Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context

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Perceived risk of predation is considered to influence individual prey vigilance, but little is known about the extent to which the context (e.g. distance to cover, group size) and the immediate presence of predators determine individual prey vigilance. We combined behavioural data on individual vigilance of herbivores at waterholes with fine-scale spatiotemporal data from 27 African lions, *Panthera leo*, fitted with GPS radiocollars to test whether individual prey vigilance increases when predators are in the vicinity and whether this relationship is influenced by group size and presence of other herbivores. The study was conducted on giraffe, *Giraffa camelopardalis*, greater kudu, *Tragelaphus strepsiceros*, and plains zebra, *Equus quagga*, in Hwange National Park, Zimbabwe, between mid-September and mid-November 2008. Kudu was the only species to adjust its vigilance level significantly in the presence of lions, arguably owing to its higher contribution to lion diet in Hwange. Kudu devoted a significantly higher proportion of time to vigilance when lions were in the vicinity. Furthermore, the proportion of time spent on individual vigilance decreased as group size increased during the approach and drinking phases, particularly when lions were in the vicinity. Finally, the presence of other herbivores at the waterhole enabled kudu to spend less time vigilant while drinking. These adjustments involved changes in the length of vigilance bouts, but not in their frequency. Our study suggests that the interplay between the context (group size, presence of other prey) and the immediate presence of predators determines the level of vigilance in prey.

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The effect of predation risk on group size is one of the most studied aspects of interactions between predators and prey (Elgar 1989; Lima & Dill 1990; Beauchamp 2003), and predation pressure is thought to have played a major role in the evolution of group living and sociality in prey species (Jarman 1974; Caro et al. 2004). Indeed, compared to solitary animals, individuals within a group benefit from not only the greater number of individuals available to scan the surroundings and thus to detect an approaching predator (the 'many eyes effect'; Pulliam 1973; Lazarus 1979), but also a lower individual risk of being preyed upon because of a 'dilution effect' (Hamilton 1971; Dehn 1990). To detect an approaching predator, an individual can rely on its own monitoring of the surroundings, or it can await signals from other wary individuals. In our study we focused on individual prey vigilance, which is classically viewed in the context of an aggregation that confers protection against predators and is commonly expected to decline with increasing group size (Lima 1987, 1995; Roberts 1996). By allowing each individual within a group to devote less time to vigilance activities and hence more time to other activities, group living may influence the trade-offs that individuals face between vigilance and foraging activities (Illius & Fitzgibbon 1994; Fortin et al. 2004). Even though they have been far less studied, similar mechanisms may occur at the interspecific level. Presence of individuals from other prey species and formation of mixed-species groups may decrease the perceived risk of predation and allow an individual to decrease its vigilance level (Morse 1977; Fitzgibbon 1990).

Prey vigilance is commonly considered to be context dependent (e.g. depending on group size, visibility); however, less is known of how prey adjust their vigilance to the perceived risk of predation associated with the immediate presence of predators (but see Childress & Lung 2003; Lung & Childress 2007 for the influence of

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predator density). Most studies on predator–prey relationships have resorted to using indirect proxies of predation risk (e.g. distance to cover, vigilance). Consequently one limitation to understanding behavioural effects of predation is that accurate data on prey behaviour are rarely complemented by comparable information on their predators (Lima 2002). Recent studies have provided evidence that behavioural responses to the risk of predation may be different when predators are or are not in the vicinity (Creel & Winnie 2005; Valeix et al. 2009). In particular, Creel & Winnie (2005) showed that in elk, Cervus elaphus, herd size increased as distance to protective cover increased (commonly interpreted as the a result of the 'many eyes effect' and the 'dilution effect' of grouping) but only on days when wolves, Canis lupus, were absent. When wolves were present, elk herd size remained small at all distances from cover, possibly because of a lower probability that a predator will encounter prey (Scheel 1993) or that it will attack once it has detected prey (Carbyn & Trottier 1987). Hence, there is a need to take predator data into account when investigating antipredator behavioural responses.

Our goal in this study was to assess how individual prey vigilance is affected by the immediate presence of predators and by the presence of conspecifics and heterospecifics. We used the example of African lions, Panthera leo, and three large herbivores (giraffe, Giraffa camelopardalis, greater kudu, Tragelaphus strepsiceros, and plains zebra, Equus quagga) at waterholes in the semiarid savannah of Hwange National Park, Zimbabwe. Previous studies have shown that, at the group level, the behaviour of herbivores at waterholes (e.g. time taken to approach the waterhole, time spent drinking) is influenced by indirect indices of the risk of predation such as distance to cover (Valeix et al. 2007), and by the long-term risk of encountering lions and the presence of lions in the vicinity of the waterhole (Valeix et al. 2009). These studies carried out at the group level strongly suggested that the risk of predation by lions influences individual vigilance in herbivores at waterholes, but individually based information was lacking. In the present study, therefore, we went one step further and combined behavioural data on individual herbivores with spatiotemporal fine-scale data from GPS radiocollars on lions to test whether individual prey vigilance increases when predators are in the vicinity and whether this relationship is influenced by group size and presence of other herbivores. In particular, we expected individual prey vigilance to decrease as group size increased and when there were other herbivores at the waterholes. We also tested whether individual drinking time decreased when lions were in the vicinity and whether this relationship was influenced by group size and presence of other herbivores. In particular, individual drinking time was expected to increase as group size increased and when there were other herbivores at the waterhole. Because herbivores can adjust either the frequency with which they scan their surroundings or the duration of their vigilance bouts, or both, to adjust their vigilance level, we further explored whether changes in individual prey vigilance were due to changes in the frequency, or in the length, of vigilance bouts. Lions are known to ambush their prey in the vegetation surrounding water sources (Schaller 1972; Hopcraft et al. 2005). Consequently, it would be expected that herbivores (1) need to scan more frequently when they are close to vegetation, where the distance to the potential danger and hence the time to react are short, and (2) can afford to scan less frequently when drinking at a waterhole since they are further from vegetation, but may need to scan for longer periods to check all the possible surroundings. Hence, when predators were in the vicinity, we expected herbivores to modulate their vigilance level mainly by changing the frequency of vigilance bouts when they left the vegetation to approach a waterhole, and mainly by changing the length of vigilance bouts when they drank at the waterhole.

METHODS

Study Site

We conducted field observations from mid-September to mid-November 2008 in the Main Camp area of Hwange National Park (HNP), Zimbabwe (Fig. 1). HNP is located in northwestern Zimbabwe (19°00′S, 26°30′E) and covers ca. 15 000 km². The vegetation is typical of southern African dystrophic (low-nutrient soil) wooded savannah, with patches of grassland (Rogers 1993). The altitude ranges from 900 to 1100 m. The climate is semiarid (long-term mean annual rainfall = 606 mm) and the rainy season occurs from the end of October to the end of April. During the dry season, natural water is scarce, and surface water available to animals is mainly found in artificial waterholes, which have been developed since the 1930s by pumping ground water. Lion density in HNP is estimated at around 2.7 lions/100 km² (Loveridge et al. 2007a). Approval for the study was obtained from the Zimbabwe Parks and Management Wildlife Authority; the Wildlife drugs Subcommittee of the Drugs Control Council of Zimbabwe and the Zimbabwe Veterinary Association, Wildlife Group.

Vigilance Behaviour Monitoring

We studied the influence of immediate predation risk by lions on three water-dependent herbivore species: giraffe, greater kudu and plains zebra. Their average body size is 750 kg, 135 kg, and 200 kg, respectively (unit mass as per Cumming & Cumming 2003). These species represent, respectively, 10%, 11–24% and 5–7% of lion kills in HNP (Loveridge et al. 2007b). After buffalo, Syncerus caffer, kudu, giraffe and zebra are, respectively, the second, third and fourth species most preyed upon by lions in HNP (Loveridge et al. 2007b). Giraffe and kudu are browsers that spend most of their time in bushy/woody areas whereas zebra are grazers and usually stay in grassland areas. Additionally, zebra are more water dependent. We monitored individual prey vigilance behaviour at three pumped waterholes: Kennedy 1, Makwa and Nyamandhlovu (Fig. 1). The three waterholes were monitored from dawn to dusk from a platform (Nyamandhlovu) or from a car parked at a reasonable distance (ca. 150 m from the waterhole) not to disturb the behaviour of herbivores (Kennedy 1 and Makwa).

For each herbivore group that entered the waterhole area (defined as a 150 m radius around the waterhole, which was initially determined using a rangefinder), we monitored the vigilance behaviour of one focal animal during (1) the approach to the waterhole, (2) the drinking phase and (3) the departure from the waterhole area. An animal was considered vigilant when it stood still on all four legs, with head raised above shoulder level and looked attentively at the surroundings, often with ears held forward (Alados 1985). We did not consider an animal moving as being vigilant; hence our approach is conservative. Focal animals were chosen randomly within the pool of animals corresponding to the following two criteria in the group. (1) Since position in the group is known to influence the level of vigilance (Blanchard et al. 2008), we consistently measured behavioural responses for adults in a central position within the group. Central individuals are less exposed to predation than peripheral ones; hence if an increase in vigilance is detected then it is highly probable that the level of vigilance increased for all individuals in the group. Moreover, it was more rigorous to monitor central individuals, as peripheral ones are less likely to remain peripheral throughout the observation phase. (2) The presence of dependent offspring is likely to increase female vigilance (Wolff & Van Horn 2003). However, the study was conducted in the late dry season when young giraffes and kudus can be considered as subadults (calving season ca. December). For
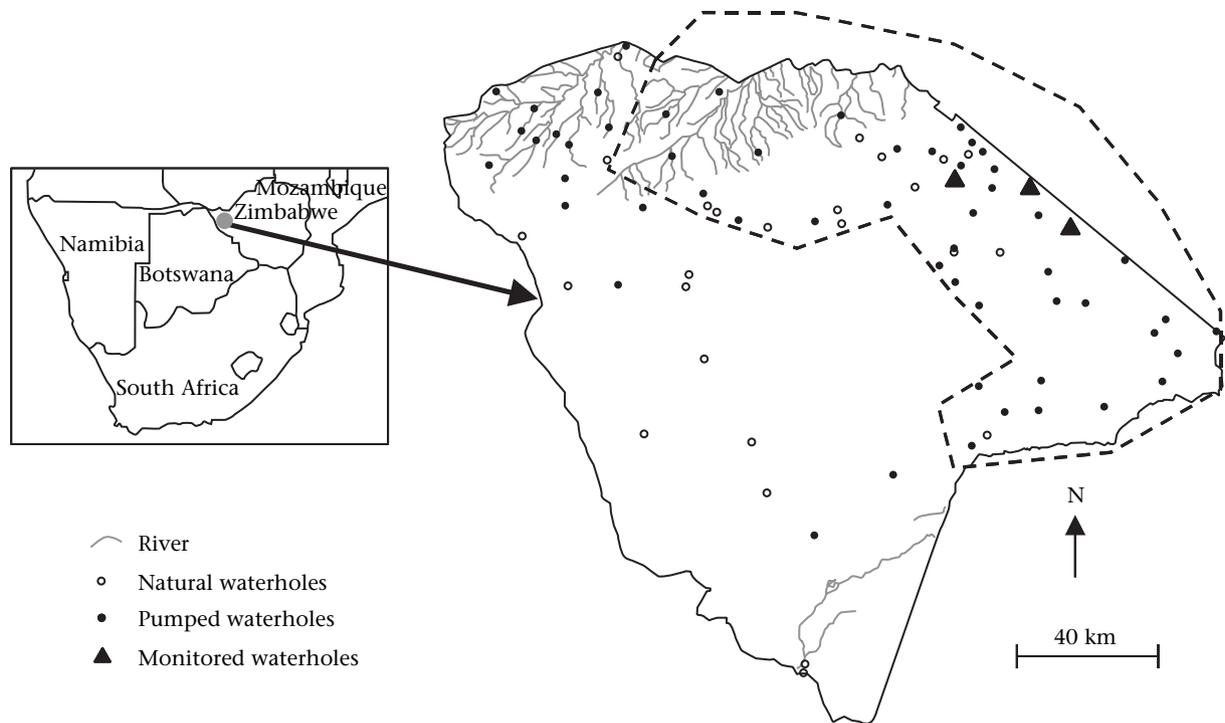
Figure 1. Map of Hwange National Park showing surface water sources and the study area. The dotted polygon represents the area where lions are closely monitored with GPS radiocollars.

zebras, for which births are spread throughout the year, we only measured the behavioural responses of females without dependent offspring. For each focal observation, we recorded the date, the presence/absence of lions, the sex of the individual, the group size and the presence of other herbivores at the waterhole. Information on the total time spent on each phase (approach, drinking and departure) is provided for each study species in Fig. 2a.

For each phase (approach, drinking and departure), we monitored the behaviour of the focal individual over a 5 min period or during the whole phase if it was shorter. During these focal observations, we recorded the total time spent vigilant, the number of vigilance bouts and the length of each vigilance bout. Additionally, during the drinking phase, we also recorded the total time spent drinking, the number of drinking bouts and the length of each drinking bout. The study comprised 49 days (ca. 600 h) of observations. We obtained a total of 156 individual focal observations (61 giraffes, 47 kudus and 48 zebras), including 48 observations when lions were in the vicinity (21 giraffes, 11 kudus and 16 zebras). Information on group size is provided in Table 1.

Lion Data

Information on lion presence around waterholes was provided by fine-scale spatiotemporal data from GPS radiocollars. We used data from 17 female and 10 male adults which were already instrumented with GPS Simplex radiocollars in the framework of the long-term monitoring of the lion population in HNP (female: 900 g; male: 950 g; Televilt Positioning AB, Lindesberg, Sweden; see Loveridge et al. 2007a for details of the captures) in the northern area of HNP. The three study waterholes were located in the home ranges of GPS-collared lions (Fig. 1). Consequently, we could detect whether lions were in the vicinity of the study waterholes during the observations. The presence of lions in the vicinity of the study waterholes was detected during the monitoring by radiotracking from the platform or the vehicle, using

a four-element Yagi antenna (Sirtrack Ltd., Havelock North, New Zealand) and either a Telonics TR4 or TR5 (Telonics Inc. Mesa, AZ, U.S.A.) or Televilt RX900 telemetry receiver (Televilt Positioning AB). Such radiotracking permits detection of collared lions within a range of ca. 2 km. Herbivores are likely to react to lion presence in such a radius (Valeix et al. 2009). Hence presence of lions in the vicinity of the waterhole is taken to mean presence of lions within 2 km of the waterhole hereafter.

One possible limitation to our study could be the presence of undetected lions or other predators. However, their presence would work against our hypotheses. Additionally, (1) there was at least one collared lion in all known lion prides and coalitions in the study area and (2) preliminary analyses revealed that lions from the same group stay together most of the time (with females from a pride sighted together in 89.2 ± 7.4% of sightings). No comparable data were available for other predators such as spotted hyaena, *Crocuta crocuta*, or wild dog, *Lycaon pictus*. However, it is unlikely that any of them were around during our observations because (1) hyaenas are strictly nocturnal hunters (Drouet-Hoguet 2007) and (2) wild dogs have become very rare in the study area. Moreover, among the study herbivore species, only kudu are potential prey of hyaenas or wild dogs (Owen-Smith & Mills 2008).

Statistical Analysis

We carried out a preliminary investigation of the effect of the phase (approach, drinking, departure) on the proportion of vigilance for the three study herbivores. Proportion of time spent vigilant was arcsine transformed to meet the assumption of normality (Sokal & Rohlf 1995). For each species, we performed an analysis of variance of the proportion of vigilance with phase as a factor and with Bonferroni correction for multiple comparisons.

We first analysed the effect of presence of lions (binary variable), group size (continuous variable), presence of other herbivores (binary variable), the interaction between presence of lions and
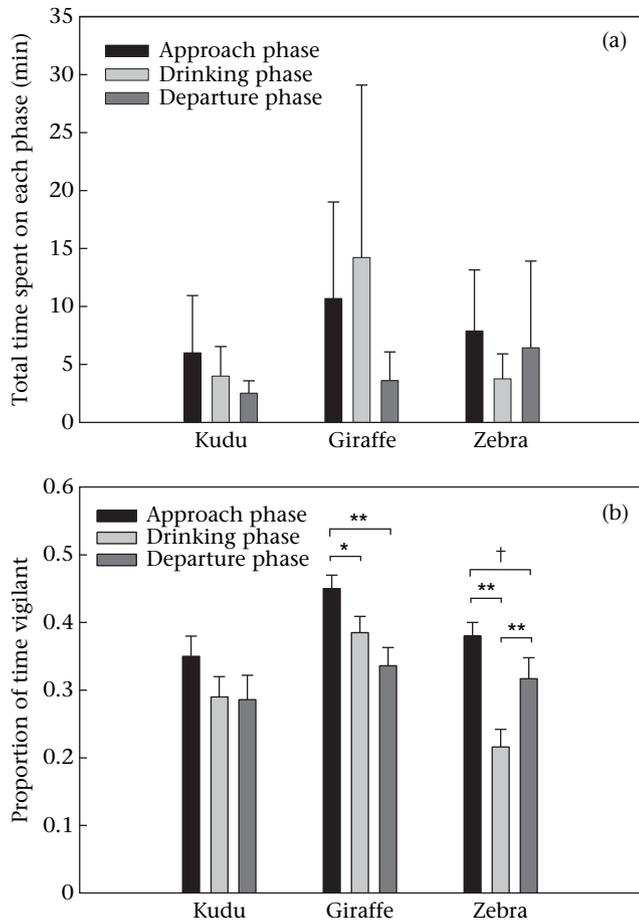
Figure 2. (a) Average time + SD spent on each phase and (b) average vigilance levels + SE across the different phases (approach, drinking and departure) for the different study species. †$P < 0.10$; *$P < 0.05$; **$P < 0.01$; t test with Bonferroni correction for multiple comparisons.

group size, and the interaction between presence of lions and presence of other herbivores on the proportion of time spent vigilant during each phase (approach, drinking, departure) for each herbivore species. Proportion of time spent vigilant was arcsine transformed to meet the assumption of normality. Initially, we used linear mixed-effect models with waterhole identity and date as random factors. In all models, none of the random factors was significant (all $P > 0.10$); hence models were simplified to general linear models (GLMs).

As the proportion of time spent vigilant can be influenced by both the frequency and the length of vigilance bouts, we then further analysed the effect of presence of lions, group size, presence of other herbivores, the interaction between presence of lions and group size, and the interaction between presence of lions and presence of other herbivores on (1) the frequency of vigilance bouts, and (2) the length of vigilance bouts during each phase (approach, drinking, departure) for each herbivore species.

Table 1
Size of the herbivore groups observed at waterholes in Hwange National Park, Zimbabwe

Species	Group size mean±SD (range)
Giraffe	2.58±2.41 (1–11)
Kudu	5.28±2.91 (1–16)
Zebra	6.20±2.97 (1–15)

Frequency of vigilance bouts was calculated as the number of vigilance bouts per min. It was log transformed to meet the assumption of normality. We calculated the average length of vigilance bouts for each individual that was observed. Both frequency and average length of vigilance bouts were investigated using GLMs for the same reason as above.

We also assessed whether presence of lions, group size, presence of other herbivores, the interaction between presence of lions and group size, and the interaction between presence of lions and presence of other herbivores influenced (1) the proportion of time spent drinking, (2) the frequency of drinking bouts, and (3) the average length of drinking bouts during the drinking phase for each species.

To distinguish between an effect of the presence of other herbivores at the waterhole and an effect of the number of other herbivores at the waterhole, we also ran the analyses described above with the variable 'number of other herbivores' instead of the variable 'presence of other herbivores'. Backward variable selection was used with successive removal of nonsignificant variables. Statistical analyses were performed with SAS software version 8.2 (SAS Institute Inc., Cary, NC, U.S.A.), using GLM procedure.

RESULTS

Levels of vigilance were generally high (between 30 and 50% of time observed on average; Fig. 2b). Preliminary analyses revealed that the phase (approach, drinking or departure) influenced the proportion of time spent vigilant (giraffe: $F_{2,145} = 7.73$, $P = 0.001$; kudu: $F_{2,87} = 2.64$, $P = 0.077$; zebra: $F_{2,106} = 21.23$, $P < 0.0001$), with higher vigilance levels during the approach phase for all three species (Fig. 2b).

Kudu Individual Vigilance

During the approach phase, the proportion of time spent vigilant was higher when lions were in the vicinity of the waterhole, and decreased as kudu group size increased, with this decrease being more pronounced in the presence of lions (Table 2, Fig. 3a). This was due to changes in the length of vigilance bouts and not to changes in their frequency (Table 2). During the drinking phase, the proportion of time spent vigilant was higher when lions were in the vicinity (Table 2). This change was also due to a change in the length of vigilance bouts (Table 2). Kudu group size influenced the proportion of time spent vigilant only when lions were in the vicinity (Table 2, Fig. 3b). Additionally, the presence of other herbivores was associated with kudu decreasing their vigilance while drinking (Fig. 3c), with both the frequency of vigilance bouts and their length decreasing (Table 2). No factor influenced the proportion of time spent vigilant during the departure phase (Table 2). The results were similar when we considered the number of other herbivores at the waterhole instead of their presence/absence.

Giraffe and Zebra Individual Vigilance

None of the measured factors influenced the proportion of vigilance during approach, drinking and departure phases for either giraffe or zebra. However, the relationship between presence of lions and the proportion of vigilance while drinking approached statistical significance for giraffe ($F_{1,58} = 3.32$, $P = 0.07$) with higher levels of vigilance when lions were in the vicinity. Additionally, the frequency of vigilance bouts was higher when lions were in the vicinity for giraffe during the drinking phase (estimate in the log-transformed scale when lion absent: 0.38 ± 0.04; when lion present: 0.47 ± 0.04; $F_{1,58} = 5.05$, $P = 0.028$).

Table 2
Results of the different models on kudu vigilance at waterholes in Hwange National Park

	Explanatory variables				
	Lion	Group size	Other herbivores	Lion*group size	Lion*other herbivores
Approach phase					
Proportion of vigilance (arcsine transformed)	−45.65±18.35 $F_{1,28}=6.19, P=0.019$	−10.13±3.66 $F_{1,28}=8.37, P=0.007$	$(F_{1,27}=0.07, P=0.79)$	9.13±3.84 $F_{1,28}=5.65, P=0.025$	$(F_{1,26}=0.46, P=0.50)$
Frequency of vigilance bouts (log transformed)	$(F_{1,29}=0.21, P=0.65)$	$(F_{1,27}=0.01, P=0.99)$	$(F_{1,30}=0.24, P=0.62)$	$(F_{1,26}=0.08, P=0.78)$	$(F_{1,28}=0.94, P=0.34)$
Length of vigilance bouts	−31.66±10.38 $F_{1,28}=9.31, P=0.005$	−7.06±2.08 $F_{1,28}=12.93, P=0.001$	$(F_{1,27}=0.01, P=0.97)$	6.30±2.18 $F_{1,28}=8.36, P=0.007$	$(F_{1,26}=2.52, P=0.12)$
Drinking phase					
Proportion of vigilance (arcsine transformed)	−20.72±6.83 $F_{1,33}=9.21, P=0.005$	$(−2.12±0.81, F_{1,33}=2.05, P=0.16)$	12.54±3.41 $F_{1,33}=13.55, P=0.001$	2.72±1.08 $F_{1,33}=6.34, P=0.017$	$(F_{1,32}=1.18, P=0.29)$
Frequency of vigilance bouts (log transformed)	$(F_{1,34}=0.23, P=0.63)$	$(F_{1,32}=1.30, P=0.26)$	0.09±0.05 $F_{1,35}=4.17, P=0.049$	$(F_{1,31}=0.20, P=0.65)$	$(F_{1,33}=3.77, P=0.06)$
Length of vigilance bouts	−4.50±2.16 $F_{1,35}=4.33, P=0.045$	$(F_{1,34}=0.42, P=0.52)$	3.88±2.05 $F_{1,35}=3.58, P=0.050$	$(F_{1,33}=2.71, P=0.11)$	$(F_{1,32}=0.35, P=0.56)$
Departure phase					
Proportion of vigilance (arcsine transformed)	$(F_{1,17}=0.13, P=0.72)$	$(F_{1,18}=1.18, P=0.29)$	$(F_{1,15}=0.15, P=0.71)$	$(F_{1,16}=1.10, P=0.31)$	$(F_{1,14}=0.14, P=0.71)$
Frequency of vigilance bouts (log transformed)	$(F_{1,17}=0.69, P=0.42)$	$(F_{1,18}=4.21, P=0.06)$	$(F_{1,15}=0.01, P=0.98)$	$(F_{1,16}=0.85, P=0.37)$	$(F_{1,14}=0.39, P=0.54)$
Length of vigilance bouts	$(F_{1,18}=0.52, P=0.48)$	$(F_{1,17}=0.01, P=0.99)$	$(F_{1,15}=0.79, P=0.39)$	$(F_{1,16}=2.59, P=0.13)$	$(F_{1,14}=1.01, P=0.33)$

Results are presented as slope estimates ± SE for continuous variables (group size). For the variables 'lion' and 'other herbivores', results are presented as the difference estimate between the 'no lion'/'no other herbivore' class and the reference class 'lion present'/'presence of other herbivores'. Results are in italics and between parentheses when $P > 0.05$. See also Fig. 3 for interpretation of the interaction results. Degrees of freedom may differ within one row because of the backward variable selection used with successive removal of nonsignificant variables.

Individual Drinking Behaviour

We found no significant result except for the proportion of time spent drinking which decreased as group size increased for kudu (slope estimate ± SE in the arcsine-transformed scale = $−1.80 ± 0.88$; $F_{1,39} = 4.18$, $P = 0.048$), but it increased as group size increased for giraffe (slope estimate ± SE in the arcsine-transformed scale = $1.76 ± 0.56$; $F_{1,60} = 9.76, P = 0.003$). For giraffe, the increase was due to an increase in the frequency of drinking bouts (slope estimate ± SE in the log-transformed scale = $0.02 ± 0.01$; $F_{1,63} = 8.70, P = 0.005$).

DISCUSSION

Higher perceived risk of predation leads to increased individual vigilance in many species (Hunter & Skinner 1998; Wolff & Van Horn 2003; Winnie & Creel 2007). However, the extent to which prey adjust their vigilance to the context (distance to cover, group size), or to a perceived risk of predation associated with the immediate presence of predators, or both, remains poorly understood. For kudu, the proportion of time spent on individual vigilance decreased as group size increased during the approach phase and during the drinking phase when lions were absent, suggesting that perceived predation risk and associated vigilance level are context dependent. This corroborates findings from the few existing studies on drinking behaviour at waterholes which revealed the importance of the context (Burger & Gochfeld 1992; Burger 2001; Valeix et al. 2007, 2009). Additionally, the proportion of time devoted to vigilance by individuals changed when lions were in the vicinity (during the approach and drinking phases), suggesting that perceived predation risk and associated vigilance level also depend on the immediate presence of predators. The relationship between group size and vigilance was particularly apparent when lions were in the vicinity (Fig. 3a, b). Hence, in the presence of a predator, individual prey vigilance decreased as group size increased as expected from the 'many eyes' and 'dilution' effects (Lima 1987, 1995; Roberts 1996). However, the relationship between group size and individual prey vigilance was either very weak (approach phase) or nonexistent (drinking phase)

when lions were not in the vicinity. All three herbivore species were highly vigilant (kudu and giraffe spent on average ca. 30% and ca. 40% of their time at waterholes being vigilant, respectively) in comparison to other reports (e.g. ca. 20% of vigilance for Defassa waterbuck, *Kobus ellipsiprymnus defassa*, in Central African Republic; Pays et al. 2007). Perhaps herbivores in HNP are already close to the peak of vigilance and cannot adjust their behaviour further in response to group size.

The presence of other herbivores at the waterhole enabled kudu to spend less time vigilant while drinking as suggested by Morse (1977) and Fitzgibbon (1990). Kudu individual vigilance was influenced by both group size and the presence of other herbivores during the drinking phase whereas there was no effect of the presence of other herbivores during the approach phase. A possible interpretation is that when a herbivore approaches a waterhole, its vigilance is influenced only by the size of its own group; however, once drinking, it responds to the size of the multispecies group and it relies on the vigilance of both conspecifics and heterospecifics. Our results strongly suggest that kudu are aware of the presence of their predators. While in some cases lions were visible from the waterhole, in many others they were not. Prey may sense the lions' odour (Kats & Dill 1998) or take account of their roaring activity at night. The mechanisms of, and time lags in, these effects merit further research.

The vigilance of all three species was higher during the approach than the drinking and departure phases. Waterhole areas are particularly risky for prey since lions ambush their prey there (Schaller 1972; Hopcraft et al. 2005). In HNP, most lions' kills occur within 2 km of waterholes (Valeix et al. 2009). Herbivores entering the open area surrounding a waterhole probably assess predation risk before advancing, explaining why they are most vigilant during the approach phase. After drinking, it is likely that they leave quickly to minimize the time spent at risk. This may explain why the effects we detected were apparent only in the approach and drinking phases.

Our results did not support the hypotheses regarding the influence of distance to cover on changes in frequency and duration of vigilance bouts. They revealed that kudu appear to adjust the length of vigilance bouts instead of their frequency, whereas giraffe
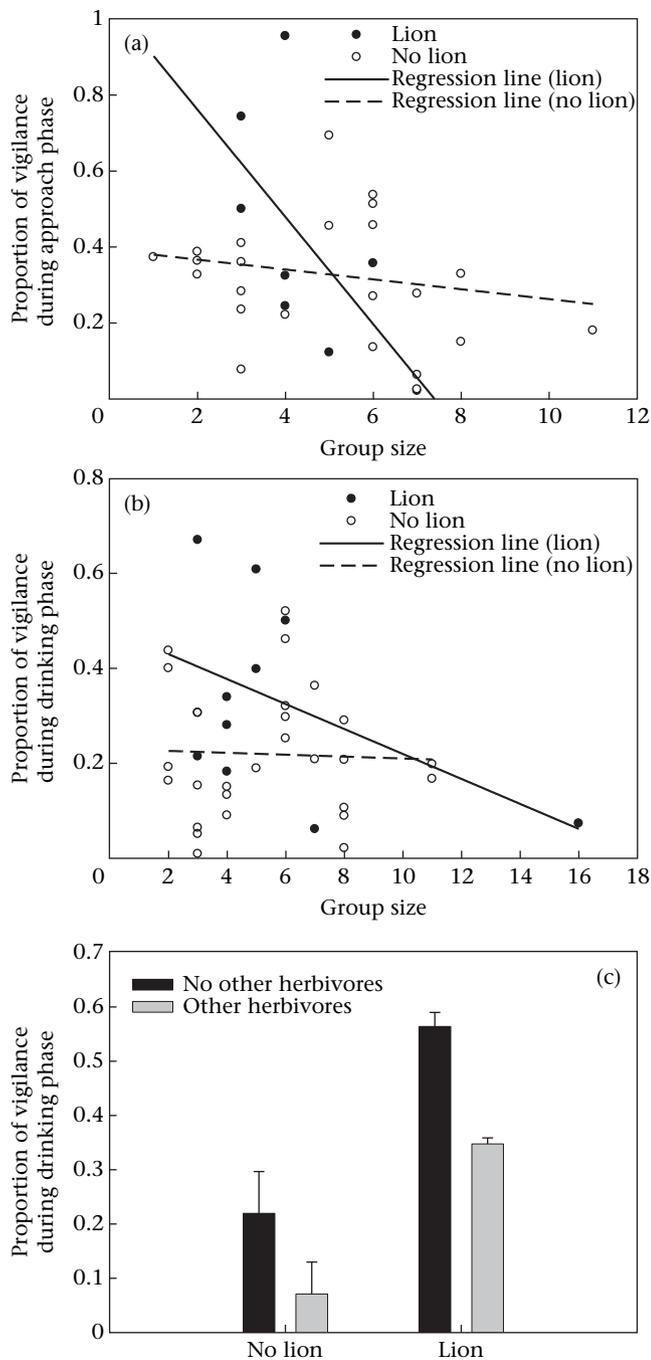
Figure 3. Relationships between the proportion of time spent on vigilance by kudus at waterholes in Hwange National Park and (a) the presence of lions and kudu group size during the approach phase, (b) the presence of lions and kudu group size during the drinking phase, and (c) the presence of lions and the presence of other herbivores during the drinking phase (mean + SE). Estimates from models were back transformed.

generally did the opposite. It is possible that different prey might have different strategies to regulate their vigilance because they differ intrinsically in their morphology and physiology, and extrinsically in their vulnerability to predation. These interspecific differences merit further research.

The presence of lions did not influence the proportion of time spent drinking. Whereas giraffe in large groups devoted significantly more time to drinking (group size effect) kudu in large groups devoted significantly less time to drinking. The latter result could be caused by increased intraspecific interactions.

Kudu was the only species to adjust its vigilance to lion presence significantly. In HNP, kudu is the lion's second most frequent prey (after buffalo) representing 11–24% of lion kills (Loveridge et al. 2007b). Hence it is not surprising that kudu was the most responsive species to the immediate risk of predation by lions in our study. Giraffes are particularly vulnerable to predators when drinking because of the splay-legged posture they adopt. They generally spent the longest time drinking and showed the highest vigilance levels. Possibly they are already close to vigilance peak. Giraffes increased the frequency of vigilance bouts when lions were in the vicinity during the drinking phase, which was close to translating into a significantly higher proportion of time devoted to vigilance. The case of zebras is different, as they are grazers, and usually stay in the grasslands to feed. They are accustomed to open environments and might be less stressed in open waterhole areas. This is consistent with previous findings that for zebras the probability of drinking was not influenced by any of the indices of the risk of predation that we recorded (Valeix et al. 2007).

In this study, the vigilance behaviour of prey was observed not just in reference to indirect risk factors (such as distance to cover) but specifically in the presence/absence of the predator. Our findings therefore clearly illustrate how the vigilance and drinking behaviour of a substantial prey item for lions (kudu) is specifically influenced by the presence of its predator, together with number of conspecifics and presence of heterospecifics.

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