine scale prey vigilance behavior. For this study, we monitored the vigilance of plains zebra (*Equus quagga*) and impala (*Aepyceros melampus*) in and around Hwange National Park, Zimbabwe. We assessed how the presence of radio-collared lions (*Panthera leo*) affected the vigilance of their prey. To evaluate the factors affecting vigilance behavior, we measured routine and intense vigilance. Routine vigilance can be conducted while chewing, although during intense vigilance chewing is halted and thus imposes foraging costs as food processing is delayed. As the most acute form of vigilance, we predicted that the presence of lions would lead to an increase in intense vigilance in both species. We found this to be the case for zebra, a key prey species for lions, while impala adjusted their intense vigilance to risk cues less specific to the presence of lions. Potential predation risk posed by lions in the immediate vicinity differs not only between species but also for a given species in different contexts. Our results also reveal how other environmental risk indicators influence the structure of vigilance behavior of large prey species in a manner that reflects their respective ecologies. *Key words:* antipredatory behavior, impala, intense vigilance, *Panthera leo*, zebra. *[Behav Ecol]*

INTRODUCTION

Vigilance behavior contributes to herbivore fitness in several ways, including avoidance of within-group competition (Blanchard et al. 2008), facilitation of group cohesion (Treves 1999), and predator detection (FitzGibbon 1989). In the latter, it is part of a suite of behavioral adaptations that facilitate increased prey fitness via predation avoidance (Lima and Dill 1990; Hunter and Skinner 1998). These adaptations have repercussions for the ecology of prey species, including effects on group size (Hamilton 1971; Pulliam 1973; Childress and Lung 2003), spatial, and temporal habitat use (Ripple and Beschta 2004; Valeix, Fritz, et al. 2009; Valeix, Loveridge, et al. 2009).

The majority of observational studies of antipredatory vigilance are limited by the fact that accurate behavioral data on prey, which are generally abundant and easy to observe, are rarely complemented by comparable information on their predators, which are often rare and difficult to observe (Lima 2002). Group size

and distance to cover have been widely used as proxies for the risk of predation (Pays et al. 2012), but recent work indicates that the physical presence of predators itself influences prey behavior (Creel and Winnie 2005; Valeix, Fritz, et al. 2009; Valeix, Loveridge, et al. 2009; Périquet et al. 2010), with prey adjusting antipredator vigilance differently to these parameters when a predator is detected in the immediate vicinity.

Vigilance generally involves foraging costs (Brown 1999; Fortin, Boyce, Merrill, et al. 2004). Time spent vigilant can conflict with foraging, thereby reducing rate of food intake (Houston et al. 1993). Optimal foragers should therefore reduce their vigilance as the marginal value of energy increases (Brown 1999; Fortin, Boyce, and Merrill 2004). Seasonality in forage quality (Blanchard and Fritz 2008) implies that costs of vigilance are most pronounced in the dry season because forage quality is lower and therefore intake needs to be greater, a phenomenon hereafter referred to as the forage quality hypothesis (see Rubenstein 1994 and Blanchard et al. 2008 for social amplification of this effect in zebra, *Equus quagga* and impala, *Aepyceros melampus*, respectively).

In some species, such as maras (*Dolichotis patagonum*), vigilance costs are shared among mates, as males keep guard while their female is feeding (Taber and Macdonald 1992). Other prey mitigate foraging costs by being vigilant while handling food. This antipredatory behavior has been referred

to as a routine vigilance (sensu Blanchard and Fritz 2007). Such multitasking can be observed in birds handling seeds (Baker et al. 2010, 2011) or herbivores swallowing or chewing food while vigilant (Fortin, Boyce, Merrill, et al. 2004; Blanchard and Fritz 2007; Pays et al. 2012). The main disadvantage of routine vigilance is that the quality of information gathered for predator detection is impaired as the chewing process disturbs both hearing and, to a lesser extent, vision (Fortin, Boyce, and Merrill 2004; Molinari-Jobin et al. 2004; Amft et al. 2005). Therefore, it might not be an optimal strategy for predator detection if routine vigilance does not allow prey to detect the predator in time. In some cases, such as when a specific risk-stimulus is detected, a more acute form of vigilance can be advantageous (Brown 1999). During such "intense vigilance" (induced vigilance, sensu Blanchard and Fritz 2007), the individual postpones all other activities while conducting vigilance, including chewing. As it is exclusive, this high-quality vigilance therefore involves higher immediate foraging costs than does routine vigilance (Blanchard and Fritz 2007) that can be performed while continuing to eat. Very few studies have made such a distinction between the 2 vigilance types. This is despite their relative contributions to total vigilance being different in that the costs of intense vigilance in terms of forging are much higher than the ones of routine vigilance (Fortin, Boyce, and Merrill 2004). To understand the ecological role of vigilance, it might be advantageous to distinguish between routine vigilance and intense vigilance because these 2 vigilance types impose different foraging costs and provide information of different quality on predation risk. Accordingly, the functional relationships between the optimal level of vigilance and habitat features should vary depending on the type of vigilance examined (Fortin, Boyce, and Merrill 2004). Nonetheless, few vigilance studies have made this distinction.

Here, we used radiotelemetry data from African lions (*Panthera leo*) to measure the effect of immediate predator presence on both components of individual vigilance: routine vigilance and intense vigilance. Because of the high quality of intense vigilance, we tested the hypothesis that prey increase their intense vigilance rather than their routine vigilance when a predator is known to be in the vicinity. We also explored the role of body size and associated vulnerability to predation in vigilance behavior by studying 2 contrasting herbivore species: zebra and impala whose average body masses are 200 and 45 kg, respectively (Cumming D and Cumming G 2003). Although both species are potential prey for lions (Owen-Smith and Mills 2008), lions preferentially prey on species within a weight range of 190–550 kg (Hayward and Kerley 2005), and zebras are known to be highly preferred prey of lions. This is the case in Hwange National Park (HNP) where zebra represent ~7.1% of all prey killed by lions, whereas impala represent only 2.5% (Loveridge et al. 2006) while both species are approximately equally abundant in the study area (1.15 zebras/km^2 [standard deviation {SD} 0.42]; 1.43 impalas/km^2 [SD 0.63], Chamaillé-Jammes et al. 2009). Additionally, lions account for most predation of zebra, but impala are more often taken by other predator species. Indeed, impala are significantly preferred by African wild dogs, cheetahs, and leopards (Hayward and Kerley 2008). In light of this, we expected these 2 species, which differ in their body size, perception of predation risk, predator preference, and energy requirements to differ in their strategy for dealing with predation risk (i.e., to optimize their survival) and limiting costs on foraging. Additionally, we expected vigilance to be negatively associated with group size, and as lions are ambush predators, we expected zebra vigilance to increase when close to cover. We did not expect impala to react strongly to the presence of lions because they are preyed on by predator species with a wide range of hunting tactics (Pays et al. 2012). However, we expected them to adjust their behavior according to their group size and distance to cover in the same way as do zebra.

MATERIALS AND METHODS

Study site

Data collection was carried out in the Main Camp area of Hwange National Park (HNP), located in north-west Zimbabwe, 19°00′S, 26°30′E. The habitat is dystrophic semiarid savannah, composed primarily of vegetation characteristic of woodland and bushland, though this is interspersed with small grassland patches (Roger 1993). The long-term mean annual rainfall for the area is 606 mm and characterized by high variability. During the dry season, natural water is scarce, and surface water available to animals is mainly found in artificial water holes, which are pumped with ground water. Lion density in HNP has been estimated at 2.7 lions/100 km^2 (Loveridge, Searle, et al. 2007). The rainy season occurs from the end of October to the end of April. Field observations were conducted in both the wet season from February to April 2008 and in the early dry season from mid-July to September 2010.

Vigilance monitoring

Vigilance data were collected from plains zebra and impala. Both are gregarious ungulates that form harem groups. Whereas zebras are grazers and usually stay in grassland areas, impalas are mixed feeders utilizing grassland and bushland habitats. Due to the practicalities of maintaining visual contact with the focal individual throughout the observation period, data collection was conducted when animals were feeding in areas open enough to film for 5 min. Filming was conducted from a parked vehicle between 100 and 150 m from the focal individual, following a period of habituation (the observers waited until no vigilance was directed toward them, usually between 2 and 5 min) allowed between switching off the vehicle's engine and data collection, so as best to capture their natural behavior.

Focal individuals were chosen randomly within the pool of animals corresponding to criteria designed to remove intraspecific variation in vigilance levels. First, observations focused on adult females without dependent offspring (Burger and Gochfeld 1994). Second, selecting individuals from the center of their group meant that we collected conservative estimates, without amplification of vigilance levels as a product of within-group positioning (Blanchard et al. 2008).

For each 5-min filming session, additional information was collected for individuals successfully recorded. This included date, time of day, location (GPS coordinates), and whether lions could be detected using a very high frequency receiver (if no detection, it meant than no radio-tagged lion was present within 2 km of the prey). Individual's species and group size were also recorded (group size was defined as the number of individuals foraging within 50 m of each other). Additionally, the distance between the focal individual and the closest cover was determined using a range finder.

For impala, pseudoreplication was avoided by only filming an individual from a given group once per day. As impala groups are very dynamic in terms of composition and numbers, this method reduced the chance of focusing on the same individual twice. For zebra, we avoided pseudoreplication by focusing on different individuals, based on their unique stripe patterns.

Using the footage collected from appropriate individuals, the type, order, and duration of behavior categories were recorded. Analysis of film footage was carried out without

reference to individual- and case-specific data to avoid introducing bias. Vigilance types were distinguished using the following criteria:

Routine vigilance

Individual's head is raised above shoulder height in an alert posture, usually with ears pushed forwards, and the individual is scanning its environment while chewing or walking. Routine vigilance could be used to detect food competition between conspecifics or be an antipredatory behavior.

Intense vigilance

Individual's head is raised above shoulder height in an alert posture, both ears pushed forwards fully, exclusively scanning their surroundings without chewing or moving. This type of vigilance is often referred to as "induced" vigilance (Blanchard and Fritz 2007) and is mainly used to describe antipredatory behavior. We chose to use the term "intense" as the cause of the vigilance is not always known.

Each observation period began when the focal individual was displaying feeding behavior. All forms of vigilance bout were considered finished when the individual had lowered its head, even momentarily. Similarly, intense vigilance bouts were considered finished when one or both ears were pushed back, even briefly, or the animal began chewing again.

Lion data

Data on lion presence in the study area were collected from radio-collared lions. We used data from 17 female and 10 male adults that were already instrumented with GPS radio collars in the framework of the long-term monitoring of the lion population in HNP (for details, see Loveridge, Davidson et al. 2007). Consequently, we could detect whether lions were in the vicinity during the observations. The presence of lions was detected during observations by radio tracking using a four-element yagi antenna (Sirtrack Ltd.) and either a Telonics TR4 or TR5 (Telonics Inc., Mesa, AZ) or Televilt RX900 telemetry receiver (Televilt Positioning AB). Such radio tracking permits detection of collared lions within a range of $\sim$ 2 km. Even though the cues on which herbivores base their knowledge of the presence of the lions in this vicinity are far from being understood, previous studies have shown that herbivores adjust their behavior to lion presence within such a radius (Valeix, Fritz, et al. 2009; Valeix, Loveridge, et al. 2009). Hence, hereafter, presence of lions in the vicinity is taken to mean the presence of radio-tagged lions within 2 km of the observation site.

The presence of undetected lions or other predators may be a source of noise in our data. However, we feel that this noise is likely to be minimal. Indeed, there was at least one collared lion in all known lion prides and coalitions in the study area, and preliminary analyses revealed that lions from the same group stay together most of the time (with all females from a pride sighted together in 89.2 ± 7.4% of sightings). No comparable data were available for other large predators in the area, but the presence of untagged large predators would simply make any vigilance response to lion less detectable rather than create an artificial effect. Our assumptions are therefore conservative in terms of the hypothesis we are testing.

Statistical analyses

We considered a baseline model that accounted for group size, absence or presence of lion, distance to cover, and season to determine how these parameters influenced the proportion of time spent in intense vigilance and routine vigilance as well as the frequency of intense vigilance and routine vigilance bouts. Whenever needed, these independent variables were transformed to linearize the relationship. We also tested the interaction between these variables and only presented the significant ones ($P \leq 0.05$). We used the function lm in the package nlme in R (version 2.13.1 for Mac OS X 10.7.2).

RESULTS

Impala

The proportion of time spent in routine vigilance per observation period averaged 27.5% (confidence interval [CI] 95% 24.5–30.4) and was best predicted by log group size and season (Table 1, Figure 1). Similarly, the group size and season influenced the frequency of routine vigilance bouts (Table 2). In both cases, vigilance was negatively associated with group size and higher in the wet season relative to the dry season. The proportion of intense vigilance per observation period averaged 8.8% (CI 95% 6.4–11.2) and was determined by group size and distance to cover (Table 1, Figure 1). Impala spent less time in intense vigilance when they were in larger groups or farther from cover. None of the variables explained variations in the frequency of intense vigilance bouts (Table 2).

None of the interactions tested had a significant impact on impala vigilance behavior.

Zebra

The proportion of routine vigilance per observation period was negatively associated with group size as was the frequency of routine vigilance bouts (Tables 1 and 2) and averaged 24.5%

Table 1

Average coefficient for multiple regressions relating the effect of different parameters on the proportions of routine and intense vigilance

Parameter	Proportion of routine vigilance				Proportion of intense vigilance			
	Zebra		Impala		Zebra		Impala	
	Value	SE	Value	SE	Value	SE	Value	SE
Intercept	0.40	0.05	0.57	0.07	0.02	0.03	0.27	0.06
Log(group size)	−0.22***	0.05	−0.15***	0.03	−0.01	0.04	−0.09*	0.04
Season[a]	NS	NS	−0.15***	0.04	NS	NS	NS	NS
Lion	NS	NS	NS	NS	0.33 ***	0.07	−0.02	0.03
Distance cover[2]	NS	NS	NS	NS	NS	NS	−0.00006*	0.00002
Log(Gr size) × lions	NS	NS	NS	NS	−0.29***	0.07	NS	NS

SE, standard error.

[a] Dicotomic variable with wet season being the season of reference.

*$P \leq 0.05$, **$P \leq 0.01$, ***$P < 0.001$, and NS, not significant

Table 2

Average coefficient for multiple regressions relating the effect of different parameters on the frequencies of routine and intense vigilance

| | Frequency of routine vigilance | | | | Frequency of intense vigilance | | | |
| | Zebra | | Impala | | Zebra | | Impala | |
Parameter	Value	SE	Value	SE	Value	SE	Value	SE
Intercept	1.13	0.2	2.65	0.39	0.078	0.062	0.48	0.18
Log(group size)	−0.63**	0.2	−0.90***	0.24	NS	NS	NS	NS
Season[a]	NS	NS	−0.62**	0.19	−0.02	0.05	NS	NS
Lion	NS	NS	NS	NS	0.032	0.05	NS	NS
Distance cover[2]	NS	NS	NS	NS	0.00007 *	0.00003	NS	NS
Season × lion	NS	NS	NS	NS	0.55 ***	0.01	NS	NS

SE, standard error.

[a] Dicotomic variable with wet season being the season of reference.

$*P \leq 0.05$, $**P \leq 0.01$, $***P < 0.001$, and NS, not significant.

(CI 95% 21.6–27.4). The proportion of time spent in intense vigilance, averaging 4.7% (CI 95% 2.8–6.6), was best predicted by the model that contained the group size × lion presence interaction term (i.e., the proportion of time spent in intense vigilance increased in the presence of lions more in small than large groups, Figure 2) and positively associated with distance from cover (Table 1). The frequency of routine vigilance bouts was only influenced by group size, with members of larger groups raising their head less frequently to scan their surroundings (Table 2). The intense vigilance bouts frequency was best predicted by the model with the season × lion presence interaction term, where lion presence increased intense vigilance frequency more in the dry than the wet season (Table 2, Figure 3).

None of the other interactions tested had a significant impact on zebra vigilance behavior.

DISCUSSION

The body size of prey species largely determines the suite and characteristics of their predators, and consequently, prey of different body sizes have different susceptibility to predation (Sinclair et al. 2003; Owen-Smith and Mills 2008; Fritz et al. 2011). Our study revealed size-dependent differences in the vigilance behavior of 2 herbivore species in response to dynamic and static features of their habitat. We found that the presence of lions in the vicinity, which varies dynamically over time and space, led to a 5.2-fold increase in frequency of intense vigilance bouts in zebra and a 3-fold increase in the average proportion of intense vigilance. In contrast, we detected no change in the vigilance of impala in the presence versus absence of lions. This predator might be a greater threat for zebra than impala, given that lions would be responsible for at least 80% of zebra mortality but cause only less than 25% of impala mortality (Hayward et al. 2007; Owen-Smith and Mills 2008; Thaker et al. 2011). Furthermore, as impala and zebra are approximately equally abundant in HNP (Chamaillé-Jammes et al. 2009) but impala are found in larger groups (impalas mean group size: 23.3 [CI 95% 20–26.6, $n = 122$], zebras mean group size: 9.2 [CI 95% 8–10.5; $n = 131$]), a given attack would represent a smaller "per capita" risk for impala than for zebra. Our finding that impala do not reduce the risk imposed by the proximity of lions through changes in individual vigilance supports the hypothesis that they react in a different way to zebras to the presence of the predator. Finally, it is also possible that their antipredatory behavior to decrease the risk of predation by lions is based on other behavioral
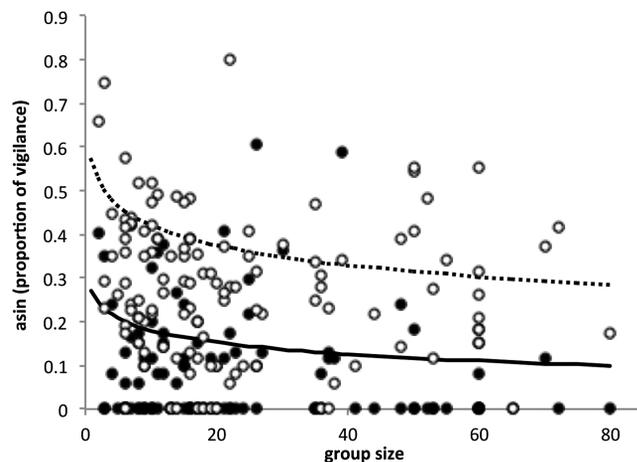
Figure 1
Proportion (arcsine transformed) of routine (solid line and filled circles) and intense (dotted line and empty circles) vigilance for impala in function of their group size.
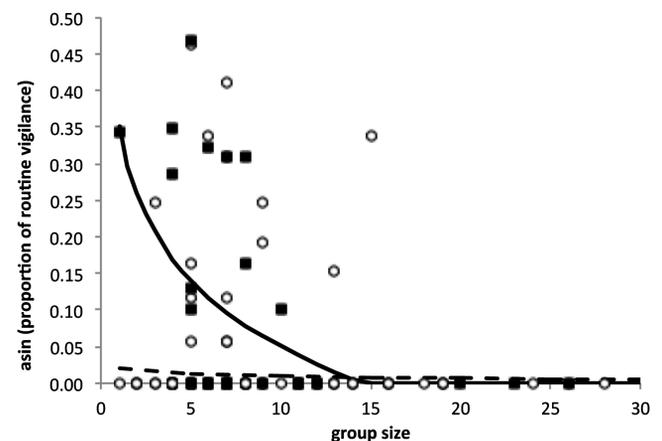
Figure 2
Proportion of intense vigilance (arcsine transformed) for zebra in function of the group size with (filled squares) and without lions (empty circles) in the vicinity.
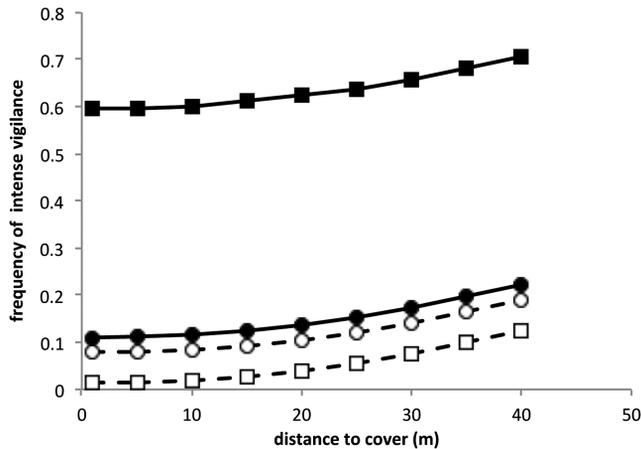
Figure 3
Frequency of intense vigilance for zebra in function of the distance to cover during the 2 seasons (squares: dry season; circles: wet season) with (filled symbols) and without lions (empty symbols) in the vicinity.

adjustments, such as changes in habitat selection or group formation.

As we expected in the presence of lions, zebra increased their use of intense vigilance. Intense vigilance is a high quality process of information acquisition to improve predator detection, thus allowing prey to respond to an immediate temporal and spatial predator risk. However, they avoid using intense vigilance when lions are not in the vicinity because it is a costly posture. Thus, they limit foraging costs of vigilance.

We further observed a 13-fold increase in the proportion of intense vigilance in the presence of lions in the dry season compared with only a 2-fold increase in the wet season, indicating that zebra perceive lions as a greater threat during the dry than the wet season. This conclusion is supported by lion kill data from HNP, which indicates that lions consume a greater proportion of zebra in the dry (6% in the early dry season, increasing to 13% in the late dry season) than the wet season (4%) (Hwange Lion Research Project, unpublished data). No such seasonal pattern in predation risk was detected for impala. The seasonal effect for zebra is also consistent with the food quality hypothesis: because there is more high-quality forage available in the wet than the dry season at our study site (Blanchard and Fritz 2008), the foraging costs of vigilance should have a greater impact on herbivore behavior in the dry season (Fortin, Boyce, Merrill, et al. 2004). Indeed, optimality principles predict a decrease in vigilance following an increase in the marginal value of food (Brown 1999).

In the dry season, herbivores have to face several constraints: low forage quality but also the need to access surface water regularly to meet their drinking requirements. As a consequence, herbivore distribution is largely influenced by the distance to a water source in the dry season (Redfern et al. 2005; Valeix, Loveridge, et al. 2009) and predators such as lions tend to hunt and ambush their prey in the vicinity of these water sources (Valeix, Fritz, et al. 2009; Valeix et al. 2011). Hence, vigilance behavior in herbivores is likely to be maximal when in the vicinity of a water source: in Hwange, kudu and giraffe spend on average 30% and 40% of their time at water sources being vigilant (Périquet et al. 2010). Although our study did not address the interplay between season, food quality, and distance to a water source, these factors are likely to interact in the prey to exhibit vigilance.

In addition to the effect of the presence of lions and season, we found that group size and distance to cover also affected the structure of individual vigilance both in zebra and impala. The

negative correlation between vigilance and group size has become a classic example of adjustable predator avoidance behavior (Roberts 1996). A number of mechanisms are thought to contribute to this, including Hamilton's (1971) dilution effect, the confusion effect (Welty 1934), and Pulliam's (1973) "many eyes" effect. The reduction in individual risk that these factors collectively convey is widely considered as a driving force behind the evolution of aggregation behavior in social herbivores (Turchin and Kareiva 1989; Reluga and Viscido 2005; Wood and Ackland 2007). In addition, interindividual competition for food access in large groups might also force individuals to reduce the time spent in intense vigilance. Indeed, in such groups constrained by a large number of competitors but taking advantage of a dilution effect, the best strategy should be an increase of the foraging time limiting vigilance posture and using the low-cost posture (i.e., routine vigilance). A group-size effect can also interact with individual choice to determine time allocated to vigilance (intense or routine vigilance), as individuals might bet on a dilution effect (and collective detection) in large groups, thereby limiting intense vigilance. This is in accordance with our result that the effect of group size on zebra intense vigilance only became evident in the presence of lions (Figure 2). However, the group-size effect was a far more dominant factor for impala in shaping intense vigilance levels. This suggests that, because they have more potential predators than do zebra, impala assess their predation risk based more on their group size rather than the actual presence or absence of one of these predators in the vicinity. In contrast to our predictions, and other results (Burger et al. 2000; Beauchamp 2010), distance to cover was positively associated with zebra vigilance (Figure 3), though the effect was comparatively small.

Finally, the way in which impala and zebra adjust their intense vigilance in response to risk cues is noteworthy. Zebra do so primarily by changing vigilance bout frequency. This strategy minimizes the length of time spent with the head lowered, hence increasing the likelihood of detecting an ambush predator, such as a lion. In contrast, impala adjusted the proportion of vigilance but not the frequency of bouts (Pays et al. 2007; Carter et al. 2009; Sirot and Pays 2011). This may reflect a more generalized approach to predator detection, fitting the risk posed by potential predators with a range of hunting strategies.

In conclusion, our results illustrate that prey body size and ecology influence how herbivores gage risk of predation, including from lions in the vicinity, and how they reduce this risk through changes in individual vigilance. These patterns are most obvious when the distinction is drawn between routine and intense types of vigilance. During the wet season, kudu (*Strepsiceros zambesiensis*) are the main prey of lions (Loveridge, Davidson, et al. 2007; Davidson 2009) so a study of their reaction to the presence of lions would add depth to the conclusions drawn here. To our knowledge, this study is one of the first to assess the effect of the immediate presence of a predator on prey behavior at such a fine scale.

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