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

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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.

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.

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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 km^2 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 km^2; Gwayi Intensive Conservation Area South, Gwayi ICA South, ca. 880 km^2). 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 km^2; four hunting properties in Gwayi ICA South, ca. 300 km^2; Fig. 1). In nonhunting areas (nonHA), we covered the blocks that were adjacent to those hunting concessions (i.e. Main camp, ca. 1300 km^2; Robins, ca. 1000 km^2) 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; Crosmary 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 (Crosmary 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 Crosmary et al. 2012) and are harvested in