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Herbivores employ a suite of antipredator behaviours to minimize risk from ambush and cursorial predators

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Prey species may adjust their use of antipredator behaviours to counter the hunting strategies (e.g. ambush versus cursorial) and the level of risk imposed by different predators. Studies of suites of behaviours across well-defined contrasts of predation risk and type are rare, however. Here we explored the degree to which six herbivore species adjusted their antipredator behaviours to two predator treatments (lion, *Panthera leo*, versus cheetah, *Acinonyx jubatus*, and wild dogs, *Lycaon pictus*). We focused on prey behaviour (vigilance, grouping, temporal use) at waterholes. We predicted that if the hunting strategy of the predator was the key driver of antipredator behaviour, ambushing lions would elicit a greater response than cursorial cheetah and wild dogs. Alternatively, if predator preference was the main driver, then we expected prey species to adjust their antipredator behaviours in response to the predators that specifically target them (i.e. preferred prey of the different predators). Overall, we found that the herbivores maintained greater vigilance, generally moved in larger groups and used waterholes less at dawn, at dusk or at night (when lions are active) when exposed to the potential threat of ambushing lions. However, some species within the accessible prey range of cheetah and/or wild dogs (i.e. red hartebeest, warthog, gemsbok) moved in larger groups when exposed to these predators. Yet, the magnitude of the differences in group size for these herbivores were small. Thus, we suggest that, overall, the potential threat of ambushing lions was the main driver of antipredator behaviour around waterholes, probably determined by prey weight preference and the possibility of being ambushed.

Prey possess a whole suite of behaviours that they may employ to reduce predation risk (Caro, 2005; Lima & Dill, 1990). In particular, vigilance and grouping are flexible behaviours that can be used to reduce risk, although they come with associated costs. For example, increased vigilance allows individuals to detect attacks earlier, providing a greater chance of escaping (Lima & Bednekoff, 1999), but often reduces food intake rate (Fortin, Boyce, Merrill, & Fryxell, 2004). Living in larger groups allows individuals to potentially benefit from dilution, collective vigilance and/or deterrence effects (Beauchamp, 2003; Schmitt, Stears, Wilmers, & Shrader, 2014), but could increase intragroup competition (Krause & Ruxton, 2002). Because of these costs, prey are not expected to always display a full suite of antipredator behaviours, but rather to finely adjust antipredator behaviours to the level of risk, by prioritizing certain behaviours over others (e.g. vigilance, grouping, temporal shifts; Creel, Schuette, & Christianson, 2014).

Predation risk varies both temporally and spatially across the landscape. This translates into a 'landscape of fear' (Laundré, Hernández, & Altendorf, 2001) that is shaped by differences in the prey's perception of the likelihood of meeting a specific predator (e.g. predator density, similar landscape use between predator and prey, shared time of activity), and of the likelihood of being killed when attacked (i.e. 'threat' of the predator). However, as not all predators are the same, prey species probably adjust the extent to which they utilize different antipredator behaviours (e.g. vigilance levels, group size) in response to different predators or predator combinations.

One factor that probably greatly influences antipredator strategies is the hunting strategy of a predator. For instance, large mammalian predators are usually classified as either cursorial or stalking/ambush predators. Cursorial predators roam over large areas looking for prey, and then approach prey rapidly and silently when found (Creel & Creel, 2002; Pomilia, McNutt, & Jordan, 2015). As a result, their distribution in the landscape is generally unpredictable, and thus prey tend not to associate specific places with predation risk from these species (see discussion in Preisser, Orrock, & Schmitz, 2007). In contrast, ambush predators rely on

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places where the likelihood of meeting prey is high, relying on small-scale vegetation cover, rather than speed, to approach prey (Preisser et al., 2007). Thus, areas attracting prey usually also attract ambush predators, and thus prey should increase their antipredator behaviour when using these areas (Valeix, Fritz, et al., 2009). For example, within the arid and semiarid environments that we studied here, water sources attract both large mammalian herbivores and their ambush predators such as lions, *Panthera leo* (Ogutu et al., 2014; Thaker et al., 2011; Valeix et al., 2010; de Boer et al., 2010).

In addition to a predator's hunting strategy, prey species probably also consider the degree of threat posed by a specific predator. Predators tend to target prey species within specific body size ranges (for lion: Clements, Tambling, Hayward, & Kerley, 2014; Hayward, 2006; Hayward, Hayward, Tambling, & Kerley, 2011). Thus, some predators will be more of a threat than others. For example, lions are more likely to attack a 290–340 kg zebra, *Equus quagga*, than a 40–70 kg impala, *Aepyceros melampus* (Hayward & Kerley, 2005). As a result, prey species should increase the extent to which they utilize specific behaviours (e.g. increase vigilance levels) in response to their primary predators, compared to more peripheral predators. Yet, an overarching factor that greatly influences predation risk is the overlap in the activity patterns of predators and prey (i.e. whether they are nocturnal or diurnal; Kronfeld-Schor & Dayan, 2003). To minimize contact with predators, prey species can shift their temporal use of the landscape to periods when predators are least active. For example, in Hwange National Park, Zimbabwe, most ungulate species appear to avoid coming to drink at night when lions are in the vicinity of the waterholes (Valeix, Fritz, et al., 2009).

Here we explored the degree to which prey species adjust their antipredator strategies in response to different predators. We focused our observations at waterholes in a semiarid ecosystem as a model of key interaction areas between predators and prey, and studied the antipredator behaviour (grouping, vigilance, time of use) of six large herbivore species (i.e. eland, *Taurotragus oryx*; gemsbok, *Oryx gazella*; plains zebra, red hartebeest, *Alcelaphus buselaphus caama*; warthog, *Phacochoerus africanus*; blue wildebeest, *Connochaetes taurinus*) at these waterholes. We did this in two sections of the same reserve that were separated by fences, one with only lions (ambush predators), the other with cheetah, *Acinonyx jubatus*, and wild dogs, *Lycaon pictus* (both cursorial predators) and no lions.

In many ecosystems, lions select and kill in areas close to water (Ogutu et al., 2014; Thaker et al., 2011; Valeix et al., 2010; de Boer et al., 2010). Cheetah and wild dog may also do this, but their presence near waterholes might be less predictable as their cursorial hunting strategies probably increase their use of areas away from water sources, more so than lions (e.g. Ndaimani, Tagwireyi, Sebele, & Madzikanda, 2016). Thus, we predicted that if hunting strategy was a key driver of prey antipredator behaviour, lions would elicit a greater antipredator response from prey species than the less spatially predictable cheetah and wild dogs. This could be through all the prey species changing their antipredator behaviours (e.g. increased vigilance and larger groups) and/or adjusting their temporal activity patterns more in response to lions than to cheetah and wild dogs. Alternatively, if antipredator behaviours of prey species are driven more by prey preferences of predators, then we would expect individual prey species to change their antipredator behaviours more in response to the predators that specifically target them (i.e. prey falling within the predator's preferred prey weight range) than if the prey species falls outside the predator's prey weight range. This could then result in species-specific differences both within and between the predator sections.

METHODS

Ethical Note

The University of KwaZulu-Natal approved all aspects of the research design (Ethics code: 058/14/Animal).

Data Collection

We conducted our study in Tswalu Kalahari Reserve (Tswalu hereafter) in the Northern Cape, South Africa (S 27°13′30″ and E 022°28′40″) from October 2013 to April 2015. The fenced reserve encompasses 1000 km^2 of restored farmland (Cromhout, 2007) located in the southern Kalahari (Roxburgh, 2008). Tswalu has a mean annual rainfall of 250 mm, with an extended dry season lasting from May to September/October when there is less than 10 mm rainfall (Roxburgh, 2008). Large mammalian herbivores found in the reserve include kudu, *Tragelaphus strepsiceros*, springbok, *Antidorcas marsupialis*, gemsbok, eland, sable, *Hippotragus niger*, zebra, red hartebeest, warthog and wildebeest.

Tswalu is divided into two adjacent sections which support different large predator populations, but are separated by about 50 m comprising a road and two predator fences. The western section of the reserve (200 km^2) contains lion ($N = 24$), while the eastern section (800 km^2) contains populations of cheetah (N ~10) and wild dog ($N = 14$). Habitat types across both sections are similar, made up of *Digitaria polyphylla*-dominated hills, *Stipagrostis uniplumis*-dominated plains and valleys and *Anthephora pubescens*-dominated sand dunes (see Van Rooyan, 1999). Likewise, both sections have a similar mean annual rainfall (mm), with 326 ± 40 mm falling within the western section compared to 345 ± 42 mm within the eastern section recorded over a 9-year period. We limited data collection to the herbivore species that occurred in both sections of the reserve. These included eland, gemsbok, zebra, red hartebeest, warthog and wildebeest. The herbivores living in the two sections face different levels of predation risk due to the hunting strategy employed, their activity patterns and the prey weight preferences of the different predator species (Hayward & Slotow, 2009; Hayward et al., 2007). Lion are stalk and ambush predators that are predominantly active at night, while cheetah and wild dogs are mostly diurnal and hunt by chasing down their prey (Hayward & Somers, 2009). Comparing prey weight preferences from a multisite analysis, Clements et al. (2014) determined that lion have an accessible prey weight class range of 32–632 kg and therefore all six herbivores species monitored in our study fall within their prey weight range. However, they tend to prefer prey weights of 92–632 kg (Clements et al., 2014) with wildebeest and zebra often preferentially targeted over other prey (Sinclair, Mduma, & Brashares, 2003). In contrast, cheetah and wild dogs have smaller accessible prey weight ranges of 14–135 kg (with a peak weight mode of 36 kg; Hayward, Hofmeyr, O'Brien, & Kerley, 2006) and 10–289 kg (peak weight modes of 16–32 kg and 120–40 kg; Hayward, Hofmeyr, et al., 2006), respectively. Therefore, only warthog and red hartebeest fall within the accessible range of cheetah, while all the herbivores, except eland, fall within the accessible prey range of wild dogs (Clements et al., 2014). However, although warthog fall within the accessible prey range of both cheetah and wild dogs, they are generally avoided (Clements et al., 2014; Hayward, Hofmeyr, et al., 2006). Despite discrepancies in prey weight range preferences, cheetah and wild dogs have the highest recorded dietary overlap (73.5%; Hayward & Kerley, 2008) of the large African predator guild and therefore present a significant cumulative predation risk to shared prey species. Within Tswalu, lion prey upon wildebeest and gemsbok (Roxburgh, 2008), while cheetah prey on red hartebeest and