



Vulnerability to predation and water constraints limit behavioural adjustments of ungulates in response to hunting risk

William-Georges Crosmary^{a,b,c,*}, Peter Makumbe^{d,1}, Steeve D. Côté^{b,2}, Hervé Fritz^{a,3}

^a Université de Lyon, CNRS Université Claude Bernard Lyon 1, Laboratoire Biométrie et Biologie Evolutive, Villeurbanne, France

^b Département de Biologie, Université Laval, QC, Canada

^c CIRAD - EMVT, Integrated Wildlife Management Research Unit, Campus International de Baillarguet, Montpellier, France

^d National University of Science and Technology, Ascot, Bulawayo, Zimbabwe

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The magnitude of behavioural adjustments by prey in response to predation risk is constrained by the necessity to maintain resource acquisition. In systems with high predation risk, prey display adjustments that can challenge resource acquisition. In such cases, prey may be limited in their ability to adjust their behaviour further in response to additional risk, such as that posed by human hunters (hunting risk). We investigated whether large African herbivores adjust their behaviour in response to hunting risk. In Hwange National Park (HNP), Zimbabwe, and in the peripheral hunting areas (HA), we monitored behaviour of impala, *Aepyceros melampus*, greater kudu, *Tragelaphus strepsiceros*, and sable antelope, *Hippotragus niger*, at waterholes. Once groups entered waterhole areas, their probability of returning to vegetation cover without drinking was higher in HA than in HNP. Individuals were more vigilant in HA than in HNP when they were approaching and leaving waterholes, but not during drinking. This suggests that drinking was prioritized over vigilance once individuals reached waterholes. The time that groups spent in waterhole areas did not differ significantly between HA and HNP, but individuals in HA were more vigilant, suggesting that groups limited their exposure to hunters. Greater kudus were the most vigilant, probably because they are the most vulnerable to predators. Sable antelopes were the least prone to compromise the acquisition of surface water. Both species consequently displayed adjustments of lower magnitude than impala in response to hunting risk. Our multispecies study illustrates how vulnerability to natural predators and environmental constraints limit behavioural responses of large herbivores to hunting risk.

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Human activities are potential sources of disturbance in animal populations (reviewed in Frid & Dill 2002). This is particularly true for hunting because animals experience direct risk of mortality and therefore habituation is unlikely in hunted populations (but see Colman et al. 2001). Hunting, like predation, may alter population dynamics directly, by increasing mortality (e.g. Caughley 1977; Solberg et al. 1999), or indirectly, by constraining animals to divert part of their time and energy budgets to safety-related behaviours (e.g. waterbird species, reviewed in: Madsen & Fox 1995; large herbivores: Kufeld et al. 1988; Benhaiem et al. 2008). Investment in antipredator behaviours may compromise other fitness-enhancing

activities (e.g. foraging), potentially altering individuals' reproductive output and/or long-term survival (Lima & Dill 1990; Lima 1998), and eventually population dynamics (Creel & Christianson 2008).

Sutherland (1998) stressed the importance of behavioural studies in conservation biology, but Gill et al. (2001) argued that behavioural indicators may not always properly indicate animal responses to human disturbance. Animals may indeed make state-dependent decisions (McNamara & Houston 1996). Those in lower condition or that have higher constraints on resource requirements may be less likely than others to adjust their behaviour in response to human disturbance (e.g. Beale & Monaghan 2004). The trade-off between safety and exposure to predators should be particularly exacerbated in systems with high predation risk and environmental constraints on resource acquisition. In such systems, further behavioural adjustments in response to any extra risk, such as human hunting (hunting risk), may be highly constrained by the need to satisfy resource requirements.

* Correspondence: W.-G. Crosmary, Département de Biologie, Université Laval, Pavillon Alexandre-Vachon, 1045 avenue de la Médecine, Université Laval, QC G1V 0A6, Canada.

E-mail address: william.crosmary.1@ulaval.ca (W.-G. Crosmary).

¹ E-mail address: pmakumbe7@gmail.com (P. Makumbe).

² E-mail address: steeve.cote@bio.ulaval.ca (S. D. Côté).

³ E-mail address: herve.fritz@univ-lyon1.fr (H. Fritz).

Understanding constraints acting on behavioural adjustments is of prime importance for the conservation and management of hunted populations. This is particularly true for ungulates because they are hunted worldwide (Festa-Bianchet 2007) and they play a prominent role in the functioning of ecosystems (Gordon et al. 2004). However, whether and how ungulates adjust their behaviour to hunting risk under high predation risk remain poorly understood. Most studies have focused on ungulates of temperate ecosystems (e.g. moose, *Alces alces*: Altmann 1958; white-tailed deer, *Odocoileus virginianus*: Kilgo et al. 1998; caribou, *Rangifer tarandus*: Aastrup 2000; roe deer, *Capreolus capreolus*: de Boer et al. 2004), where human activities have widely reduced the diversity and densities of natural predators (Berger 1999). Moreover, these studies essentially focused on single species, which limits our understanding of how different ecological requirements may influence behavioural response to disturbance (Blumstein et al. 2005).

Here, we investigated behavioural adjustments displayed by ungulates of semi-arid African savannas in response to hunting risk. African savannas host the richest guild of large terrestrial carnivores (Andersen et al. 2006), and ungulates in this system must thus adjust their behaviour in response to predation risk (e.g. FitzGibbon 1994; Hunter & Skinner 1998). Semi-arid African savannas are moreover characterized by the scarcity of surface water. Water is a key resource for African ungulates, which make regular visits to waterholes to drink, despite the high risk of being ambushed by predators (Valeix et al. 2009, 2010). The risk of predation is accentuated during the dry season when surface water becomes scarcer. McNamara & Houston (1996) suggested that as physiological stress increases, resource acquisition is prioritized at the expense of antipredator behaviours. Therefore, at the peak of the dry season, African ungulates should invest more heavily in drinking water than in antipredator behaviours (e.g. Valeix et al. 2007; Périquet et al. 2010) and be limited in their ability to make further adjustments in these behaviours in response to the additional risk posed by human hunters.

We compared antipredator behaviours and water acquisition of impala, *Aepyceros melampus*, greater kudu, *Tragelaphus strepsiceros*, and sable antelope, *Hippotragus niger*, at waterholes in a hunting-free environment, Hwange National Park, Zimbabwe, and in the neighbouring hunting areas. We expected these ungulates to leave waterholes without drinking more often (i.e. lower drinking probability) and to be more vigilant in hunting areas than in the National Park. However, we also predicted that the magnitude of these behavioural adjustments would vary with species, according to their vulnerability to natural predation and the constraint of surface water availability. We predicted that greater kudu, the species most often preyed upon (Drouet-Hoguet 2007; Loveridge et al. 2007), would display the strongest antipredator behavioural adjustments in the National Park (i.e. lowest drinking probability and highest vigilance at waterholes). To maintain water acquisition, we predicted that greater kudu would be less likely to adjust these behaviours further in hunting areas despite increased overall predation risk (i.e. drinking probability should decrease less and vigilance should increase less than for species less vulnerable to predation). Sable antelope, which are particularly constrained by access to surface water (Western 1975; Redfern et al. 2003; Rahimi & Owen-Smith 2007), should be less likely to compromise drinking opportunities at waterholes than impala and greater kudu. We expected sable antelope to display the highest drinking probability and the lowest vigilance level in the National Park, and to adjust these behaviours minimally in hunting areas despite the hunting risk. Impala, being less vulnerable to natural predation than greater kudu and less constrained by access to surface water than sable antelope, should be able to decrease their drinking probability and

increase their vigilance in response to hunting risk more than the two other species.

METHODS

Study Site

We conducted field observations during the late dry season (from August to late-October) in 2008 in Hwange National Park (HNP), an area of 15 000 km² in northwestern Zimbabwe (19°00'S, 26°30'E) and in two hunting areas (HA) immediately adjacent to HNP (i.e. Matetsi Safari Area South, MSA South, ca. 1890 km²; Gwayi Intensive Conservation Area South, Gwayi ICA South, ca. 880 km²). In the peripheral hunting areas, we selected hunting concessions from which we had obtained the authorization to carry out wildlife surveys during the study period (i.e. Unit 3 in MSA South, ca. 360 km²; four hunting properties in Gwayi ICA South, ca. 300 km²; Fig. 1). In nonhunting areas (nonHA), we covered the blocks that were adjacent to those hunting concessions (i.e. Main camp, ca. 1300 km²; Robins, ca. 1000 km²) in the northern part of Hwange National Park (Fig. 1). The hunting concessions and the adjacent blocks in nonHA that we selected for our study presented similar vegetation types and environmental conditions (i.e. rainfall, temperature, soil characteristics; Ganzin et al. 2008; Peace Parks Foundation 2009).

During the past century, the study area received an average of 600 mm of rainfall during the rainy season, and 830 mm of rainfall in 2008, with most rain occurring during December–March. Most water sources are seasonal and eventually dry up after the early part of the dry season (i.e. June/July). Provision of water during the dry season mainly comes from artificially filled waterholes through ground water pumping in both HNP and HA (Fig. 1). Vegetation is typical of southern African dystrophic wooded and bushed savannas with patches of grasslands (Rogers 1993), dominated by *Colophospermum mopane* and *Combretum* spp. in MSA South and Robins, and by *Baikiaea plurijuga*, *Burkea africana*, *Terminalia sericea* and *Brachystegia* woodlands in Main Camp and Gwayi ICA South (Ganzin et al. 2008).

HNP is a state land administrated by Zimbabwe Parks and Wildlife Management Authority (ZPWMA). No permanent settlement is allowed within the limits of HNP, aside from ZPWMA headquarters and some outlying ranger posts. Illegal activities, such as poaching and timber extraction, are controlled and limited by regular vehicle and foot patrols both in HNP and in HA; hence, we assumed that the level of illegal exploitation was similar between the two land uses. Trophy hunting does not occur in HNP, but ZPWMA allocates quotas to its staff for food rations, mainly on elephants, *Loxodonta africana*, and buffalos, *Syncerus caffer*. Trophy hunting has occurred since the 1970s in HA, and hunting season ranges from March to December. Although hunters are not allowed to hunt at waterholes (ZPWMA, personal communication), they occasionally do, and they often visit waterhole areas to look for signs of targeted species. Overall, the main large predators of the system were present in HNP and HA in comparable densities (Elliot 2007; Crosmarj et al. 2012). We thus studied a contrasted system, where the risk undergone by ungulates in nonHA was exclusively exerted by natural predators, whereas the risk in HA originated both from natural predators and human hunters (Crosmarj et al. 2012).

Study Species

We selected impala, greater kudu and sable antelope as our biological models because they share common ecological features (ruminants, group living), are fairly observable in reasonable numbers (see densities in Crosmarj et al. 2012) and are harvested in

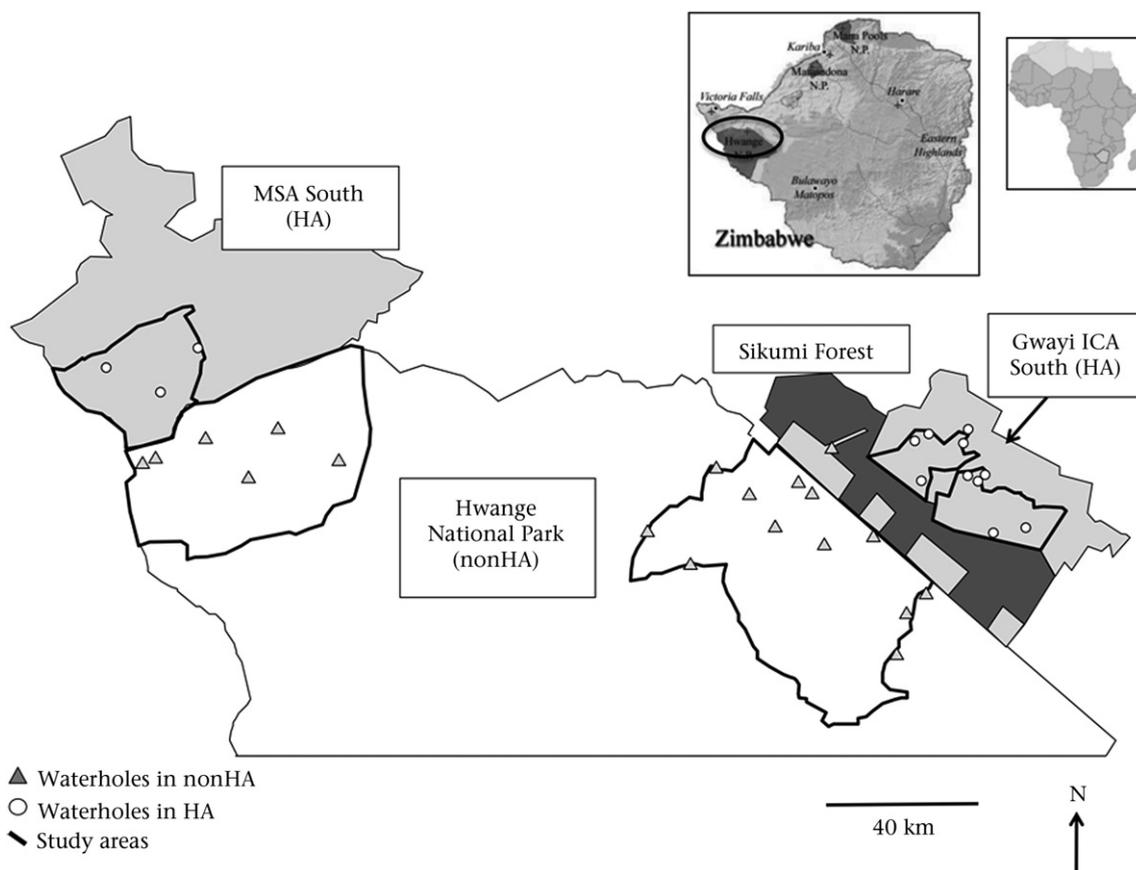


Figure 1. Hwange National Park (HNP, nonhunting area) and adjacent sport hunting areas (HA, Gwayi ICA South and MSA south) in Zimbabwe, Africa. The study area is delineated by thick black lines. Triangles: locations of waterholes monitored within HNP; circles: locations of waterholes monitored in HA.

the hunting areas, but their vulnerability to natural predators and their dependency on surface water differ. Greater kudu and impala, to a lesser extent, are preyed upon by every large African carnivore species and are among the main prey species in these predator diets (reviewed in Hayward & Kerley 2005; Hayward 2006; Hayward et al. 2006a, b, c). Sable antelope conversely is essentially preyed upon by lion, *Panthera leo* (Hayward & Kerley 2005), and generally avoided by other large carnivores. Diet studies in our system confirmed this broad African pattern (Loveridge et al. 2007; Drouet-Hoguet 2007; Rasmussen 2009). Greater kudu and impala, to a lesser extent, were therefore expected to be more vulnerable to natural predation than sable antelope.

Browsers such as greater kudu are less dependent on surface water than grazers like sable antelope and mixed feeders like impala (Western 1975). As the dry season advances, grazers and mixed feeders are compelled to forage farther from waterholes to mitigate limitations in nutritional requirements (Redfern et al. 2003). Sable antelopes, in particular, travel longer distances between waterholes and feeding sites in the dry season, which may increase their energy expenditure and exposure to predators (Rahimi & Owen-Smith 2007). Thus, sable antelopes should be more constrained by surface water than greater kudu and, to a lesser extent, impala.

Harvest rates are traditionally set at about 2% of population size for most ungulates in Zimbabwean hunting areas (Cumming 1989), and the perceived hunting risk is comparable among the three ungulate species (Crosmarj et al. 2012). Note, however, that female sable antelope are not hunted, but both sexes of greater kudu and impala are. The magnitude of behavioural adjustments to hunting

risk should therefore vary among our three biological models mainly according to differences in vulnerability to predation and constraints imposed by access to surface water (Table 1).

Behavioural Monitoring

We monitored the behaviour of ungulates in the vicinity of 31 waterholes (18 in HNP, 13 in HA) (Fig. 1). We selected waterholes according to the availability of surface water and signs of recent ungulates presence (i.e. fresh spoor and faeces). We used binoculars (10 × 42) to conduct behavioural observations during daytime (i.e. from 0600 to 1800 hours), from viewing platforms, a hide on the ground or a car parked at 100–150 m away from

Table 1

Comparisons of vulnerability to predation and constraints on access to surface water for impala, greater kudu and sable antelope in Hwange National Park, Zimbabwe, and in surrounding hunting concessions

	Impala	Greater kudu	Sable antelope
Vulnerability to predation	++	+++	+
Surface water constraint	++	+	+++
Time spent in vigilance	++	+++	+
Drinking probability	++	+	+++
Response to hunting risk	++	+	+

The '+' ranks the species in each context (i.e. the species with the most '+' ranked first, and the species with the fewest '+' ranked last). The expected behavioural adjustments around waterholes (i.e. time spent in vigilance and drinking probability) are compared among species, as well as the predicted response to hunting risk in hunting concessions (i.e. further increase in time spent in vigilance, further decrease in drinking probability).

waterholes to avoid disturbing the animals. Because the studied species are gregarious and adjust their behaviour both at the group level and at the individual level (e.g. Valeix et al. 2007; Périquet et al. 2010), we performed behavioural observations on groups and on individuals.

Monitoring of individuals

We monitored individuals at waterholes during (1) approach, which corresponded to the moment that the individual first appeared in the waterhole area (i.e. the open area around the waterhole) to the moment it started drinking, (2) drinking, from the moment the individual started drinking to the moment it stopped drinking, including all drinking and vigilance bouts and (3) departure, the moment the individual stopped drinking to the moment it left the waterhole area. We considered these three phases separately because vigilance may be unevenly distributed during these phases (Périquet et al. 2010).

During each phase, we performed 2 min focal observations to monitor the behaviour of adult individuals within groups. The duration of focal observations was limited by the high turnover of groups around waterholes. These 2 min focal observations were, however, sufficient to capture several behavioural bouts (i.e. mean \pm SD number of behavioural bouts in 2 min for the three species: 12 ± 5 during approach, 15 ± 5 during drinking, and 20 ± 9 during departure), which allowed us to test for behavioural differences between HNP and HA. During the 2 min focal observations, we measured the time that individuals spent (1) vigilant, (2) drinking and (3) walking while approaching or leaving the waterhole. Vigilance was clearly distinct from other behaviours, with vigilant animals typically standing and raising their head above the shoulders with ears held forward (Alados 1985). During our observations, all focal animals that were vigilant were standing, so we considered standing bouts as vigilance bouts. Times spent walking, drinking and vigilant were exclusive from one another, as the time an individual spent in vigilance was negatively correlated with time spent walking or drinking (see [Supplementary Table S1](#)). We also recorded the total duration of the drinking phase of focal individuals. We recorded the sex of focal individuals, group size, presence of young in the group (yes/no), and the minimal distance to vegetation cover (measured with a rangefinder as the distance from the waterhole to the closest scrub/treeline), because these factors may influence the perception of predation risk (e.g. Dehn 1990; Burger & Gochfeld 1994; Burger et al. 2000).

Monitoring of groups

For each group entering the waterhole area, we recorded whether the group drank (i.e. at least one individual drank) or not (i.e. none of the individuals drank). When the group drank, we measured the group (1) approach time (i.e. from the moment the group entered the waterhole area to the moment the first individual of the group began to drink), (2) drinking time (i.e. from the moment the first individual of the group began to drink to the moment the last individual of the group stopped drinking) and (3) departure time (i.e. from the moment the last individual of the group stopped drinking to the moment the group left the waterhole area). Distances walked by groups in approach and departure phases may influence the group approach and departure times. We therefore recorded the approach and departure distances in categories (i.e. 0–50 m, 50–100 m, 100–150 m, 150–200 m, >200 m) for each group, and accounted for this in the analyses.

The study comprised 84 days of observations in HNP (ca. 1000 h) and 46 days of observations in HA (ca. 550 h). We observed 268 groups in HNP ($N = 133$ impala, $N = 120$ greater kudu, $N = 15$ sable antelope) and 226 groups in HA ($N = 134$ impala, $N = 54$ greater kudu, $N = 38$ sable antelope). We obtained a total of 154 individual

focal observations in HNP ($N = 52$ impala, $N = 60$ greater kudu, $N = 42$ sable antelope) and 166 individual focal observations in HA ($N = 68$ impala, $N = 58$ greater kudu, $N = 40$ sable antelope). Group size ranged from 1 to 110 in impala (mean \pm SD = 10 ± 14), 1 to 20 in greater kudu (5 ± 4) and 1 to 50 in sable antelope (10 ± 12).

Statistical Analyses

Drinking probability

We used mixed logistic regressions to calculate the probability of drinking once animals had entered the waterhole area. We tested the effect of land use (i.e. HNP (no hunting) versus HA (hunting)). We included presence of young in the group, group size and minimal distance to vegetation cover as covariates. We added waterhole identity as a random factor. We then compared the probability of drinking among species by running logistic models for each land use separately, with species as a single factor.

Individual behaviour

For each species, we first computed the proportion of time spent in vigilance by individuals during the 2 min focals in each phase and the total duration of their drinking phase. We arcsine square-root transformed these proportions and square-root transformed the total durations of the drinking phase to meet assumptions of normality and homogeneity of variance (Sokal & Rohlf 1995). We used linear mixed models, with waterhole identity as a random factor, to test the effect of land use on the proportion of time individuals spent in vigilance and on the total duration of each individual's drinking phase. In addition to testing for the effect of land use, we tested for effects of presence of young, sex, group size and minimal distance to vegetation cover as covariates. We then used linear models to test for the effects of phase and species, and their interaction, on the proportion of time individuals spent in vigilance.

Group approach, drinking and departure times

The time spent in the different phases by groups was log transformed to meet the assumptions of normality and homogeneity of variance. For the approach and departure phases, we used linear mixed models with approach and departure distances and waterhole identity as random factors to test for the effect of land use. For the drinking phase, we used linear mixed models with waterhole identity as a random factor. In each case, we also tested for the effects of presence of young, group size and minimal distance to vegetation cover as covariates.

For the selection of models, we used the Akaike's Information Criterion (AIC) to select the best model with the small sample adjustment AICc (Burnham & Anderson 2002). The model with the lowest AICc value (i.e. the best compromise between accuracy and precision) was retained. When Δ AICc between two models was less than two, we selected the simplest model according to the parsimony rules (Burnham & Anderson 2002). We defined a set of a priori models for each species and each dependent variable (see [Supplementary Table S2](#)). Statistical analyses were performed with R nlme and lme4 packages for linear and generalized linear mixed models (<http://cran.r-project.org/web/packages/index.html>).

RESULTS

Drinking Probability

The selected model for the probability of drinking in impala included land use, minimal distance to vegetation cover, and their interaction ([Supplementary Table S2](#)). The probability of drinking was lower in HA than in HNP ([Table 2](#)). This probability decreased as the minimal distance to vegetation cover increased, but less

Table 2

Estimated parameters and 95% confidence intervals for the most parsimonious models of drinking probability for groups of impala, greater kudu and sable antelope that visited waterhole areas in Hwange National Park (HNP, nonhunting area), Zimbabwe, and in peripheral hunting areas (HA) during the 2008 dry season

Drinking probability	Selected model	k^*	Parameter	df	Estimate	95% CI
Impala	Land use \times distance to cover	18	Intercept	1	6.17	3.25, 9.09
			HA [†]	1	-4.59	-7.92, -1.25
			Distance to cover	1	-0.06	-0.09, -0.02
			HA \times distance to cover	1	0.05	0.01, 0.1
Greater kudu	Group size	15	Intercept	1	0.67	-0.19, 1.55
			Group size	1	0.15	0.02, 0.29
Sable antelope	Null	12	Intercept	1	9.04	-4.21, 22.3

* Number of parameters includes the random factor 'waterhole'.

[†] Results are presented as the difference estimate between HA and the reference class HNP.

rapidly in HA (Table 2). For greater kudu, the model selected only included group size (Supplementary Table S2), with the probability of drinking increasing with group size (Table 2). In sable antelope, land use and the covariates did not influence the probability of drinking (Table 2, Supplementary Table S2).

In HNP, the drinking probability of groups was lower for greater kudu than for impala (ca. 83% versus 93%, respectively; estimate \pm SE = -1 ± 0.4 ; Wald test: $Z = -2.4$, $N = 276$, $P = 0.02$), but did not differ between groups of sable antelope and impala (ca. 94% and 93%, respectively; $Z = 0.1$, $P = 0.9$). However, in HA, this probability was higher for groups of sable antelope than for groups of impala (ca. 95% versus 76%, respectively; estimate \pm SE = -1.8 ± 0.8 ; $Z = -2.4$, $N = 244$, $P = 0.02$) and greater kudu (ca. 95% versus 67%, respectively; estimate \pm SE = -2.2 ± 0.8 ; $Z = -2.9$, $N = 244$, $P = 0.004$), whereas there was no significant difference between impala and greater kudu ($Z = -1.6$, $N = 244$, $P = 0.1$).

Individual Level

Approach phase

For the three species, the selected model for the proportion of time in vigilance during approach only included land use (Supplementary Table S2). The proportion of time that individual impala, greater kudu and sable antelope spent in vigilance while they were approaching waterholes was 2.5, 1.5 and 3.7 times higher, respectively, in HA than in HNP (Table 3, Fig. 2a).

Drinking phase

The selected model for the proportion of time in vigilance during drinking only included land use for impala, whereas none of the variables influenced this proportion in greater kudu and sable antelope (Supplementary Table S2). Impala were 1.7 times more vigilant in HA than in HNP while drinking, whereas there was no difference for greater kudu and sable antelope (Table 3, Fig. 2b).

The total duration of the individual drinking phase did not differ between HA and HNP for any of the three species (ANOVA: impala: $F_{1, 62} = 2.4$, $P = 0.1$; greater kudu: $F_{1, 43} = 3.4$, $P = 0.07$; sable antelope: $F_{1, 38} = 3.6$, $P = 0.07$).

Departure phase

The selected model for the proportion of time in vigilance during departure only included land use for impala and sable antelope; none of the variables influenced this proportion for greater kudu (Supplementary Table S2). Impala and sable antelope were 1.8 and 1.3 times more vigilant, respectively, in HA than in HNP while leaving waterholes, whereas there was no difference for greater kudu (Table 3, Fig. 2c).

Effects of species and phase on individuals' time spent vigilant

The phase influenced the proportion of time that individuals spent in vigilance in HNP ($F_{2, 168} = 28.2$, $P < 0.0001$; Fig. 3a) and in HA ($F_{2, 193} = 103.5$, $P < 0.0001$; Fig. 3b). In both land uses, individuals of the three species were less vigilant while drinking than

Table 3

Estimated parameters and 95% confidence intervals for the most parsimonious models of the proportion of time that individual impala, greater kudu and sable antelope were vigilant while approaching and while drinking and departing from waterholes in Hwange National Park (HNP, nonhunting area), Zimbabwe, and in peripheral hunting areas (HA) during the 2008 dry season

Individual vigilance*	Species	Selected model	k^{\dagger}	Parameter	df	Estimate	95% CI	
Approach	Impala	Land use	9	Intercept	1	0.44	0.28, 0.60	
				HA [‡]	1	0.42	0.20, 0.65	
				Intercept	1	0.64	0.74, 0.55	
	Greater kudu	Land use	9	HA	1	0.24	0.09, 0.39	
				Intercept	1	0.40	0.22, 0.59	
				HA	1	0.42	0.15, 0.69	
Drinking	Impala	Land use	9	Intercept	1	0.26	0.37, 0.15	
				HA	1	0.18	0.08, 0.29	
	Greater kudu	Null	9	Intercept	1	0.53	0.47, 0.59	
	Sable antelope	Null	9	Intercept	1	0.31	0.22, 0.39	
	Departure	Impala	Land use	9	Intercept	1	0.58	0.46, 0.71
					HA	1	0.32	0.15, 0.50
Greater kudu		Null	11	Intercept	1	0.85	0.75, 0.95	
Sable antelope		Land use	9	Intercept	1	0.73	0.60, 0.85	
				HA	1	0.25	0.07, 0.43	

* Proportion of time spent in vigilance (arcsine square-root-transformed data) during 2 min focals.

[†] Number of parameters includes the random factor 'waterhole'.

[‡] Results are presented as the difference estimate between 'HA' and the reference class 'HNP'.

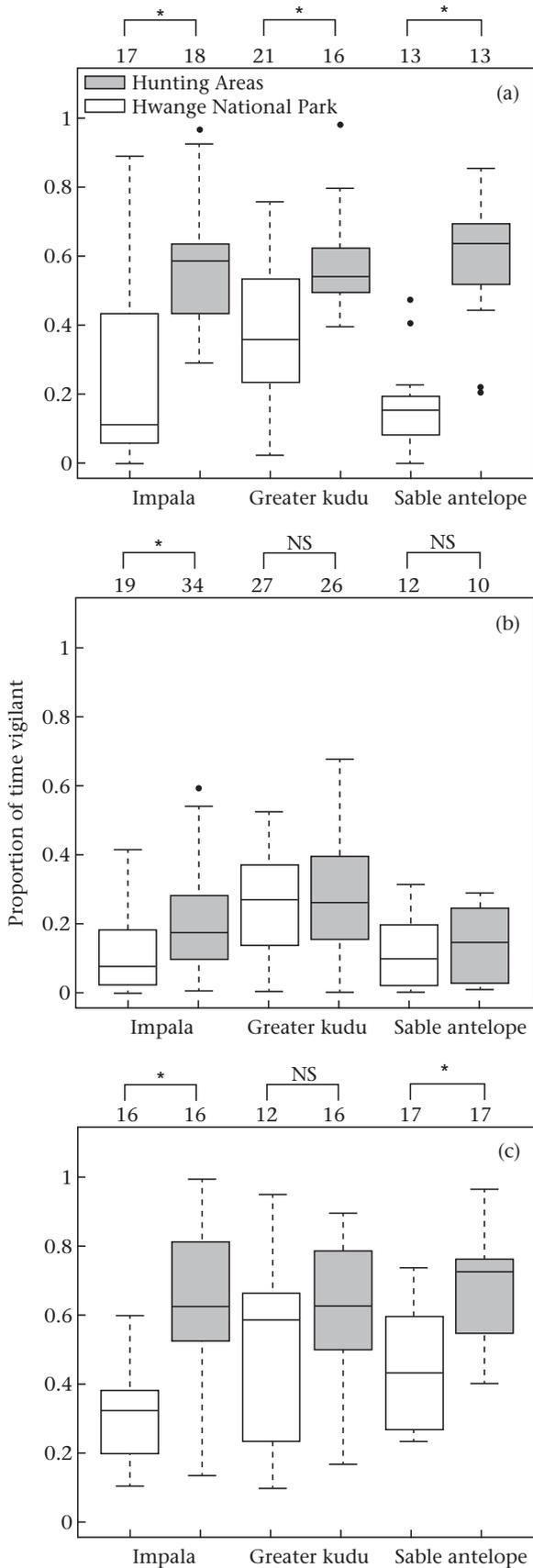


Figure 2. Proportion of time that individual impala, greater kudu and sable antelope spent in vigilance while (a) approaching and (b) drinking and (c) departing from waterholes in Hwange National Park (nonhunting area), Zimbabwe, and in adjacent

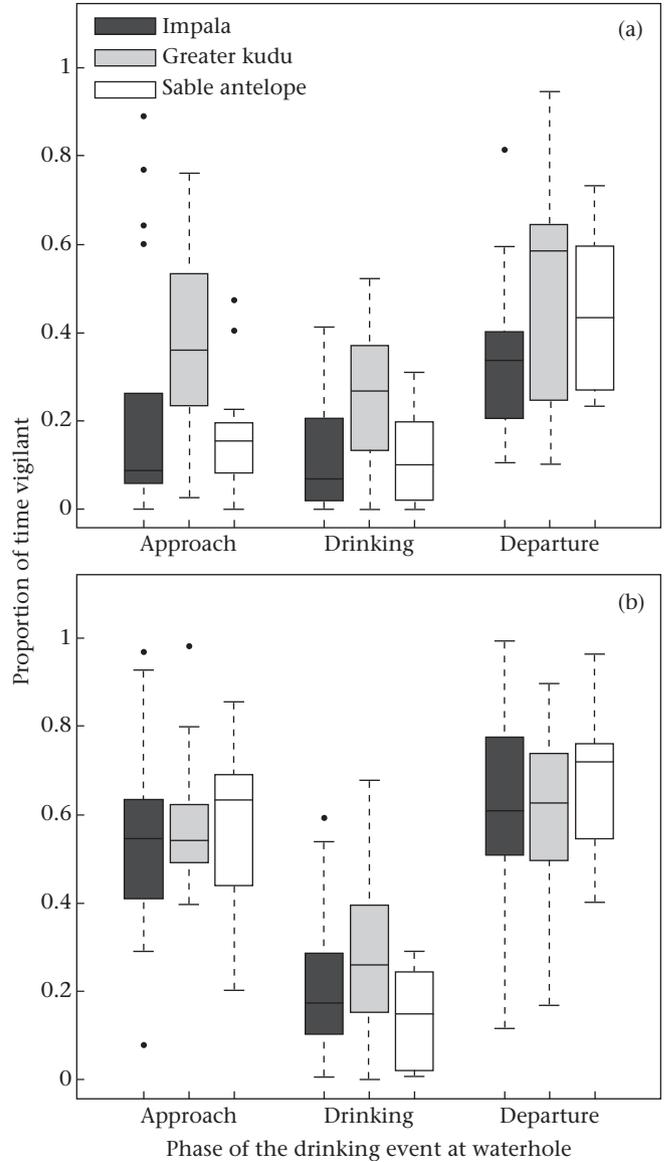


Figure 3. Proportion of time that individual impala, greater kudu and sable antelope spent in vigilance while approaching and while drinking and departing from waterholes in (a) Hwange National Park (nonhunting area), Zimbabwe, and (b) adjacent sport hunting areas. The horizontal line within the box represents the median, the box illustrates the range between the 25th and 75th percentile, the two dotted segments outside the box represent the 10th and 90th percentiles, and the black dots are observations <10th or >90th percentile.

while approaching (in HNP: estimate \pm SE = -0.1 ± 0.07 ; Student's *t* test: $t_{1, 168} = -2, P = 0.05$; in HA: estimate \pm SE = -0.4 ± 0.06 ; $t_{1, 193} = -7.1, P < 0.0001$) and leaving (in HNP: estimate \pm SE = -0.3 ± 0.07 ; $t_{1, 168} = -4.6, P < 0.0001$; in HA: estimate \pm SE = -0.4 ± 0.06 ; $t_{1, 193} = -7.6, P < 0.0001$) waterholes.

In HNP, the proportion of time that individuals spent in vigilance differed with species (ANOVA: $F_{2, 168} = 14.2, P < 0.0001$). Greater kudu were more vigilant than impala (estimate \pm SE = 0.2 ± 0.08 ;

sport hunting areas. * $P < 0.05$. Sample sizes are given above each box plot. The horizontal line within the box represents the median, the box illustrates the range between the 25th and 75th percentiles, the two dotted segments outside the box represent the 10th and 90th percentiles, and the black dots are observations <10th or >90th percentile.

Student's *t* test: $t_{1, 168} = 2.7, P = 0.008$), whereas we observed no difference between sable antelope and impala ($t_{1, 168} = -0.5, P = 0.6$). In HA, conversely, the proportion of time that individuals spent vigilant did not vary with species (ANOVA: $F_{2, 193} = 1.3, P = 0.3$). The interaction between phase and species was not significant in HNP ($F_{4, 168} = 0.8, P = 0.5$) and in HA ($F_{4, 193} = 1.7, P = 0.1$).

Group Approach, Drinking and Departure Times

Approach time

The null models were selected for all three species, meaning that the time for groups to approach waterholes was not influenced by land use or by the covariates (Fig. 4a, Table 4, Supplementary Table S2).

Drinking time

For the three species, land use was not included in the selected models and thus had no effect on drinking time of groups (Fig. 4b, Table 4, Supplementary Table S2). Drinking time, however, increased with group size in impala (Table 4) and was shorter for groups without juveniles in greater kudu (Table 4).

Departure time

For the three species, land use was not included in the selected models and thus had no effect on the departure time of groups (Fig. 4c, Supplementary Table S2). Departure time, however, was shorter for groups without juveniles in greater kudu (Table 4).

DISCUSSION

Behavioural adjustments in response to hunting risk have been outlined in several large herbivores (e.g. Kilgo et al. 1998; Austrup 2000; Matson et al. 2005; Reimers & Colman 2006; Setsaas et al. 2007; Benhaiem et al. 2008). However, the extent to which large herbivores can adjust their behaviour in response to both hunting risk and predation risk remains poorly understood, because most studies have concentrated on northern ecosystems where human activities have widely reduced the diversity and densities of natural predators, and hence, the predation risk for large herbivores (Berger 1999).

In Hwange National Park (hunting-free area), Zimbabwe, more than 90% of the groups of impala and sable antelope and nearly 85% of the groups of greater kudu eventually drank once they entered waterhole areas. This suggests that most large African herbivores depend on surface water (Western 1975; Thrash et al. 1995; Owen-Smith 1996; Redfern et al. 2003). It also shows that the greater kudu is more likely to leave waterholes without drinking, possibly as a result of the combined effect of its greater vulnerability to natural predators and its lower dependence on surface water. In the neighbouring hunting areas, however, up to 24% of groups of impala and 33% of groups of greater kudu left waterhole areas without drinking. Groups of sable antelope, conversely, showed no decrease of drinking probability in hunting areas compared to nonhunting areas in the National Park. This is consistent with the observation that sable antelope are more constrained by surface water than are greater kudu and impala (Redfern et al. 2003; Rahimi & Owen-Smith 2007). Animals that are more constrained by resource requirements are indeed less likely to adjust their behaviour in response to disturbance (Gill et al. 2001; Beale & Monaghan 2004).

Results at the individual level clearly showed, however, that sable antelope, like impala and greater kudu, behaviourally responded to hunting risk. In groups that eventually approached waterholes to drink, individuals of all three species spent more

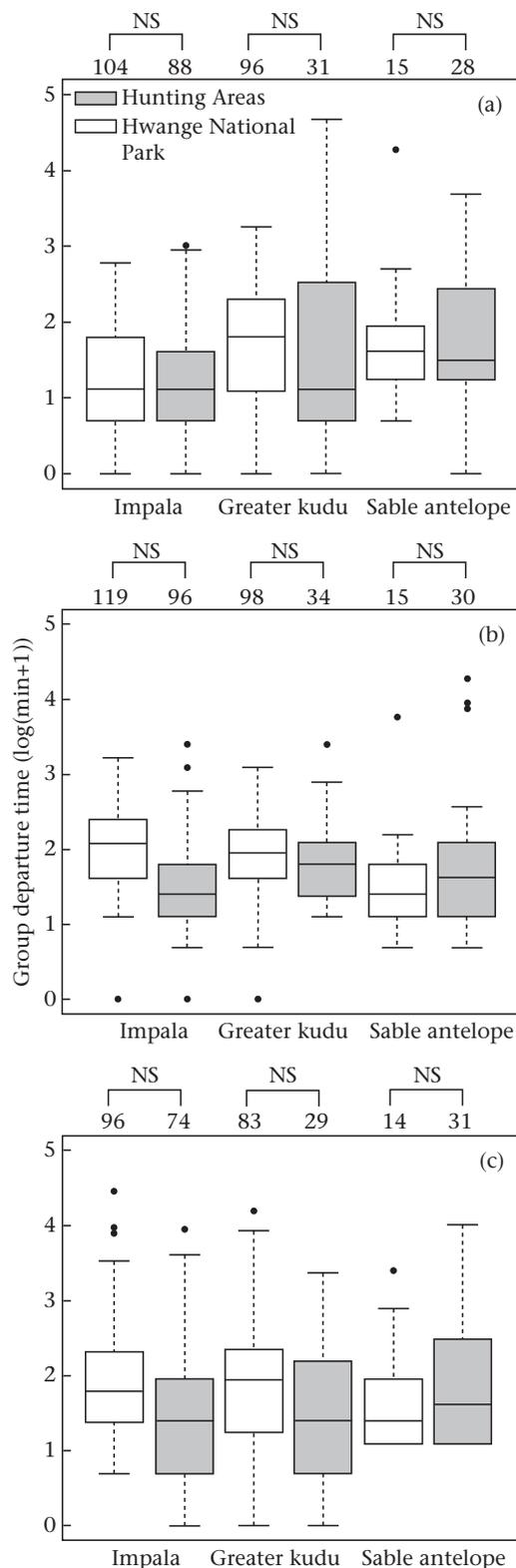


Figure 4. Time that groups of impala, greater kudu and sable antelope spent (a) approaching and (b) drinking and (c) departing from waterholes in Hwange National Park (nonhunting area), Zimbabwe, and in adjacent sport hunting areas. Sample sizes are given above each box plot. The horizontal line within the box represents the median, the box illustrates the range between the 25th and 75th percentile, the two dotted segments outside the box represent the 10th and 90th percentiles, and the black dots are observations <10th or >90th percentile.

Table 4
Estimated parameters and 95% confidence intervals for the most parsimonious models of the time that groups of impala, greater kudu and sable antelope spent approaching and drinking and departing from waterhole areas in Hwange National Park (HNP, nonhunting area), Zimbabwe, and in peripheral hunting areas (HA) during the 2008 dry season

Group time*	Species	Selected model	k_{\dagger}	Parameter	df	Estimate	95% CI
Approach	Impala	Null	24	Intercept	1	1.31	1.06, 1.56
	Greater kudu	Null	31	Intercept	1	1.51	1.08, 1.95
	Sable antelope	Null	16	Intercept	1	1.57	1.15, 2.00
Drinking	Impala	Group size	14	Intercept	1	1.49	1.30, 1.67
				Group size	1	0.025	0.019, 0.032
	Greater kudu	Status	17	Intercept	1	2.01	1.83, 2.18
				No juvenile‡	1	-0.31	-0.52, -0.10
Sable antelope	Null	10	Intercept	1	1.77	1.51, 2.03	
Departure	Impala	Null	27	Intercept	1	1.64	1.32, 1.96
				Greater kudu	Status	19	Intercept
	Sable antelope	Null	16	No juvenile			1
				Intercept	1	1.74	1.47, 2.02

* Log-transformed data.

† Number of parameters includes the random factors 'waterhole' and 'approach distance' or 'departure distance' for the approach and departure phases.

‡ Results are presented as the difference estimate between 'no juvenile' and the reference class 'presence of juveniles'.

time in vigilance in hunting areas than in nonhunting areas. Greater kudu was the most vulnerable species to natural predation in our study (Loveridge et al. 2007; Drouet-Hoguet 2007) and was accordingly the most vigilant in the National Park. As predicted, greater kudu displayed the lowest increase in vigilance in response to hunting risk. Indeed, vigilance overall increased by 32% in greater kudu (from 34% in HNP to 45% in HA), compared to 65% (from 20% to 33%) and 85% (from 27% to 50%) for impala and sable antelope, respectively. Périquet et al. (2010) suggested that greater kudu in Hwange national Park are already close to a maximum level of vigilance and therefore could hardly increase their vigilance further in response to additional risk. The time allocated to vigilance is indeed limited because the costs associated with an increase in vigilance may eventually outweigh the benefits of reduced risk (Lima & Dill 1990; Lima 1998). Feeding rate, for instance, decreases with increasing vigilance (Beauchamp & Livoreil 1997; Fritz et al. 2002). In our study, vigilance increased at the expense of walking and drinking. Increased vigilance may thus force individuals to extend their stay at waterholes, away from shade and protective cover, and so may alter thermoregulation (e.g. Jarman & Jarman 1973; Owen-Smith 1998) and increase exposure to natural predators (Valeix et al. 2007).

Vigilance varied according to the main activity that individuals were engaged in. For the three species, individuals were indeed more vigilant while they were approaching or leaving waterholes than while they were drinking. They thus prioritized drinking over vigilance once they reached a waterhole, even though they were furthest from protective cover and thus at greater risk relative to the other two phases. In hunting areas, moreover, vigilance greatly increased during approach and departure, whereas it did not vary much during drinking. By not increasing their vigilance during drinking, individuals managed to satisfy their water requirements without extending their drinking period, and thus the time they remained exposed to predators and hunters. Vigilance during foraging periods is limited (Illius & FitzGibbon 1994; Shipley et al. 1999; Cowlshaw et al. 2004). Interestingly, only impala increased vigilance during drinking in response to hunting. This supported our prediction that species less vulnerable to natural predators and less constrained by key resources are more likely to adjust further their behaviour in response to hunting because they have the capacity to do so.

At the group level, the increase in individual vigilance should have resulted in extended periods spent in waterhole areas. Groups in hunting areas, however, approached, drank and left waterholes

as fast as groups in the National Park. This indicates that groups in hunting areas were more cohesive than groups in the National Park (i.e. distances between group members were reduced; e.g. Lingle 2001). Enhanced cohesion would therefore allow groups in hunting areas to reduce time spent in waterhole areas, thus limiting their exposure to hunters. Greater cohesion in groups moreover promotes the dilution effect (Hamilton 1971; Dehn 1990) and increases confusion in predators (Neill & Cullen 1974; Milinski 1977). However, it also requires greater synchrony in behaviour among group members. Such synchrony may be costly for individuals because they have to compromise their own activity budgets to follow the behaviour of other group members (e.g. Côté et al. 1997; reviewed in Conradt & Roper 2005).

Group size positively influenced drinking probability in greater kudu. The risk perceived by individuals decreases in larger groups because of dilution (Hamilton 1971; Dehn 1990) and because there are more eyes to detect danger ('many eyes' effect; Pulliam 1973). Drinking probability, however, did not increase with group size in impala and sable antelope, possibly because these species form larger groups than greater kudu, making the effect of increased group size in these two species negligible. The time that groups spent drinking increased with group size in impala, probably because it took longer for all group members in larger groups to complete the drinking phase. In approach and departure phases, however, there was no effect of group size. We suspect that larger groups managed to limit the duration of approach and departure, and thus the time they spent in waterholes areas, by increasing their cohesion. This, however, remains to be investigated.

Sex did not influence the time that individuals spent vigilant, whereas we could have expected males to be more vigilant than females in hunting areas (e.g. Matson et al. 2005), because hunting is male biased in sable antelope and, to a lesser extent, in greater kudu. Hunters frequently target males in mixed groups (ZPWMA, personal observations); thus, females are often disturbed as much as males. Presence of young in groups had no effect on individual vigilance. At the time of our study, young were about 10 months old, and thus, less vulnerable to predators than earlier in the year (Bourgarel 2004). Risk perceived in groups with young was therefore possibly not higher than in groups without young. However, greater kudu spent less time drinking and departing from waterholes when there were no juveniles in the group. As the minimal distance to vegetation cover increased, drinking probability decreased. This is consistent with previous studies suggesting that the perceived risk increases with distance to protective cover (Creel

& Winnie 2005; Valeix et al. 2007). The absence of such effects in greater kudu is consistent with the idea that greater kudu are close to a maximum level of vigilance and cannot increase their vigilance further (Périquet et al. 2010). Similarly, sable antelope are less likely to adjust their vigilance at waterholes because they are more constrained by access to surface water than are greater kudu and impala (Western 1975; Redfern et al. 2003; Rahimi & Owen-Smith 2007).

Conclusion

Our study illustrates how both vulnerability to natural predation and resource requirements constrain the behavioural adjustments of prey species to hunting risk. Species that naturally display strong adjustments in response to predation risk, such as greater kudu, and species that are strongly constrained by resource requirements, such as sable antelope, are less likely to adjust their behaviour in response to the additional risk imposed by hunting. This challenges the risk-disturbance hypothesis that predicts that prey species that naturally experience higher predation risk are more likely to respond to human disturbance (Frid & Dill 2002). Our work, moreover, illustrates how changes in behaviour may not always be good measures of the relative susceptibility of species to human disturbance (Gill et al. 2001) and urges for the importance of multispecies studies in the investigation of wildlife responses to human disturbance (Blumstein et al. 2005). In terms of management and conservation, further research is needed on the associated costs of behavioural adjustments in response to hunting risk (e.g. alteration of activity budgets, costs of synchrony and increased exposure to natural predators). This would help managers decide whether the design of 'hunting-free sanctuary zones' around key resources, such as waterholes in semi-arid African savannas, is desirable in hunting areas.

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Supplementary Material

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