

Does the risk of encountering lions influence African herbivore behaviour at waterholes?

Marion Valeix · Hervé Fritz · Andrew J. Loveridge ·
Zeke Davidson · Jane E. Hunt · Felix Murindagomo ·
David W. Macdonald

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Abstract A central question in the study of predator–prey relationships is to what extent prey behaviour is determined by avoidance of predators. Here, we test whether the long-term risk of encountering lions and the presence of lions in the vicinity influence the behaviour of large African herbivores at waterholes through avoidance of high-risk areas, increases in group size, changes in temporal niche or changes in the time spent in waterhole areas. In Hwange National Park, Zimbabwe, we monitored waterholes to study the behaviour of nine herbivore species under different risks of encountering lions. We radio-collared 26 lions in the study area which provided the opportunity to monitor whether lions were present during observation sessions and to map longer-term seasonal landscapes of risk of encountering lions. Our results show that the preferred

prey species for lions (buffalo, kudu and giraffe) avoided risky waterholes. Group size increased as encounter risk increased for only two species (wildebeest and zebra), but this effect was not strong. Interestingly, buffalo avoided the hours of the day which are dangerous when the long-term and short-term risks of encountering lions were high, and all species showed avoidance of waterhole use at night times when lions were in the vicinity. This illustrates well how prey can make temporal adjustments to avoid dangerous periods coinciding with predator hunting. Additionally, many herbivores spent more time accessing water to drink when the long- and short-term risks of encountering lions were high, and they showed longer potential drinking time when the long-term risk of encountering lions was high, suggesting higher levels of vigilance. This study illustrates the diversity of behavioural adjustments to the risk of encountering a predator and how prey respond differently to temporal variations in this risk.

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M. Valeix · A. J. Loveridge · Z. Davidson · J. E. Hunt ·
D. W. Macdonald
Wildlife Conservation Research Unit,
Zoology Department, Oxford University,
Tubney House,
Abingdon OX13 5QL, UK

F. Murindagomo
Zimbabwe Parks and Wildlife Management Authority,
P.O. Box CY140, Causeway,
Harare, Zimbabwe

M. Valeix (✉) · H. Fritz
Université de Lyon, CNRS Université Claude
Bernard Lyon 1 UMR 5558,
Laboratoire Biométrie et Biologie Evolutive,
Bât Gregor Mendel 43 Bd du 11 novembre 1918,
69622 Villeurbanne cedex, France
e-mail: mvaleix@yahoo.fr

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Introduction

To reduce the risk of predation, prey make behavioural decisions to decrease the probabilities of encounter, attack and capture, and the time spent vulnerable to predation (Lima and Dill 1990). The two major and most studied behavioural adjustments are group formation and vigilance (Lima 1995; Roberts 1996). 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) but also a lower risk of being preyed upon because of a “dilution effect” (Hamilton 1971; Dehn 1990). Additionally, increased vigilance allows earlier detection of an approaching predator and is a common and important response to predation risk (Underwood 1982; Hunter and Skinner 1998; Liley and Creel 2008). However, behavioural responses to predation are many and diverse. For example, they include avoidance of risky environments and spatial redistribution of animals (Ripple and Beschta 2004; Valeix et al. 2009), and selection of specific habitat types and features (Creel et al. 2005). Additionally, prey may make temporal adjustments to avoid dangerous periods coinciding with predator hunting (Fenn and Macdonald 1995; Roth and Lima 2007).

All these behavioural adjustments to predation may be particularly prevalent around scarce and patchily distributed resources, around which prey have no option but to aggregate, and consequently by which predators are likely to be attracted. In arid and semi-arid savannas, surface-water resources become depleted as the dry season progresses, resulting in scarcity and consequently in high levels of animal aggregation (Thrash et al. 1995). In such ecosystems, the distribution of herbivores in the landscape is largely influenced by the distribution of surface water in the dry season (Valeix et al. 2009), and predators, such as the African lion (*Panthera leo*), thus have a greater chance of encountering potential prey at these water sources. Indeed, 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 should be particularly alert in such areas, and employ behavioural adjustments to minimise the risks of predation.

It seems likely that it would be adaptive for prey to vary their behaviour in accordance with perceptions of risk at multiple temporal scales. Recently, elk (*Cervus elaphus*) herd size was found to increase as distance to protective cover increased (as expected from the “many eyes” and “dilution” effects). However, this only occurred on days when wolves (*Canis lupus*) were absent. Interestingly, when wolves were present, herd size remained small at all distances from cover (Creel and Winnie 2005). These findings strongly suggest that prey respond differently to temporal variations in the risk of predation.

Whereas the present study focuses on the responses of prey to the risk of encountering a predator, predators also respond to prey distribution and behaviour. Large mammalian prey and predators thus respond to one another in behaviourally sophisticated ways since the predator attempts to maximise its success rate on prey that actively avoid predation (e.g. van Balaan and Sabelis 1993). Owing to the reciprocal evolutionary effects that predators and

prey have on one other, predator–prey relationships are extremely complex and often considered in the context of game theory (Brown et al. 1999).

Here, we studied the influence of long-term and short-term risks of encountering lions on the behaviour of several large African herbivore species at waterholes in Hwange National Park, Zimbabwe. We used GPS radio collars that recorded the location of lions to map a long-term landscape of encounter risk, which can be compared to a cumulative understanding of encounter risk, and to test whether herbivore behaviour at a waterhole was influenced by the long-term probability of encountering lions. We also used GPS radio-collar data to test whether herbivore behaviour changed on days when lions were locally present or absent. We tested four hypotheses: (1) that herbivores avoid the waterholes located in risky areas or where lions are present; (2) because lions are largely nocturnal (Schaller 1972), high-risk hours encompass night as well as dawn and dusk for herbivores. Herbivores should thus avoid use of waterholes during such dangerous hours when the probability of encountering lions is high or when lions are in the vicinity; (3) groups are larger in riskier areas or when lions are in the vicinity; and (4) herbivores are more vigilant under high encounter risk and consequently are expected to spend longer time approaching water in riskier areas or when lions are in the vicinity.

Our study was carried out during 2 years of contrasted rainfall (a normal rainy season and a drought), which provided an opportunity to investigate the trade-off between exposure to risk of predation by lions and necessity to access water. In Hwange National Park, African buffalo (*Syncerus caffer*) is the most frequently taken prey species (making up 30–35% of lion kills, whereas it represents only 2% of herbivore groups and 13% of individuals encountered), followed by greater kudu (*Tragelaphus strepsiceros*) (11–24% of lions kills, whereas it represents only 10% of herbivore groups and 8% of individuals encountered), and giraffe (*Giraffa camelopardalis*) (8–10% of lion kills, which is in proportion with its availability) (Loveridge et al. 2007a). We therefore investigated whether these preferred prey species adjusted their behaviour more than others to the risk of encountering lions, or whether lions select these prey species specifically because they do not adjust their behaviour as much as other prey.

Materials and methods

Study site

Hwange National Park (HNP) covers c. 15,000 km² of semi-arid dystrophic savanna in north-western Zimbabwe

(19°00' S, 26°30' E). Altitude varies from 800 to 1,100 m. The vegetation is primarily woodland and bushland savanna (64%) and plant communities are dominated by *Colophospermum mopane*, *Combretum* spp., *Acacia* spp., *Baikiaea plurijuga* and *Terminalia sericea* (Rogers 1993). The long-term mean annual rainfall is 606 mm, which falls primarily between October and April. Annual rainfall was 362.6 mm in 2003 and 695.8 mm in 2004, which are the years corresponding to our study. The surface water available to animals is found in natural as well as artificial waterholes. We preliminarily compared the distribution of lion kill sites to the distribution of the study area with regard to the distance to water. This preliminary analysis revealed that the two distributions differed significantly ($\chi^2=103.3$; $df=9$; $p<0.0001$) and that most lion kills occur within 2 km of a waterhole (Fig. 1). Further, other analyses showed that habitat selection is more or less influenced by the distance to a waterhole depending on the herbivore species (Valeix et al. 2009; Appendix). For species that generally make no or very little use of areas far from waterholes (e.g. wildebeest (*Connochaetes taurinus*), roan (*Hippotragus equines*)), the per capita risk of predation may not be higher close to waterholes. However, for the other herbivores (e.g. giraffe, kudu, impala (*Aepyceros melampus*)), these preliminary analyses revealed that waterhole areas are particularly dangerous. Lion density is estimated around 2.7 lions/100 km² in the northern region of HNP (Loveridge et al. 2007b). We studied the influence of the risk of encountering lions on nine water-dependent herbivore species: African buffalo, giraffe, impala, greater kudu, roan antelope, sable antelope (*Hippotragus niger*), warthog (*Phacochoerus aethiopicus*), blue wildebeest and plains zebra (*Equus quagga*).

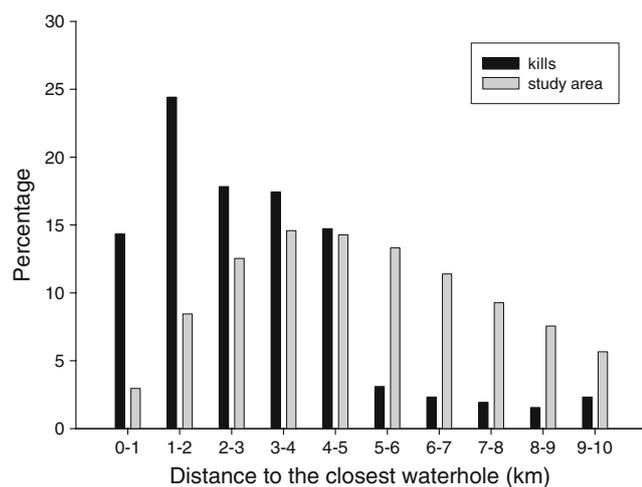


Fig. 1 Distribution of lion kills ($n=261$) and of the study area (7,000 km²) with regard to the distance to the closest waterhole. The two distributions differ significantly ($\chi^2=103.3$; $df=9$; $p<0.0001$)

Data

Since 2002, lions have been closely monitored in the northern part of HNP (c. 7,000 km²), of which 17 female and ten male adults were instrumented with GPS Simplex radio collars (female=900 g, male=950 g; Televilt Positioning AB, Lindesberg, Sweden; see Loveridge et al. 2007b for details; precision=10 m). Positional data from the GPS Simplex radio collars were downloaded regularly and animals' locations were available since 2003. For each individual, one location was available hourly from 18h00 to 07h00, plus fixes at 09h00 and 16h00.

Waterholes were monitored throughout the dry season, from early May to late October when the first significant rains fell. Observations included 12-h and 24-h surveys at 11 waterholes in 2003 (1,644 observation hours) and eight waterholes in 2004 (1,680 observation hours). The observations were done from a tourism platform, from a hide in a tree, or from a car parked at sufficient distance not to disturb the animals. For all herbivores entering a 100-m radius around the waterhole (the waterhole area), we recorded the time at which they entered the waterhole area, the group size and composition, and we measured (1) the time spent accessing water as the difference between the time when the herd entered the waterhole area and the time when the first herbivore of the herd drank (hereafter referred to as the 'approach time'), (2) the potential drinking time as the difference between the time when the first herbivore of the herd drank and the time when the last herbivore of the herd stopped drinking, and (3) the time spent in the waterhole area after drinking as the difference between the time when the last herbivore of the herd stopped drinking and the time when the last herbivore of the herd left the waterhole area (hereafter referred to as the 'time after drinking').

Most lion groups were collared in the study area (80% of the lion groups seen during the observations at waterholes included one collared individual). Because there are factors other than lion presence that characterise predation risk (e.g. activity of other predators, habitat characteristics; see Hebblewhite et al. 2005), our work is restricted to the study of the short-term and long-term probability of lion presence (hereafter short-term and long-term encounter risk). No accurate data on the spatial ecology of other large predators was available to allow us to consider them in this study. However, lions contribute to the major share of herbivores killed across a wide body size range (Owen-Smith and Mills 2008) and consequently should have a detectable influence on the behaviour of most herbivores.

We used data from the lion GPS radio collars to build seasonal landscapes of encounter risk, integrating histor-

ical information on lion presence calculated over the past 4 months. To build such landscape, we calculated the consecutive 10% isopleths kernel, using the reference smoothing factor h_{ref} as recommended by Hemson et al. (2005), for each individual lion using Ranges 7 (version 0.811, South and Kenward 2006). Where gaps in the data set occurred, owing to poor satellite detection, we used averaged isopleths kernels over all the locations available for individuals who were confirmed to be alive and present in the area during the specified period (19% of seasonal home ranges). We then approximated the probability of a lion presence by $0.10/(A_i - A_{i-1})$; with A_i the area of the surface of isopleths i and 0.10 because 10% of all locations are located between two consecutive isopleths. For each waterhole, the value derived from the seasonal landscape of encounter risk was used as a proxy for long-term risk of encountering lions (see also Valeix et al. 2009).

Short-term encounter risk was quantified by presence of lions within 2 km of the study waterhole (herbivores are likely to react to lion presence in such radius; Valeix et al. 2009) in the preceding 24 h, as revealed by fine-scale spatio-temporal data collected by the lion GPS radio collars and by direct observations during the waterhole monitoring. We contrasted observation sessions characterised by ‘lion presence’ and ‘lion not detected’, a conservative approach insofar as the effects of any undetected lions will work against our hypotheses. The number of herbivore groups/individuals observed for each situation is provided in Table 1. Preliminary analyses revealed that group size and abundance of herbivores were significantly correlated for all study species (all $p < 0.05$).

Table 1 Number of herbivore groups and individuals recorded at waterholes

Species	Total number of groups/individuals	Number of groups/individuals when lions were absent	Number of groups/individuals when lions were present
Buffalo	268/11,235	224/9,467	44/1,768
Giraffe	708/1,643	618/1,450	90/193
Impala	474/5,893	323/3,984	151/1,909
Kudu	543/2,255	441/1,849	102/406
Roan	121/310	95/236	26/74
Sable	243/971	189/774	54/197
Warthog	321/890	221/594	100/296
Wildebeest	146/2,647	118/1,934	28/713
Zebra	879/5,988	708/4,679	171/1,309

Data recorded during 32 waterhole monitoring sessions with lions and 32 waterhole monitoring sessions without lions

Analyses

Use of waterholes: visit rate and group size

We first tested whether herbivores avoided visiting waterholes located in areas of high long-term encounter risk, by using mixed models. For each species, we performed a covariance analysis on the number of groups and the number of individuals counted per hour at a waterhole, with waterhole identity as a random effect and with the long-term encounter risk as the fixed effect. Because the average long-term encounter risk was significantly higher in 2003 than in 2004 ($F_{1,171} = 16.13$; $p < 0.0001$), the analyses were run separately for each year to avoid any confounding effect. We also tested whether herbivores avoided waterholes when lions were in the vicinity in the preceding 24 h by comparing the number of groups and the number of individuals counted per hour at a waterhole depending on whether or not lions were known to be present. We preliminarily tested for equality of variance between the two groups (lion present and lion absent) and we used the pooled t statistics when there was equality of variance, and the Satterthwaite t statistics when there was inequality of variance.

We finally tested whether group size changed as a function of year, long-term encounter risk and the interaction between the presence of young and long-term encounter risk. We included the latter interaction because the vulnerability of young can influence the behaviour of adults in their group (Berger 1991; Burger and Gochfield 1994). All species group size data followed a Poisson distribution whereas zebra group size data followed a skewed normal distribution. Consequently, for all species except zebra, we used generalised mixed models with waterhole identity as a random effect, and for zebra we used linear mixed models (group sizes were log-transformed to meet normality requirements) with waterhole identity as a random factor. Statistical analyses were performed with SAS software (version 8.2), using MIXED procedure only for zebra and MIXED procedure with the GLIMMIX macro for Poisson distributed data, using a log link function and correcting the models for over-dispersion by a scaling function: deviance⁻¹ (Firth 1991) for all other species. Backward step-wise selection procedure was used with successive removal of non-significant variables. We also tested whether the presence of lion had an effect on group size. Warthog was excluded from group size analyses since they form family groups whose size was not expected to fluctuate much.

Temporal niche

Temporal niche at waterholes was approximated by the arrival time of animals at waterholes. To evaluate whether

herbivores avoided using waterholes during the dangerous hours (night, early morning and late afternoon), we plotted a frequency distribution of herbivore group observations at waterholes by hour using Oriana 2.0 software for circular data. We compared temporal use between waterholes characterised, from the landscape of risk, by high and low chances of encountering lion. The latter were defined as the sites characterised by a long-term encounter risk among the highest quartile, and the former as the sites among the lowest quartile. We carried out the same approach between waterholes where lions were known to be present in the preceding 24 h and waterholes where lions were known to be absent.

Time spent at waterholes

We tested whether the risk of encountering lions influenced the approach time, the potential drinking time and the time after drinking by regressing these times against the long-term encounter risk and the short-term encounter risk separately. We used generalised mixed models with waterhole identity as the random variable. Statistical analyses were performed with SAS software (version 8.2), using MIXED procedure with GLIMMIX macro for Poisson distributed data, then correcting the models for overdispersion by a scaling function: deviance⁻¹ (Firth 1991).

Results

Use of waterholes: visit rate and group size

In 2003, the number of groups and of individuals counted per hour at a waterhole was independent of the long-term encounter risk (all $p > 0.05$). However, in 2004, there was a significant influence for five species. The number of buffalo groups counted per hour at a waterhole decreased as the long-term encounter risk increased (estimate \pm SE = -5.22 ± 2.49 ; $F_{1,68} = 4.44$; $p = 0.03$; $r^2 = 0.27$; waterhole identity accounted for 18% of the total variance ($p = 0.09$), but surprisingly the number of buffalo individuals did not change significantly with the long-term encounter risk. For roan, sable, wildebeest and zebra, the number of groups and individuals counted per hour at a waterhole increased as the long-term encounter risk increased.

There was a significant difference in the number of groups per hour at a waterhole depending on the presence or absence of lions for three species with more frequent use of waterholes without lion (Fig. 2a): buffalo (Satterthwaite t test— $t_{1,57} = 1.62$; $p = 0.10$; groups per hour at waterholes with lions = 0.06 ± 0.01 (S.E.), and without lion =

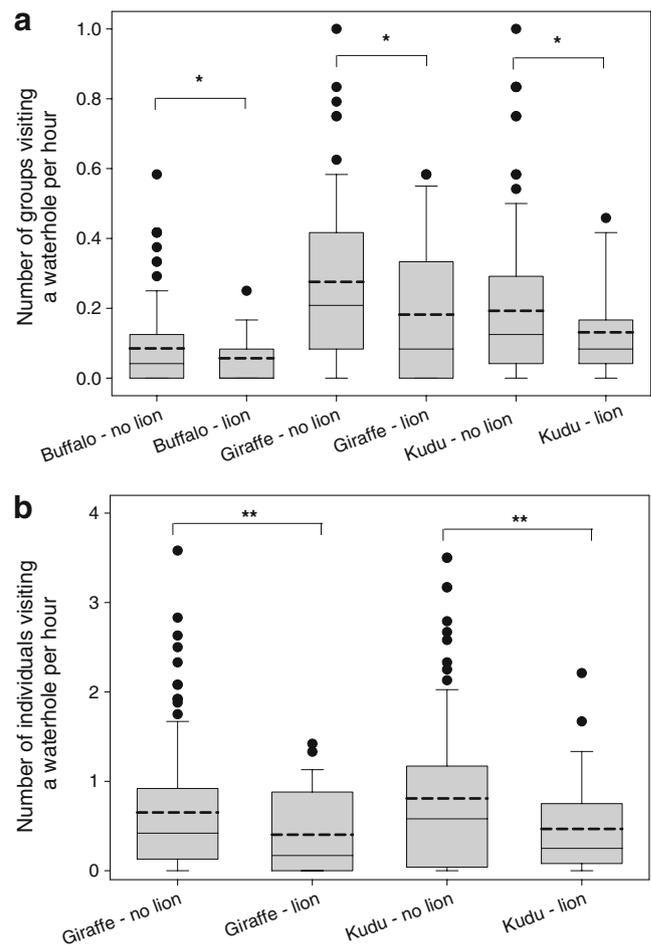


Fig. 2 Mean number of **a** groups and **b** individuals visiting a waterhole per hour according to the absence (“no lion” on the x-axis)/presence (“lion”) of lions in the vicinity of the waterhole. Boxes show medians, 25% and 75% quartiles. Bold dashed lines indicate means. Whiskers indicate the range between 10% and 90% percentiles. Dots represent data outside this range. The level of significance of the t test is indicated with * when the test is significant at the level $p < 0.1$ and ** at the level $p < 0.05$

0.09 ± 0.01 ; $r^2 = 0.01$), giraffe (pooled t test— $t_{1,152} = 1.74$; $p = 0.08$; groups per hour at waterholes with lions = 0.18 ± 0.04 , and without lion = 0.28 ± 0.02 ; $r^2 = 0.02$) and kudu (Satterthwaite t test— $t_{1,57} = 1.89$; $p = 0.06$; groups per hour at waterholes with lions = 0.13 ± 0.03 , and without lion = 0.19 ± 0.02 ; $r^2 = 0.01$). Similar results were found for the number of individuals per hour at a waterhole (Fig. 2b) for giraffe (Satterthwaite t test— $t_{1,54} = 2.28$; $p = 0.03$; individuals per hour at waterholes with lions = 0.40 ± 0.09 , and without lion = 0.65 ± 0.06 ; $r^2 = 0.02$) and kudu (Satterthwaite t test— $t_{1,64} = 2.48$; $p = 0.02$; individuals per hour at waterholes with lions = 0.47 ± 0.11 , and without lion = 0.81 ± 0.09 ; $r^2 = 0.02$).

Group size increased as the long-term encounter risk increased whether groups had young or not for wildebeest

(estimate \pm SE=20.87 \pm 8.49; $F_{1,138}=6.04$; $p=0.0152$; $r^2=0.10$; waterhole identity accounted for 1% of the total variance ($p=0.18$) and zebra (estimate \pm SE=6.81 \pm 2.10; $F_{1,865}=10.47$; $p=0.0013$; $r^2=0.03$; waterhole identity accounted for 2% of the total variance ($p=0.10$)). Additionally, there was a significant effect of year with groups being smaller in 2003 than in 2004 for three species (buffalo, giraffe and kudu). There was no significant effect of lion presence on group size for all species (all $p>0.05$) except wildebeest, which came in larger groups when there were lions in the vicinity of the waterhole ($F_{1,138}=5.05$; $p=0.0263$).

Temporal niche

All study herbivore species are rather diurnal but the data showed that most species appeared to avoid night times when the short-term encounter risk was high, i.e. when lions were in the vicinity of waterholes (Fig. 3). No such clear pattern was revealed by the comparison of low and high long-term encounter risk. Further, a focus on the day patterns only showed that buffalo were less frequently recorded at waterholes during high-risk hours of the day (dawn and dusk) when the long-term encounter risk was high (with 65% of buffalo groups that came during the “safe” hours when the long-term encounter risk was high, against only 26% when the long-term encounter risk was low; Fig. 4a) and when the short-term encounter risk was high (with 59% of buffalo groups that came during the “safe” hours when there were lions in the vicinity, against only 19% when there were no lion in the vicinity of the waterhole; Fig. 4b).

Time spent at waterholes

The predominant result is an increase in the time spent approaching waterholes and in the potential drinking time as the long-term encounter risk increases for most herbivores (Table 2). Additionally, responses in approach time to the short-term encounter risk mainly indicate longer potential drinking times when lions were in the vicinity (Table 2). Finally, impala and kudu spent less time in the waterhole areas after drinking when the long-term encounter risk was high (Table 2). Models provided significant but low fit (r^2 ranging from 0.05 to 0.21).

Discussion

The risk of predation is thought to exert a strong influence over the foraging behaviour of potential prey (see review by Lima and Dill 1990), with most individuals avoiding areas

where the risk of predation is high (e.g. Kotler et al. 1991; Doncaster 1994; Barreto and Macdonald 1999; Ward et al. 2000). However, this has to be balanced against their need to gain access to sufficient resources (McNamara and Houston 1987). This may be exacerbated in many African savanna herbivores that need to access critical water resources on an almost daily basis, with this dependence being strongly influenced by seasonal rainfall differences. In our study, buffalo was the only species that appeared to avoid risky waterholes characterised by a high long-term risk of encountering lions. Interestingly, they avoided risky waterholes only in 2004, possibly because 2003 was a severe drought (it was the second of two consecutive dry years), suggesting that buffalo were forced into shifting the trade-off between exposure to risk of encountering lions and necessity to access water. Thus, in years when water access is not limited, they can afford to avoid riskier waterholes. Furthermore, buffalo have large home ranges (>300 km²; Ryan et al. 2006) and thus in HNP, where water resources are widely spaced, especially in the dry season, they are able to avoid high-risk areas by travelling greater distances to waterholes. We suggest that buffalo may avoid the places where lions have been for the past months or where they have had recent interactions with lions. Presumably the lions, when not constrained by their home range boundaries, move to areas currently occupied by buffalo, their preferred prey species. This in turn causes the buffalo to shift to a new location to reduce the risk of encountering lions. Species other than buffalo did not avoid waterholes characterised by a high long-term encounter risk possibly because they can travel between and access only one or two waterholes or because of small home ranges, sometimes having no option but to use risky ones (with the exception of giraffe). Also, our results for grazers other than buffalo show a correlation between their abundance and the probability of encountering lions. Such result strongly suggests that lions select waterholes characterised by a high abundance of sedentary herbivores. This illustrates the other side of the predator–prey reciprocal behavioural adjustments to each other.

Drinking is an activity when giraffe are particularly vulnerable to predators because of the splay-legged posture used when drinking. Consequently, it is not surprising that giraffe appear to avoid waterholes when there are lions in the vicinity. This result is consistent with previous findings on giraffe behaviour at waterholes showing that their decision to drink is influenced by proxies of the risk of predation, such as group size and distance to cover (Valeix et al. 2007). Our results showed that buffalo and kudu also avoided waterholes when lions were in the vicinity. These results are consistent with the fact that buffalo, kudu and giraffe are the preferred prey for lions in HNP (Loveridge et al. 2007a), and may attempt to avoid areas where lions

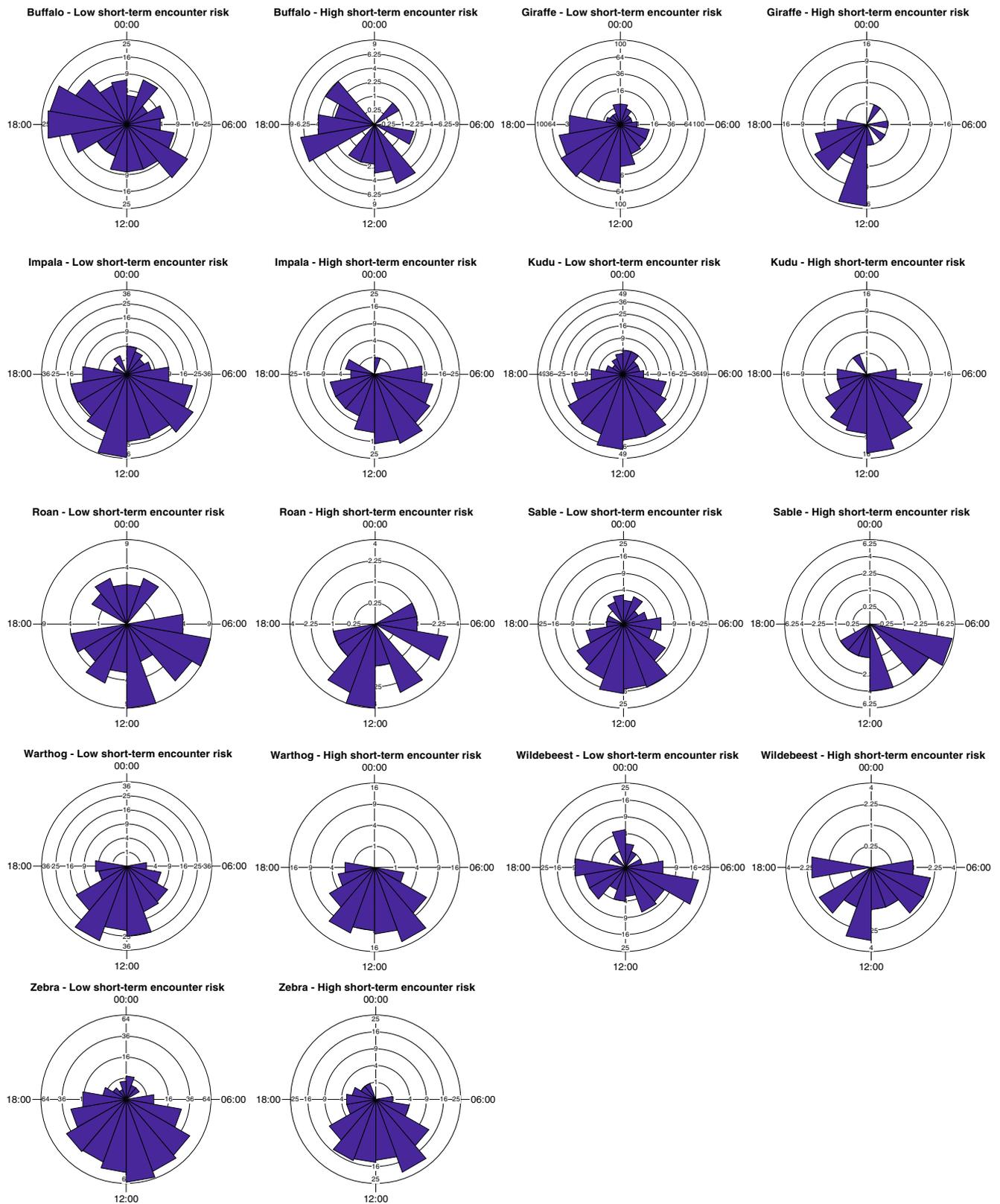


Fig. 3 Waterhole temporal use by herbivores at waterholes characterised by low or high short-term risk of encountering lions. Each bar length represents the number of groups that came during each hour and the area of each bar is proportional to the frequency of group visits

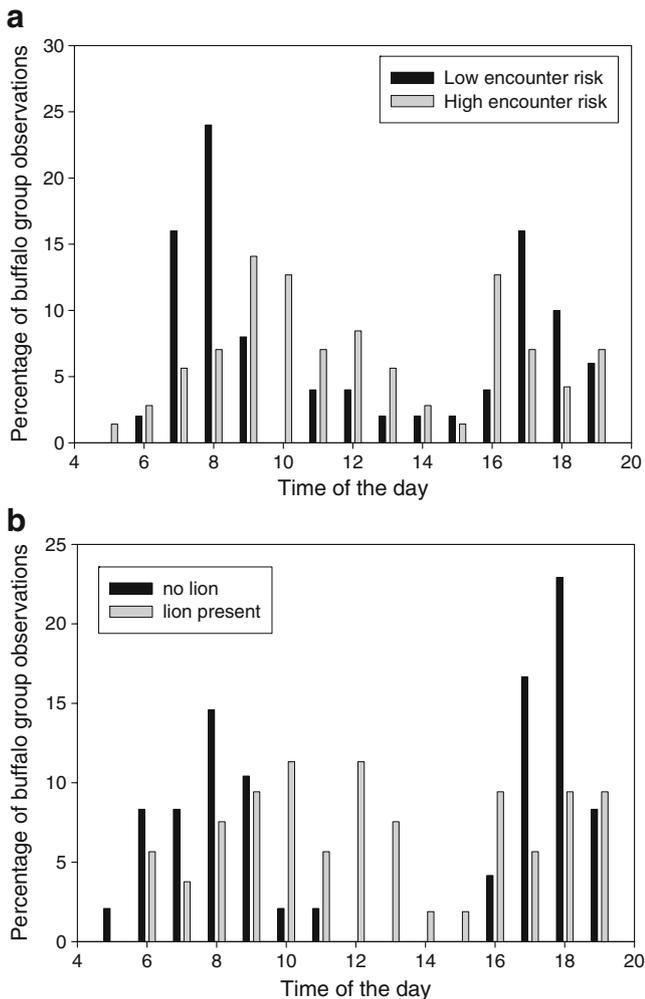


Fig. 4 Waterhole temporal use by buffalo during the day time only at waterholes characterised by **a** low and high long-term risk of encountering lions, and **b** low and high short-term risk of encountering lions

have been recently or are presently more than other prey species. Whilst the risk of encountering lions had a significant influence on the visit rates of buffalo, giraffe and kudu, the effect size was generally small ($r^2 \leq 0.27$), possibly because visit rates at a given waterhole result from several other factors (e.g. proximity of other water sources, quality of the water, presence of other predators, presence of conspecifics).

In addition to avoidance of risky areas, prey may limit their temporal overlap with predators and may exploit sub-optimal activity periods to reduce vulnerability to predation (e.g. Kotler et al. 2004; Fenn and Macdonald 1995; Roth and Lima 2007). Indeed, time can be considered as a niche dimension over which animals can minimise the risk of predation. Lion activity peaks are after 17h00 and before 08h00 (Schaller 1972). Periods between 17h00 and 08h00 are consequently more dangerous for herbivores. In our

study, when the long-term or short-term encounter risk was low, the activity peaks of buffalo at waterholes were before 8h00 and after 17h00 with nearly no use in the middle of the day. In contrast, buffalo used waterholes mainly during the middle of the day when the long-term or short-term encounter risk was high. This result strongly suggests that buffalo avoid the hours of the day which are dangerous when the risk of encountering lions is high. It corroborates a previous finding showing that the percentage of buffalo that are standing and vigilant at night is greater than during the day (Prins and Iason 1989). In our study, the avoidance of waterhole use at night times by most herbivores when lions are the vicinity of the waterhole illustrates well the temporal niche shift to reduce the risk of predation.

The general understanding is that prey group size increases with heightened risk of predation, because an individual's risk of predation decreases as a result of the combination of collective vigilance and a dilution effect (Lima 1995; Roberts 1996). Lions prefer to hunt prey that are in small groups (Scheel 1993), so prey forming larger groups in riskier environments appears to be an adaptive anti-predator response. However, our results did not show a strong effect of both long-term and short-term encounter risks on group size. This may be explained by the diversity of other factors that affect group size in herbivores such as forage abundance and quality (Fryxell 1991; Brashares and Arcese 2002), social organisation (Jarman 1974), competition (Bednekoff and Lima 2004) and type of habitat (Creel and Winnie 2005). Even if not strong, our results suggest that the long-term encounter risk may have some effect on wildebeest and zebra group size. These species are open grassland grazers and open grassland areas are scarce and often associated with waterhole areas (Rogers 1993). Consequently, wildebeest and zebra tend to remain in waterhole areas most of the time and therefore their movement is generally within these areas. One explanation to the pattern revealed could be that they form larger groups before approaching the waterhole to drink. However, the weakness of the relationships between encounter risk and group size revealed in this study strongly suggests that other anti-predator strategies may be more important.

It has been previously suggested that the time spent around waterholes is influenced by the perceived risk of vulnerability to predation (group size, distance to cover, presence of young) as well as by thermoregulatory constraints (Valeix et al. 2007). This study goes one step further in the investigation of the role of predation by taking lion presence into account, and confirms that the risk of encountering a predator influences the time spent by herbivores in their approach to water, potential drinking time or to a lesser extent leaving the waterhole area. Our results revealed some significant effect of the risk of

Table 2 Results of the mixed models modelling the time spent at waterholes with waterhole identity as a random variable

Species	Long-term encounter risk			Presence of lion		
	Approach time	Potential drinking time	Time after drinking	Approach time	Potential drinking time	Time after drinking
Buffalo	13.87 (± 6.50) <i>F</i> _{1,227} =4.55 <i>p</i> =0.0340 var _{WI} =0.02; <i>p</i> _{WI} =0.08	9.38 (± 3.46) <i>F</i> _{1,214} =7.34 <i>p</i> =0.0073 var _{WI} =0.01; <i>p</i> _{WI} =0.38	NS	NS	NS	NS
Giraffe	18.31 (± 6.18) <i>F</i> _{1,414} =8.78 <i>p</i> =0.0032 var _{WI} =0.02; <i>p</i> _{WI} =0.12	NS	NS	0<1 <i>F</i> _{1,414} =4.51 <i>p</i> =0.0344 var _{WI} =0.01; <i>p</i> _{WI} =0.12	NS	NS
Impala	NS	NS	-23.41 (± 10.70) <i>F</i> _{1,286} =4.78 <i>p</i> =0.0295 var _{WI} =0.02; <i>p</i> _{WI} =0.05	0<1 <i>F</i> _{1,317} =3.29 <i>p</i> =0.0706 var _{WI} =0.02; <i>p</i> _{WI} =0.06	NS	NS
Kudu	NS	NS	-24.72 (± 5.67) <i>F</i> _{1,349} =19.01 <i>p</i> <0.0001 var _{WI} =0.02; <i>p</i> _{WI} =0.03	0>1 <i>F</i> _{1,376} =4.37 <i>p</i> =0.0372 var _{WI} =0.01; <i>p</i> _{WI} =0.13	0<1 <i>F</i> _{1,371} =5.80 <i>p</i> =0.0165 var _{WI} =0.02; <i>p</i> _{WI} =0.03	NS
Roan	NS	NS	NS	0<1 <i>F</i> _{1,81} =9.05 <i>p</i> =0.0035 var _{WI} =0.02; <i>p</i> _{WI} =0.15	NS	NS
Sable	NS	10.10 (± 5.35) <i>F</i> _{1,197} =3.57 <i>p</i> =0.0602 var _{WI} =0.02; <i>p</i> _{WI} =0.12	NS	NS	NS	NS
Warthog	NS	13.30 (± 4.03) <i>F</i> _{1,233} =10.88 <i>p</i> =0.0011 var _{WI} =0.03; <i>p</i> _{WI} =0.07	NS	NS	NS	NS
Wildebeest	38.42 (± 18.69) <i>F</i> _{1,74} =4.23 <i>p</i> =0.0434 var _{WI} =0.02; <i>p</i> _{WI} =0.13	23.69 (± 6.09) <i>F</i> _{1,74} =15.15 <i>p</i> =0.0002 var _{WI} =0.03; <i>p</i> _{WI} =0.22	NS	NS	NS	NS
Zebra	NS	13.02 (± 3.78) <i>F</i> _{1,669} =11.87 <i>p</i> =0.0006 var _{WI} =0.01; <i>p</i> _{WI} =0.09	NS	0<1 <i>F</i> _{1,696} =3.54 <i>p</i> =0.0605 var _{WI} =0.01; <i>p</i> _{WI} =0.14	NS	NS

The proportion of total variance explained by waterhole identity (var_{WI}) and the significance of this random variable (*p*_{WI}) are indicated. Results are presented as slope estimates (\pm standard error); they are in italic when $0.05 < p < 0.10$ and NS is indicated when $p > 0.10$. For the variable “presence of lion”, 0 represents absence of lion and 1 presence of lion; 0>1 and 0<1 indicate that the time spent when lion were absent was longer and shorter respectively than the time spent when lion were present

encountering lions on the time spent around waterholes. These effects were not very strong (r^2 ranging from 0.05 to 0.21) showing that many other factors come into play in the behaviour of herbivores at waterholes (e.g. intra- and interspecific competition/facilitation, social interactions, grazing quality in the waterhole area, thermoregulation constraints). Still, the significant results showed consistent trends revealing that many herbivores spent longer time approaching the water and showed longer potential drinking time when the long-term encounter risk increased, strongly suggesting an increased level of vigilance to detect potential predators in waterhole areas that have been characterised by frequent lion presence in the past 4 months. Similarly, some species showed longer approaching time when the short-term encounter risk was high. However, if most herbivores spent longer time to approach the waterhole when lions were in the vicinity (giraffe, impala, roan and zebra), which is consistent with higher level of vigilance, kudu approached the waterhole more rapidly. Some herbivores may have detected the location of lions while entering the waterhole area, thus do not need to frequently scan the surroundings and may ultimately tend to minimise exposure to predation risk. However, our conclusions are limited by the lack of data on vigilance *per se* at waterholes, which will need to be collected in the future to reach a fine understanding of the vigilance response of prey to different temporal scales of perception of predation risk. For example, it is well documented that herbivores in larger group allocate less time to vigilance activities since they can rely on collective vigilance (Lima 1995). Further, theory predicts that individuals at the periphery of a group should be at higher risk than their more central conspecifics since they would be the first to be encountered by an approaching predator, hence the position of an individual within the group is also expected to strongly influence vigilance (Krause 1994). Finally, other activities than drinking and vigilance may play a role, and herbivores may sometimes spend more time in a waterhole area for other activities (e.g. social display may be more efficient in open areas). Consequently, the lack of data on individual patterns of vigilance limits the strength of our conclusions on suggested higher level of vigilance when the risk of encountering a predator is high.

Buffalo are the prey species most frequently killed by lions in HNP, making up 30–35% of all kills recorded (Loveridge et al. 2007a). Interestingly, this study provides evidence that buffalo shows many behavioural adjustments to high risk of encountering lions. First, buffalo avoid waterholes where (1) lions have been most active over the past 4 months or (2) lions have been active in the past 24 h. Second, they shift their use of waterholes towards the middle of the day when they use waterholes characterised

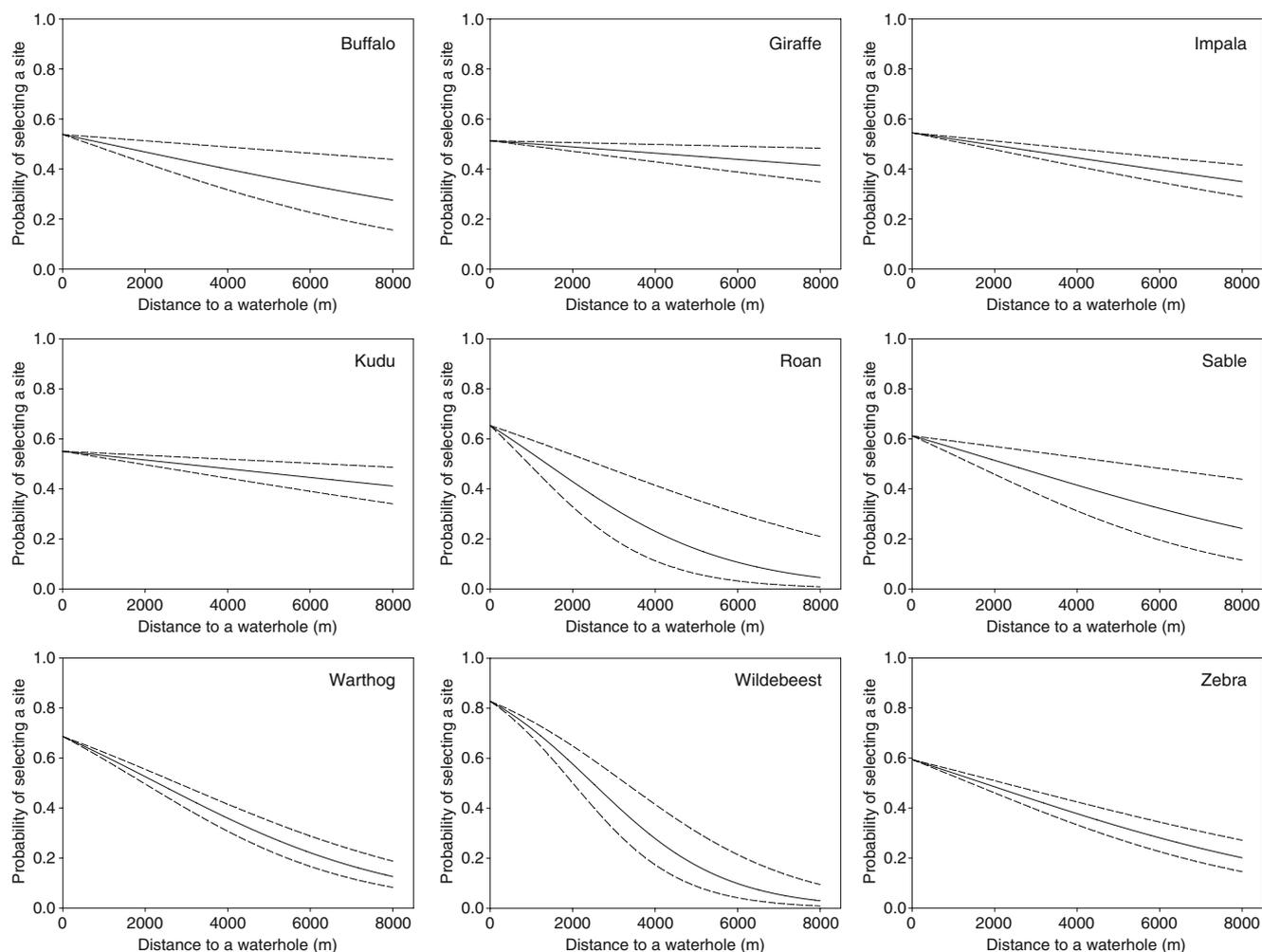
by a high long-term or short-term risk of encountering lions, and they avoid use of waterholes at night if lions have been in the vicinity recently. Third, they appear to be more vigilant when approaching and then drinking at waterholes characterised by high long-term encounter risk. All these findings reveal the diversity of anti-predator responses that buffalo employ at essential sites such as waterholes in semi-arid savannas. Other species showed a less complete array of behavioural adjustments. It is noteworthy that, unlike larger herbivores, smaller herbivores can be preyed upon by carnivores from across the spectrum of body sizes (Owen-Smith and Mills 2008), and the risk of being preyed upon by other predators may therefore have confounding effects on the behaviour of smaller herbivore species.

Our results illustrate that the risk of encountering a predator is a significant factor affecting behaviour patterns of prey species. They reinforce the idea that prey respond differently to different temporal variations in the risk of predation (Creel and Winnie 2005), by strongly suggesting that prey are responding to predation at least at two levels. The first is a cumulative understanding of the risk of encountering a predator with its concomitant responses, and the second is the more immediate predation risk where they respond to the specific situation that confronts them.

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Appendix

Relationship between the distance to the closest waterhole and the probability of selecting a site for the study herbivores. These plots are mainly based on results published in Valeix et al. (2009). *Plain lines* represent the estimate of the resource selection function model and dotted lines the estimate \pm standard error.



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