



## African ungulates and their drinking problems: hunting and predation risks constrain access to water

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Prey make several behavioural adjustments to minimize the risk of predation by their natural predators. When hunted, however, they may have to adjust their behaviour further or differently to cope with this additional mortality risk. Here, we investigated whether African large ungulates would adjust their behaviour in response to hunting risk (i.e. risk of being shot by human hunters). We predicted that they would shift their use of surface water, a key and scarce resource in African savannas, from day hours to night hours to reduce the risk of encountering human hunters. In Hwange National Park, Zimbabwe, we monitored waterholes to record the temporal drinking niche of three nonhunted ungulates (i.e. impala, *Aepyceros melampus*, greater kudu, *Tragelaphus strepsiceros*, sable antelope, *Hippotragus niger*). We also monitored waterholes in hunting areas in the vicinity of Hwange National Park. In Hwange National Park, the three species avoided waterholes at night, when the risk of natural predation was higher. Conversely, in the hunting areas, all three species visited waterholes more often at night. Impala and greater kudu, however, were less prone to switch towards night-time use of waterholes in hunting areas compared to sable antelope, although all three species were exposed to similar hunting risk. Our results suggest that hunting may force African ungulates to shift their visits at waterholes from day hours towards night hours, but that the magnitude of this shift may be constrained by the predation risk imposed by large nocturnal carnivores. We conclude that species preyed upon by natural predators adjust their antipredator behaviour in response to the additional risk of predation imposed by hunting.

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With ongoing increase of human disturbance on wildlife habitats, there is growing concern about how disturbance stimuli may affect animal behaviour (Geist 1970; Caro 1999a). Animals respond to human disturbance similarly to predation risk, that is, by adjusting their behaviour in order to reduce the disturbance, for example, by increasing flight initiation distance or vigilance, or by shifting habitats (reviewed in Stankowich & Blumstein 2005). There may be medium- to long-term costs associated with behavioural adjustments (e.g. lower resource intake rate, lower diet quality, or decreased mating opportunities; Lima & Dill 1990; Lima 1998). The repercussions of these nonlethal effects of predation or disturbance (sensu Lima 1998) might therefore alter the fitness of individuals, affect population dynamics (Creel et al. 2007; Creel & Christianson 2008), and ultimately community structure and ecosystem functioning (Brown et al. 1999; Ripple & Beschta 2004).

Hunting may be considered an extreme type of human disturbance as individuals from harvested populations experience a direct risk of mortality. Hunting disturbance disrupts normal activities, alters diurnal activity rhythms and increases flight initiation distances in many waterbird species (reviewed in Madsen & Fox 1995). In large ungulates, studies have reported increased flight initiation distance in response to hunting disturbance (reviewed in Stankowich 2008). However, much less is known about long-term behavioural responses such as shifts in habitat use (Swenson 1982) and feeding sites (Benhaiem et al. 2008), or changes in activity patterns (Kufeld et al. 1988).

Here we address an example of long-term behavioural adjustment to hunting in large game ungulates. We assessed whether ungulates adjust their temporal use of key and scarce resources in response to hunting risk (i.e. risk of being shot by human hunters). A common behavioural response of prey to predation risk is to avoid risky areas where predators are abundant (Ripple & Beschta 2004; Creel et al. 2005; Valeix et al. 2009a). In certain circumstances, however, spatial avoidance of predators may not be possible, particularly when prey have no choice but to use risky

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areas to access rare and scattered resources where predators might look for them. Under such situations, prey may shift their niche along the time axis to reduce temporal overlap with predator activity (reviewed in Kronfeld-Schor & Dayan 2003). While such temporal adjustments have been illustrated in some predator–prey studies (Kotler et al. 1991; Fenn & Macdonald 1995; Roth & Lima 2007; Valeix et al. 2009b), much less has been reported on hunted species (but see Kilgo et al. 1998; Sunde et al. 2009), particularly on how hunting risk may affect resource utilization.

Semiarid African savannas are excellent ecosystems to investigate how hunting risk may constrain temporal access of ungulates to scarce water resources. First, hunting is very common in Africa, more particularly sport hunting (Lindsey et al. 2007), or recreational hunting practised by paying tourists. Yet, only few studies have reported behavioural adjustments in response to hunting risk in African ungulates (Caro 1999b; Matson et al. 2005; Setsaas et al. 2007) compared to ungulates from the northern hemisphere (e.g. reindeer, *Rangifer tarandus*; reviewed in Reimers & Colman 2006). Second, surface water is limited in African semiarid savannas. Hence, even though the risk of encountering predators (Valeix et al. 2009a, b) and human hunters (e.g. Harrison & Bates 1991, for ungulates in deserts of the Middle East) may be high, most ungulates have to come to waterholes almost daily to satisfy their drinking requirements. Third, the richness of African ungulate communities provides the opportunity for original comparative studies. While behavioural changes in harvested populations may be used as indicators of species sensitivity to human hunting, Gill et al. (2001) stressed that behavioural indicators might not always adequately reflect animal response to human disturbance. For instance, animals of lower condition, or that undergo higher constraints on resource requirements, are less likely to adjust their behaviour in response to human disturbance (e.g. Beale & Monaghan 2004). Likewise, behavioural response to hunting risk may expose ungulate species to their natural predators (e.g. Kilgo et al. 1998). Species that are therefore more vulnerable to natural predators might be less likely to adjust their behaviour to human hunting risk. Multispecies studies are rare and greatly needed to understand how specific ecological constraints may influence behavioural responses to human hunting.

We investigated how different African ungulate species (impala, *Aepyceros melampus*, greater kudu, *Tragelaphus strepsiceros*, sable antelope, *Hippotragus niger*) adjust their temporal use of waterholes in response to hunting risk. We hypothesized that ungulates would shift their temporal use of waterholes to night-time in hunting areas to decrease temporal overlap with human hunters, in comparison to protected areas where ungulates drink mainly during daytime (Valeix et al. 2007a). We expected this shift to be partial, notably because of the constraint exerted by predation risk at night, as the main predators in our study area are mostly nocturnal (i.e. lion, *Panthera leo*: Schaller 1972; spotted hyaena, *Crocuta crocuta*: Kruuk 1972). Furthermore, we predicted the magnitude of the shift to vary according to species vulnerability to natural predation. The species more often preyed upon (i.e. greater kudu) should perform a shift of lower magnitude than the other species.

## METHODS

### Study Site

Hwange National Park (nonHA) in northwestern Zimbabwe (19°00'S, 26°30'E) is approximately 15 000 km<sup>2</sup>. Sport hunting is allowed and practised in governmental safari areas and private concessions around nonHA: Matetsi Safari Area South (MSA South, 1890 km<sup>2</sup>) and Gwayi Intensive Conservation Area South (Gwayi ICA South, ca. 880 km<sup>2</sup>) (Fig. 1). The hunting mode practised in these

hunting areas is sport hunting, and thus harvest usually represents a small fraction of total population size, contrary to culling or uncontrolled poaching. Harvest rates are traditionally set at about 2% of population size for most ungulates in Zimbabwean hunting areas (Cumming 1989). During the study period, we estimated per capita hunting risk based on the ratio of hunting quotas over population size estimates for the three species. We found, as did Cumming (1989), that percentages of harvested individuals were about 2% of population size (i.e. 2.5%, 1.7% and 1.4% for impala, greater kudu and sable antelope, respectively). This implies similar per capita risk of human predation for all ungulate species. These Hunting Areas (HA) act as buffers between the National Park and human settlements where subsistence agriculture is the principal activity and wildlife is only present at low densities (Dunham 2002).

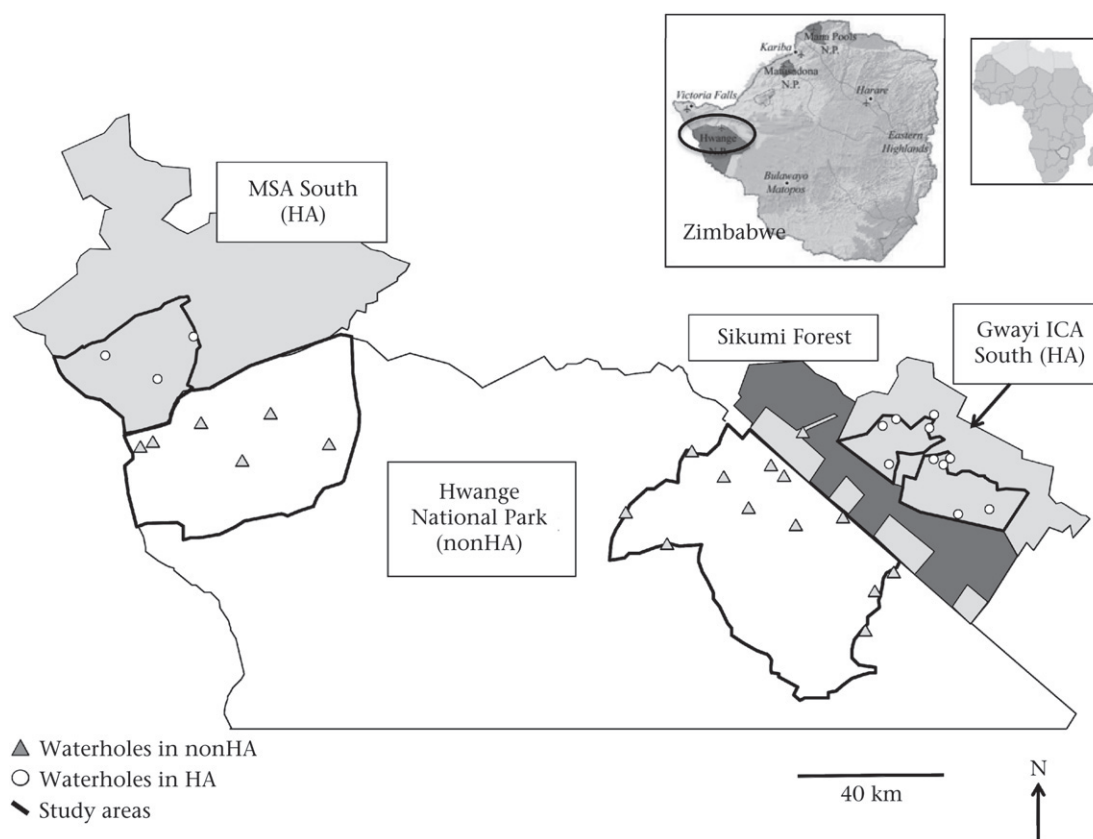
Vegetation is typical of southern African dystrophic wooded and bushed savannas with patches of grasslands, dominated mainly by *Colophospermum mopane*, *Combretum* spp., *Acacia* spp., *Baikiaea plurijuga* and *Terminalia sericea* (Rogers 1993). The rainy season ranges from November to April, and long-term annual rainfall averages 613 mm (Chamaillé-Jammes et al. 2006). Surface water is mainly found in natural and artificially filled waterholes, and in some rare rivers. During the dry season, natural waterholes and rivers dry up and most of the surface water available to animals is found in artificially filled waterholes and river pools.

No sport hunting occurs in nonHA, but the Zimbabwe Parks and Wildlife Management Authority (ZPWMA) allocates quotas to its staff for food rations, mainly on elephants, *Loxodonta africana*, and buffalos, *Syncerus caffer*, while other ungulates have not been allocated since 2007. In the surrounding HA, hunting season ranges from March to December (since the mid-1970s). Ungulates are strictly hunted during daytime, from dawn (around 0600 hours) to dusk (around 1900 hours). Hunters are not allowed to hunt from vehicles, so all hunts are performed on foot. Overall, the abundance of large carnivores appears to be comparable between the study HAs and their adjacent nonHA areas (Elliot 2007; Table 1). Hence, the main difference between HA and nonHA is the predation risk due to hunting by humans. We thus disposed of a contrasted system, where the risk to ungulates in nonHA was exclusively exerted by natural predators and the risk to ungulates in HA originated both from natural predators and human hunters (further information on the different study areas is provided in Table 1).

Our study area covered, in the peripheral HA, the hunting concessions from which we had obtained authorization to conduct wildlife surveys during the study period: Unit 3 in MSA South (ca. 360 km<sup>2</sup>) and four hunting properties in Gwayi ICA South (ca. 300 km<sup>2</sup>) (Fig. 1). In nonHA, we chose to cover the blocks that were adjacent to those hunting concessions: Main camp (ca. 1300 km<sup>2</sup>) and Robins (ca. 1000 km<sup>2</sup>) in the northern part of Hwange National Park (Fig. 1). Therefore, the hunting concessions and their adjacent blocks in nonHA presented similar vegetation types and environmental conditions (i.e. rainfall, temperature, soil characteristics; Ganzin et al. 2008; Peace Parks Foundation 2009).

### Observations

We monitored waterholes in nonHA and surrounding HA in 2007 and 2008 during the hot dry season (August–October). In HA, we selected waterholes on the basis of availability of standing water and signs of recent ungulates presence (i.e. fresh spoor and faeces). We monitored nine waterholes once in 2007 and seven waterholes once in 2008. Only two waterholes were surveyed both years (i.e. 13 different waterholes). In nonHA, each waterhole is surveyed once a year (since the 1970s) by Wildlife and Environment Zimbabwe (WEZ) and ZPWMA. Accounting for vegetation similarities with HA as well as water availability, we randomly selected, from the



**Figure 1.** Hwange National Park (nonHA) and adjacent hunting areas (Gwayi ICA South and MSA south, HA) in Zimbabwe. Study area is delineated by thick black lines.

**Table 1**

Site characteristics and densities of ungulates and large predators in nonhunting areas (NonHA) in Hwange National Park, Zimbabwe, and in hunting areas (HA) in the vicinity of Hwange National Park

	NonHA		HA	
	Main camp	Robins	Gwayi ICA South	Unit 3/MSA South
<b>Site characteristics</b>				
Area (km <sup>2</sup> )	1300	1000	300	360
Waterhole density (nb/100 km <sup>2</sup> )	1.23	1.3	4.34	2.5
Road length (km)	325	400	172	263
<b>Ungulate density (indiv./km<sup>2</sup>)</b>				
Impala	1.43 (0.47)	5.45 (0.31)	–	3.0 (0.15)
Greater kudu	1.59 (0.24)	1.52 (0.36)	–	2.5 (0.20)
Sable antelope	0.22 (0.44)	–	–	1.0 (0.45)
<b>Predator density</b>				
Lions (call-up surveys, indiv./100 km <sup>2</sup> )†	2.8–5.5	*	2–3.9	5.3–7.7
Lions (spoor transects)	2.6	*	2.2	4.5
Hyaena (call-up surveys, indiv./100 km <sup>2</sup> )†	11.3–22.1	*	5.5–10.9	6.5–11.7
Hyaena (spoons/100 km <sup>2</sup> )	27.2	*	11.6	26.5
Leopard (spoons/100 km <sup>2</sup> )	1.2	–	4.2	1.3
Wild dog (spoons/100 km <sup>2</sup> )	0.4	–	1.6	0.2
Cheetah (spoons/100 km <sup>2</sup> )	0.1	–	0.5	1.5

Coefficients of variation associated with ungulate density estimates are given in parentheses and were calculated by distance sampling (Buckland et al. 2001).

\* Density estimates were not available but were comparable to those at the Main Camp (A. J. Loveridge & N. Elliot, personal communication).

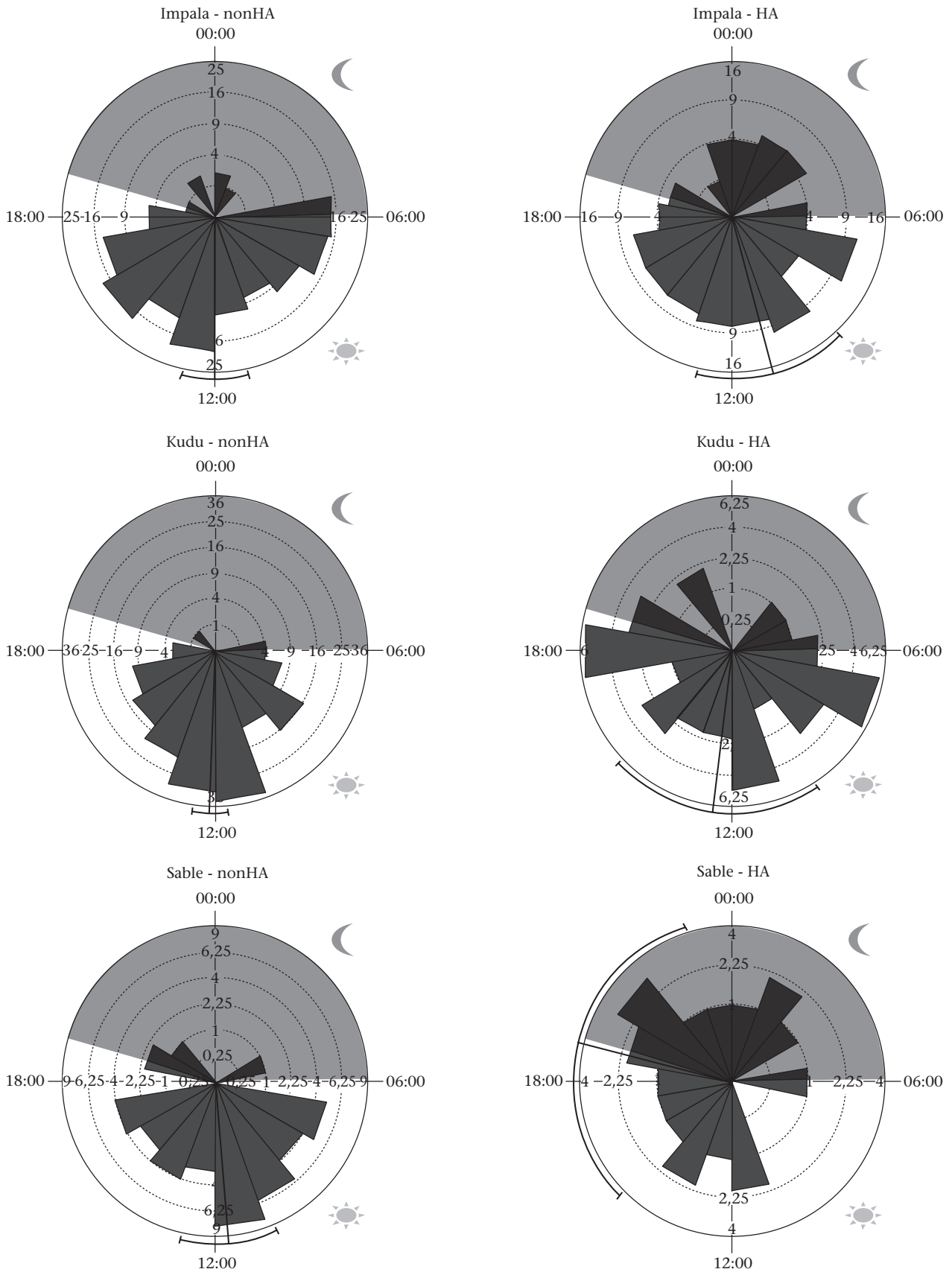
† For call-up surveys, the lower estimate corresponds to the 2.5 km response range, and the higher estimate corresponds to the 3.2 km response range (Elliot 2007).

existing database, 19 waterholes in 2007 and 13 waterholes in 2008 (i.e. 19 different waterholes).

Monitoring consisted in 24 h counts during full moon periods to document temporal drinking niches of ungulates at waterholes. Full moon nights guarantee good visibility conditions to carry out observations, particularly in the areas surrounding waterholes, which are characterized by the absence of vegetation. Observations were conducted with binoculars or spotting scopes (15–45×) from platforms, tree hides or a car parked about 100 m away from the waterholes to avoid disturbing animals. We recorded the time at which ungulate groups arrived at waterholes, as well as species, group size and presence/absence of young. We accounted for group size and presence of young as cofactors in the decision to access waterholes during daytime or at night, as both group size ('many eyes effect': Pulliam 1973; 'dilution effect': Hamilton 1971; Dehn 1990) and presence of young (Berger 1991; Burger & Gochfeld 1994) are known to influence antipredator behaviours.

#### Study Species

We focused on two browsers: impala and greater kudu, and one woodland grazer: sable antelope. These ungulates are strictly dependent on surface water and they visit waterholes regularly, mostly during daytime in nonHA (Valeix et al. 2007a). In the study area, the main predators are lions and spotted hyaenas (Table 1). Lions are ambush predators and many lion kills (~40%) occur close to a waterhole (Valeix et al. 2009a, 2011). Hyaenas are cursorial predators that commonly hunt in waterhole areas (Salnicki et al. 2001; N. Drouet-Hoguet, personal observations). Both carnivore species are nocturnal and their visits to waterholes occur mainly at night (70% and 80% of the lion visits recorded during the



**Figure 2.** Temporal visits at waterholes by groups of impala, greater kudu and sable antelope in 2007 and 2008 during daytime (0600–1900 hours) and night-time (1900–0600 hours) under two contrasted situations: natural predation and no sport hunting (nonHA, Hwange National Park, Zimbabwe) versus natural predation and sport hunting (HA). Each bar length represents the number of groups that visited waterholes during each hour; the area of each bar is thus proportional to the frequency of group visits. The black line in each graph indicates mean arrival time, with 95% confidence interval.



monitoring occurred at night in nonHA and HA, respectively, and 90% and 100% of the hyaena visits occurred at night in nonHA and HA, respectively; see also [Supplementary Material, Fig. S1](#)). Lions were not hunted in HAs at the time of the study because of a moratorium on lion hunting that took place in the study area between 2005 and 2008, and hyaenas are very rarely targeted by hunters.

Impalas are more abundant than greater kudus and sable antelopes in our study area (ca. 8800 impalas, 4700 greater kudus and 1200 sable antelopes), but they represent less than 5% of lions' diet ([Loveridge et al. 2007](#)). The four-fold difference in abundance between greater kudu and sable antelope is reflected in the diet of lions, with greater kudu representing up to 24% and sable antelope less than 5% ([Loveridge et al. 2007](#)). This is consistent with other African systems where lions prey upon greater kudu and sable antelope in accordance with the abundance of these prey species, whereas impala is avoided (reviewed in [Hayward & Kerley 2005](#)). However, in the nearby Kruger National Park, South Africa, 61.3% of encounters between impala and lion lead to hunts ([Funston et al. 2001](#)). Therefore, despite impala not being a preferred prey species for lion, impalas probably do not consider lions to be a low-level threat. Hyaenas show no prey species preference ([Hayward 2006](#)). Impala and greater kudu, which are among the commonest prey species consumed by hyaenas, are taken in proportion to their relative abundance. The sable antelope, however, is more likely to be avoided. In our study area, greater kudu, impala and sable antelope represent 8–12%, 5–10% and less than 5% of hyaenas' diet, respectively ([Drouet-Hoguet 2007](#)). However, about 80% of hyaenas' food is acquired by scavenging ([Drouet-Hoguet 2007](#)), whereas about 16% is obtained by hunting. Impalas represent 56% of the prey species hunted, and greater kudu represent 19%, whereas sable antelopes are not hunted ([Drouet-Hoguet 2007](#)). For the secondary large carnivore species of the study area (i.e. leopard, *Panthera pardus*, wild dog, *Lycaon pictus*, cheetah, *Acinonyx jubatus*), there is no equivalent information on diet composition. Nevertheless, reviews on these large carnivore diets ([Hayward et al. 2006a, b, c](#)) indicate that leopards preferentially prey upon impala, consume greater kudu in proportion to their relative abundance, and tend to avoid sable antelope. Wild dogs preferentially prey upon greater kudu and impala (see [Rasmussen 2009](#) for our study area), but they consume sable antelope in proportion to their relative abundance. Cheetahs preferentially prey upon impala, consume greater kudu in accordance with their relative abundance and tend to avoid sable antelope. Overall, these diet studies suggest that greater kudu, and impala to a lesser extent, are more vulnerable to their natural predators than are sable antelope.

The magnitude of behavioural adjustments in hunted populations is likely to increase with hunting pressure ([Caro 1999b](#); [Matson et al. 2005](#)). During road counts carried out in HA in the late dry season in 2007 and 2008, we encountered four groups of impala/100 km, three groups of greater kudu/100 km and 1.4 groups of sable antelope/100 km. In the meantime, the realized hunting quotas (i.e. actual numbers of animals shot) were 1.2 times higher for impala than for greater kudu, and four times higher for impala than for sable antelope (ZPWMA, unpublished data). Therefore, considering the dilution effect, the human hunting risk perceived by groups of ungulates was comparable among the three species. Thus, the three species differed mainly in their exposure to natural predators, and we therefore expected impala and greater kudu to be less prone to shift their visits at waterholes during night-time than sable antelopes when hunted because of their higher exposure to natural predators then. We observed 226 groups of impala (131 in nonHA, 95 in HA), 188 groups of greater kudu (149 in nonHA, 39 in HA) and 63 groups of sable antelope (41 in nonHA, 22 in HA).

### Statistical Analyses

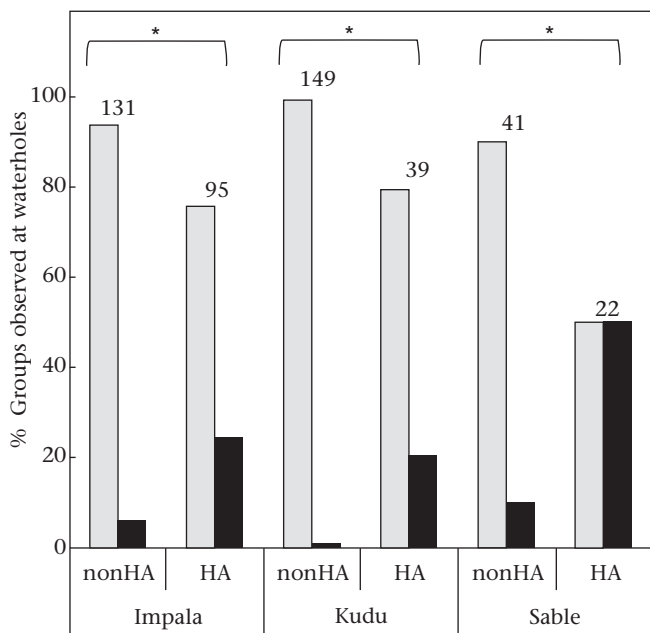
Drinking temporal niche at waterholes was approximated by the arrival time of groups at waterholes. We plotted a frequency distribution of group observations at waterholes by hour using Oriana 2.0 software for circular data ([Fisher 1993](#)). We used the group as the statistical unit. Mean arrival times per species were compared with the Watson–Williams test for circular means ([Fisher 1993](#)). To test whether waterholes were more frequently visited at night in HA than in nonHA, we compared the respective temporal distributions of visits at waterholes between the two zones. To determine the expected number of visits in HA during daytime (0600–1900 hours) and at night (1900–0600 hours), we used the distribution of visits at waterholes in nonHA where there was no sport hunting. We then compared the expected distribution with the observed distribution in HA using a contingency table (following [Zar 1984](#)), with the Pearson's chi-square test with Yates' continuity correction, and the Fisher's exact test for frequencies that were smaller than five.

For each species, we investigated the effects of zone (nonHA or HA), group size and presence/absence of young on the probability of arriving at a waterhole at night with a logistic regression model. The respective effects of group size and presence of young, however, may be confounded for the three species because these two factors were correlated (Wilcoxon signed-ranks test with continuity correction: impala:  $V = 20301$ ,  $r = 0.10$ ,  $N = 201$ ,  $P < 0.001$ ,  $N = 201$ ; greater kudu:  $V = 17020$ ,  $r = 0.19$ ,  $N = 184$ ,  $P < 0.001$ ; sable antelope:  $V = 1770$ ,  $r = 0.64$ ,  $N = 59$ ,  $P < 0.001$ ). We included all possible interactions between fixed effects but none was statistically significant. To compare the probabilities of visiting waterholes at night between species, we used a logistic regression with species and zone as factors, and their interaction. For all logistic models, we used the Akaike Information Criterion (AIC) to select the best model ([Burnham & Anderson 2002](#)). The model with the lowest AIC value (i.e. the best compromise between accuracy and precision) was retained. When  $\Delta\text{AIC}$  between two models was less than two, we selected the simplest model according to the parsimony rules ([Burnham & Anderson 2002](#)). All statistical analyses were generalized linear mixed models, with year and waterhole fitted as random effects, using R lme4 package (<http://cran.r-project.org/web/packages/lme4/index.html>).

## RESULTS

Groups of all three species visited waterholes preferentially during daytime, generally avoiding night hours ([Fig. 2](#)). However, avoidance of waterholes during night-time was less marked in HA, where proportionally more groups came at night, than in nonHA. In nonHA, 6% of groups of impala, less than 1% of groups of greater kudu and 10% of groups of sable antelope visited waterholes at night. Conversely in HA, 24% of groups of impala, 20% of groups of greater kudu and 50% of groups of sable antelope visited waterholes at night. These differences between day and night were significant for the three species (impala, Pearson's chi-square test:  $\chi^2_1 = 13.76$ ,  $N = 226$ ,  $P < 0.001$ ; greater kudu, Fisher's exact test:  $N = 188$ ,  $P = 0.001$ ; sable antelope, Fisher's exact test:  $N = 63$ ,  $P = 0.001$ ; [Fig. 3](#)).

Average arrival times at waterholes did not differ between nonHA and HA for impala (Watson–Williams test:  $F_{1, 221} = 1.56$ ,  $P = 0.2$ ; [Fig. 2](#)) or greater kudu ( $F_{1, 185} = 0.15$ ,  $P = 0.7$ ; [Fig. 2](#)). Sable antelope arrived at waterholes later in HA than in nonHA (Watson–Williams test:  $F_{1, 59} = 18.68$ ,  $P < 0.0001$ ; average arrival time in nonHA = 1140 hours; average arrival time in HA = 1856 hours). Circular variances associated with average arrival times were higher in HA than in nonHA (circular



**Figure 3.** Effect of sport hunting on attendance of groups of impala, greater kudu and sable antelope at waterholes during daytime (grey bars; 0600–1900 hours) versus night-time (black bars; 1900–0600 hours) in 2007–2008. Zones with natural predation and no sport hunting (nonHA, Hwange National Park, Zimbabwe) versus natural predation and sport hunting (HA) are compared. Numbers above bars indicate number of groups present at waterholes in each zone. Statistical tests are from comparisons of frequencies within contingency tables, but results are presented as percentages for clarity. \* $P < 0.001$ .

standard deviation: impala: nonHA =  $65^\circ$ , HA =  $90^\circ$ ; greater kudu: nonHA =  $41^\circ$ , HA =  $86^\circ$ ; sable antelope: nonHA =  $56^\circ$ , HA =  $89^\circ$ . The distribution of arrival times was thus more scattered in HA than in nonHA. Temporal distributions of arrival times were more concentrated during daytime in nonHA than in HA, particularly during the hottest hours of the day (between 1000 and 1600 hours): for impala, 49.6% of groups were observed during the hottest hours of the day in nonHA, as opposed to 35.9% in HA; for greater kudu, it was 68.5% in nonHA versus 31.5% in HA; and for sable antelope, 51% in nonHA versus 30% in HA.

Logistic regressions confirmed that the probability of visiting waterholes at night was higher in HA than in nonHA for the three species (estimate  $\pm$  SE: impala:  $2.3 \pm 1.0$ ; greater kudu:  $3.7 \pm 1.1$ ; sable antelope:  $7.0 \pm 2.2$ ; Table 2). Moreover, the probability of visiting waterholes at night was lower for groups of impala with young (estimate  $\pm$  SE =  $-2.6 \pm 1.2$ ), but not for groups of greater kudu with young (Table 2). For sable antelope, although the presence of young was retained in the selected model (Table 2), its effect on the probability of visiting waterholes at night was highly variable (estimate  $\pm$  SE =  $-20.4 \pm 2322.1$ ). Group size was not retained in the selected models and, therefore, did not affect the probability of visiting waterholes at night for any of the three species (Table 2).

Sable antelope had a higher probability of visiting waterholes at night compared to impala and greater kudu in HA, but not in nonHA (Fig. 4). In HA, impala and kudu had a similar probability of visiting waterholes during night-time, whereas in nonHA, greater kudu had a lower chance of visiting waterholes at night than did the two other species.

## DISCUSSION

Prey may shift their niche along the time axis to reduce temporal overlap with predator activity (reviewed in: Kronfeld-Schor & Dayan

**Table 2**

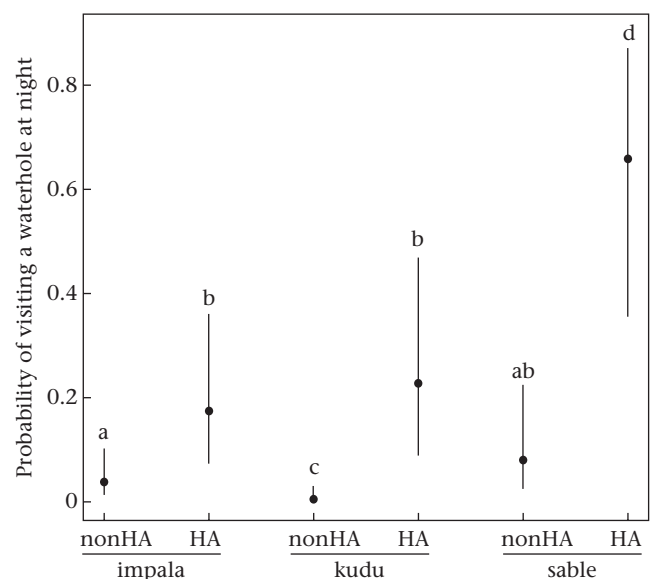
Summary of the logistic regression modelling the probability of visiting waterholes at night as a function of zone (hunting area, HA, versus nonhunting area, nonHA), group size and status (i.e. presence/absence of young) for groups of impala, greater kudu and sable antelope in Hwange National Park (Zimbabwe) and the surrounding hunting areas in 2007 and 2008

Models	$K^*$	AIC	$\Delta$ AIC
<b>Impala</b>			
Null	22	127.1	7.8
Zone	24	125.2	5.9
Status	24	121.6	2.3
Group size	24	128.7	9.4
<b>Zone + status</b>	<b>25</b>	<b>119.3</b>	<b>0</b>
Zone + group size	25	127	7.7
Group size + status	25	123.3	4
Zone + group size + status	26	120.5	1.2
<b>Kudu</b>			
Null	22	55.4	5.4
<b>Zone</b>	<b>24</b>	<b>51</b>	<b>1</b>
Status	24	56.5	6.5
Group size	24	55.6	5.6
Zone + status	25	50	0
Zone + group size	25	50.8	0.8
Group size + status	25	57.5	7.5
Zone + group size + status	26	51.6	1.6
<b>Sable</b>			
Null	15	58	21
Zone	16	49.7	12.7
Status	16	48.1	11.1
Group size	16	55.2	18.2
<b>Zone + status</b>	<b>17</b>	<b>37</b>	<b>0</b>
Zone + group size	17	42.7	5.7
Group size + status	17	50.6	13.6
Zone + group size + status	18	38.9	1.9

The selected models (lowest AIC) are shown in bold font.

\* Number of parameters. It includes the random factor 'waterholes'.

2003; Caro 2005). Human hunters, similarly to natural predators, may also induce a temporal adjustment of the niche in hunted populations (e.g. Kilgo et al. 1998). Here, we observed African ungulates' use of waterholes in semiarid savannas to examine how



**Figure 4.** Probabilities of visiting waterholes at night (1900–0600 hours) for impala, greater kudu and sable antelope in 2007 and 2008. Zones with natural predation and no sport hunting (nonHA, Hwange National Park, Zimbabwe) versus natural predation and sport hunting (HA) are compared. Estimates from logistic regression models and their confidence intervals (backtransformed) are shown. Estimates with different letters were significantly different at  $P < 0.05$ .

they adjust their temporal niche in response to both their risk of natural predation by large carnivores mostly at night and their risk of being hunted by human hunters during the day. Groups of impala, greater kudu and sable antelope visited waterholes more often at night in hunting areas than in nonhunting areas (Hwange National Park), where visits at waterholes were almost exclusively diurnal. The temporal pattern of access to water was concentrated around the hottest hours of the day in the protected area, particularly for greater kudu, while it was scattered throughout the day in hunting areas. More interestingly, we observed that groups of impala and greater kudu were less prone to switch their access to water towards night-time in hunting areas compared to groups of sable antelope, although they were exposed to similar hunting risk.

The diurnal use of waterholes by ungulates in African savannas is largely dictated by the circadian rhythms and physiology of these ungulates (Finch 1972; Ayeni 1977; Valeix et al. 2007b). It may also be a tactic to decrease the risk of encountering the main natural predators of these ecosystems (Valeix et al. 2009b), which visit waterholes essentially at night to drink or to hunt their prey. The activity of ungulates at waterholes was almost exclusively diurnal in the protected area, similar to that observed in other protected areas (Hwange National Park: Weir & Davison 1965; Valeix et al. 2007a; Tsavo National Park, Kenya: Ayeni 1975), whereas a large proportion of the groups (24% for impala, 20% for greater kudu and 50% for sable antelope) visited waterholes at night in hunting areas. We hypothesize that this significant temporal shift towards nocturnal use of waterholes in hunting areas is a behavioural adjustment of ungulates to the risk of being hunted by humans during daytime. The increase of nocturnal activities (e.g. movements, foraging, social interactions) as a way to escape human disturbance occurring during daytime has been largely documented in birds (e.g. brent goose, *Branta bernicla bernicla*: Riddington et al. 1996; sanderling, *Calidris alba*: Burger & Gochfeld 1991), but less so in ungulates (but see: white-tailed deer, *Odocoileus virginianus*: Kilgo et al. 1998; red deer, *Cervus elaphus*: Sunde et al. 2009).

The significant temporal shift towards nocturnal use of waterholes exposes ungulates to their natural predators. Hence, ungulates in the hunting areas face a trade-off between the risk of natural predation and the risk of being hunted. Such trade-off is poorly understood because most studies on hunting are carried out on ungulates of temperate ecosystems (moose, *Alces alces*, elk, *Cervus canadensis*: Altmann 1958; roe deer, *Capreolus capreolus*: de Boer et al. 2004; Benhaïem et al. 2008; fallow deer, *Dama dama*: de Boer et al. 2004; caribou and reindeer, *R. tarandus*: reviewed in Reimers & Colman 2006), where the diversity and densities of predators have been largely reduced by human activities (Berger 1999; Andersen et al. 2006). In comparison, African savannas still host a rich guild of large carnivores. Our results showed greater circular variances associated with mean arrival time at waterholes for the three species in hunting areas, whereas the great majority of observations were made during the hottest hours of the day (1000–1600 hours) in the protected area. In African savannas, the hottest hours of the day coincide with the period when large carnivores are less active (Kruuk 1972; Schaller 1972). Consequently, ungulates drinking at waterholes during this period may benefit from a reduced risk of natural predation. Conversely, visits of ungulates at waterholes were more randomly distributed over the day in hunting areas. As a consequence, their whereabouts were less predictable to human hunters. Random antipredator behaviour of prey may also be an efficient tactic against predators; for instance, Scannell et al. (2010) recently demonstrated that prey that scan at random are more difficult to catch by predators. The decrease in the predictability of the temporal pattern of visits at waterholes may be an alternative tactic adopted by ungulates to

partly reduce hunting risk during daytime without completely shifting towards night-time, thus limiting increased exposure to natural predators.

The magnitude of the temporal shift in the use of waterholes was expected to vary according to species vulnerability to natural predation and exposure to hunting. Because the three species differed mainly in their exposure to natural predation, we predicted that greater kudu, and to a lesser extent impala, should be less prone to shift their visits at waterholes during night-time than sable antelope. Interestingly, sable antelope showed the greatest shift to night use of waterholes in hunting areas, whereas greater kudu and impala showed the smallest shift. Such results are consistent with the observation that greater kudu is the second most frequent prey of lions (after buffalo) (Loveridge et al. 2007), and that greater kudu and impala represent a greater share of hyaena diet in Hwange National Park than do sable antelope (Drouet-Hoguet 2007), while sable antelope has never been identified as a main prey for one of the large carnivores in Hwange National Park. Previous studies in this ecosystem have shown that greater kudus are particularly responsive to the immediate risk of predation by lions (Valeix et al. 2009b; Périquet et al. 2010). Hence, it is not surprising that greater kudu and impala showed less shifting in their temporal niche at waterholes towards the night in hunting areas, and that sable antelope, which appears less sensitive to natural predation, shifted the most to night use of waterholes in hunting areas. Our results indicate that the higher the risk of natural predation, the lower the probability of shifting to night use of waterholes to avoid human hunters.

Note that we have limited our conclusions to nights during which visibility was good, since we carried out all of our observations during full moon nights. Lower visibility condition during other nights may change prey perception of natural predation risk. Ayeni (1975) observed that many herbivores in Tsavo National Park, Kenya, drank later into the night on moonlit nights than on moonless nights, probably because it is then much more difficult to detect approaching predators. Under moonless or cloudy nights, the situation of ungulates would be therefore even more complicated than during full moon nights because natural predation risk is probably enhanced because of lower visibility.

The propensity to shift to nocturnal use of waterholes was also influenced by presence of young in impala, and in sable antelope to a lesser extent, with the probability of coming to waterholes at night being lower for groups with young than for groups without young. Because young are highly vulnerable to predators, groups with young normally adjust their behaviour to compensate for increased vulnerability (increased vigilance: Burger & Gochfeld 1994; avoidance of risky areas and risky hours: Hamel & Côté 2007). In greater kudu, however, the presence of young in groups had no significant influence. Since greater kudu is the most vulnerable prey species, it may not be less dangerous for groups without young to come at night at waterholes than for groups with young. This however remains to be investigated. We found no effect of group size on the probability of coming to waterholes at night. Perceived predation risk, however, was expected to be lower in larger groups because more individuals are present to scan the surroundings for approaching predators ('many-eyes effect', Pulliam 1973) and because of the dilution effect of large groups (Hamilton 1971; Dehn 1990). At night, because of the lower light conditions (even under full moon light), more individuals may not sufficiently offset the increased risk of predation in large groups because of the presence of young. Moreover, the risk for groups with young to be targeted by natural predators might be higher than the risk to be targeted by human hunters, the latter usually seeking trophy males, which are often solitary or found in small bachelor groups.



We cannot fully exclude other potential alternative explanations to the nocturnal shift observed in hunting areas (e.g. differences in environmental conditions, tourism and natural predation). The studied hunting areas and Hwange National Park were adjacent and showed similar soil composition, vegetation structure, temperature and rainfall characteristics (Ganzin et al. 2008; Peace Parks Foundation 2009). Moreover, the diurnal preferential use of waterholes by African ungulates has been shown in other ecosystems (e.g. Tsavo National Park, Kenya: Ayeni 1975; Etosha National Park, Namibia: Preez & Grobler 1977). Therefore, differences in environmental conditions are unlikely to account for the difference in the temporal pattern of visits at waterholes observed in our study between Hwange National Park and the adjacent peripheral hunting areas. Tourism was generally low in Zimbabwe during our study (2007–2008) because of the economic and political crisis, and there were very few tourists in Hwange National Park and the peripheral hunting areas. Finally, densities of natural predators, proportion of waterholes visited by these natural predators, and the temporal pattern of these visits were similar between Hwange National Park and the peripheral hunting areas (Table 1, Supplementary Material, Fig. S1). Hence, we interpret the shift to night use of waterholes in hunting areas as a response to the risk of being hunted by human hunters during the day, which is the main difference between the national park and the peripheral hunting areas.

Our study illustrates how sport hunting influences the ecology of ungulates in a system where ungulates have to face a trade-off between the risk of natural predation by carnivores and the risk of being hunted, the former being higher at night and the latter higher during the day. To our knowledge, this is one of the first attempts to explore such trade-off, and one of the rare studies that contrasts different species. The three study species were characterized by a gradient in the risk of natural predation, leading to a gradient in the shift made to night use of waterholes in hunting areas. The species more often preyed upon (i.e. greater kudu) performed the shift of the lowest magnitude, whereas the species less preyed upon (i.e. sable antelope) performed the shift of the highest magnitude. Because our study did not measure the potential costs associated with the shift of visits to waterholes towards night-time in hunting areas, we cannot assume that this behavioural response to hunting risk has any impact on individual fitness. To better understand how sport hunting and induced behavioural adjustments influence ungulate population dynamics, there is a need to investigate whether the differences that we observed in ungulate behaviour between hunting-free areas and hunting areas actually lead to measurable costs in terms of physiology and survival (e.g. greater exposure to natural predators, alteration of thermo-regulation, or changes in time budget).

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## Supplementary Material

Supplementary material for this article is available, in the online version, at doi:10.1016/j.anbehav.2011.10.019.

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