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ABSTRACT

Foraging behaviour and vigilance of African ungulates are considered to be influenced by their perception of predation risk. In this experiment, I tried to obtain a better understanding of the relative importance of spatial and temporal drivers of perceived predation risk for African ungulates of various sizes. On 12 experimental plots located in Hluhluwe-iMfolozi Park (South Africa), I manipulated vegetation cover, and applied scats of lions (*Panthera leo*) and African wild dogs (*Lycaon pictus*). I recorded the number of visitations, the amount of time spent on plots, the group sizes, and the proportion of time spent vigilant of mammalian herbivores. I found that on plots with lion and African wild dog scats, small and intermediate-sized ungulates were more vigilant, large and intermediate-sized ungulates aggregated in larger numbers, and species of all size classes increased the amount of time they spent on plots. In the absence of carnivore scats, woody cover only negatively influenced patch selection of impala (*Aepyceros melampus*). However, in the presence of lion scats, woody cover was avoided by ungulates of intermediate size, while impala increased their group size and buffalo (*Syncerus caffer*) spent more time on wooded plots. On the other hand, presence of African wild dog scats did not trigger or increase any antipredator behaviour associated to woody cover. White rhinoceros (*Ceratotherium simum*), who represent nearly half of the park's ungulate biomass, did not respond to either woody cover nor carnivore scats. This study illustrates how perceived predation risk and antipredator behaviour of African ungulates is influenced by body mass and an interaction of spatial and temporal risk factors.

INTRODUCTION

Carnivores influence prey populations not only through direct predation but also via behavioural changes in prey animals, such as increased selection for safer habitats, increased vigilance levels and changing grouping patterns (Creel et al., 2014; Lima and Bednekoff 1999). Because these anti-predator responses often come at the cost of foraging quality and quantity (Barnier et al., 2014; Brown & Kotler, 2004) or reproduction (Scott Creel & Christianson, 2008) it has been argued that indirect behavioural effects might be of equal or even greater importance in shaping herbivore-plant community than direct lethal effects (Christianson & Creel, 2008; Creel & Christianson, 2008; Laundré et al., 2001; Preisser et al., 2005). To understand how ungulate species respond to perceived predation risks, studies have distinguished between predictive responses to "risky places" or structural, landscape-based variations in risk, and reactive responses to "risky times" or short-term variations in risk (Broekhuis et al. 2013; Creel et al. 2014; Périquet et al. 2012).

Ungulates in Africa, Europe and North America have been shown to display a variety of responses to risky places. In Yellowstone, female elks (*Cervus canadensis*) were more vigilant when close to escape-impediments (Halofsky and Ripple 2008). In

Hwange National Park (Zimbabwe), impala (*Aepyceros melampus*) were more vigilant in proximity to woody cover, contrary to zebra (*Equus quagga*) whose vigilance increased with increased distance to cover (Périquet et al. 2012). Ungulates can also respond to risky places by aggregating in larger groups, as has been shown in roe deer, but not in red deer by Barja and Rosellini (2008) in Spain. In Karongwe game reserve (South Africa), warthog and impala selected against risky places such as closed riverine habitat, while the larger blue wildebeest (*Connochaetes taurinus*), zebra and giraffe (*Giraffa cameleopardis*) selected for safer open scrub habitat (Thaker et al., 2011). Using the same experiment sites as in this study, Rogers (2016) found that only impala selected for habitats with increased visibility.

Ungulates also respond to risky times and the presence or absence of predators. In Hwange National Park, all ungulates avoided waterholes at night when lions (*Panthera leo*) were in the vicinity, and kudu (*Tragelaphus strepsiceros*), buffalo (*Syncerus caffer*) and giraffe – the preferred prey species of lion in this area – avoided waterholes day-round when lions were nearby (Valeix et al. 2009 (a)). In the Olkiramatian–Shompole Community Conservation Area (Mara ecosystem, Kenya), zebras and impalas aggregated into larger groups when lions or hyenas were present, while wildebeest disaggregated into smaller groups. The presence of lions and hyenas also increased vigilance levels in all ungulates, with the effect being inversely related to herd size (Creel et al., 2014). However, in Addo elephant Park (South Africa), space use of ungulates and ostriches was found to be driven by bottom-up factors rather than by predation risk by reintroduced lions (Davies, Tambling, Kerley, & Asner, 2016).

A range of studies also suggests that during risky times, ungulates might respond particularly strongly to what they perceive as risky places. In Hwange National Park, all ungulate species increased their use of grassland when lions were in the vicinity, with buffalo, giraffe and kudu also selecting against bushland. In Yellowstone, elk shifted from grassland to coniferous forests when wolves were present (Creel et al. 2005).

While most studies conducted in North America have focused on the trophic relations between one herbivore and one carnivore species (typically elk and wolf), most studies conducted in Africa have looked at the behavioural responses of herbivores of various size classes – from impala to giraffe – to the short-term and long-term space use of lions (but see Creel et al. 2014; Thaker et al. 2011). Although experimental studies on mammalian predator-prey interactions are scarce, a small number of experiments has looked at the effect of carnivore scats on the behaviour of wild and domestic ungulates. Kuijper et al. (2014) found that wolf scats significantly increased vigilance of red deer in Bialowieza Forest (Poland). In Southern Sweden, fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) avoided areas with reduced visibility in the presence of brown bear (*Ursus* arctos) scats (Sahlen et al., 2016) Other studies have found that olfactory cues of wild carnivores reduce food intake (Arnould et al.,1998; Shrader et al., 2008) and increase vigilance levels (Kluever et al., 2009) of domestic livestock. Browsing damage by white-tailed deer has also been shown to be reduced by spraying trees with predator scat and urine

extracts (Melchiors & Leslie, 1985; Swihart et al., 1991). In Hwange National Park however, kudu and impala did not behaviourally respond to dissolved African wild dog faeces and playback sounds of African wild dogs (van der Meer et al. 2012). Overall, scats of predators seem to be perceived as a reliable indicator for their presence by ungulates.

African savanna ecosystems are characterized by a rich and diverse assemblage of ungulates, including megaherbivores (i.e. species weighing more than 1000 kg), as well as by the presence of a carnivore guild containing up to five large mammalian predators. The strong variation in size exhibited by African ungulate species leads to large differences in the relative importance of predation, forage quality, and forage quantity in regulating populations, with species weighing less than 150 kg being particularly influenced by top-down effects and megaherbivores (e.g. species weighing more than 1000 kg) effectively excluded from predation (Hopcraft et al. 2010; Owen-Smith 1989). This might in turn influence the degree of perceived risk, and elicit different responses from species to species. Moreover, the different hunting modes and prey preferences displayed by African carnivores can be expected to trigger different, and sometimes opposite responses in prey species. While sit-and-pursue predators such as lions and leopards (*Panthera pardus*) are particularly efficient in wooded or bushy areas with reduced visibility, cursorial predators such as spotted hyena (*Crocuta crocuta*), cheetah (*Acynonix jubatus*) and African wild dog (*Lycaon pictus*), have hunting techniques that rely on more open terrain (Thaker et al., 2011). African predators also differ in their degree of dietary specialization, as well as the preferred weight range of their prey. For example, lions preferentially prey upon species with a weight of 190 to 550 kg, while African wild dogs prefer species within a range of 16 to 32 kg, and 120 to 140 kg (Hayward & Kerley, 2005; Hayward, O'Brien, Hofmeyr, & Kerley, 2006).

While harbouring all characteristics typical of a Southern African savanna, the Hluhluwe-iMfolozi Park in South Africa is unique in that 90% of its ungulate biomass is made of megaherbivores and African buffalos (~ 55% for megaherbivores alone, Le Roux et al. 2017) with particularly high densities of a megagrazer, the white rhinoceros (*Ceratotherium simum*), a keystone species of the Southern African savanna from which it has been largely extirpated (Owen-Smith et al. 2017). In this experiment, I investigated whether and to which extent ungulate species of different size classes show behavioural responses to perceived carnivory threat in terms of patch selection, group size, time spent on patch, and vigilance level. I looked at the effect of vegetation cover (risky places) and of cues of carnivore presence by using scats of lions and African wild dogs (risky times), respectively sit-and-pursue and cursorial predators. I was particularly interested in the interaction effect between risky places and risky times. I tested the six following hypotheses:

(1) Ungulates select against, aggregate in larger groups, spend less time and are more vigilant in habitat with reduced visibility.

(2) Ungulates select against, aggregate in larger groups, spend less time and are more vigilant on plots with lion scats.

(3) Small ungulates select against, aggregate in larger groups, spend less time and are more vigilant on plots with African wild dog scats.

(4) Among plots containing lion scats, ungulates will increase their number of visits, spend more time per plot, gather in smaller groups and exhibit lower levels of vigilance with larger visibility.

(5) Among plots containing wild dog scats, small ungulates will reduce their numbers of visits, spend less time per plot, gather in larger groups and exhibit higher levels of vigilance with larger visibility.

(6) The effect of lion scats and of visibility on patch selection, group size, time spent on plot and vigilance decreases with increasing body mass. Carnivore scats and visibility have no effect on patch selection, group size, time spent on plot and vigilance of megaherbivores.

METHODS

Study site

The experiment was conducted in the central section of Hluhluwe_iMfolozi Park (HiP), located in the KwaZulu-Natal province of South Africa (28°13′11″S 31°57′7″E). A 90 000 ha fully fenced park, HiP belongs to the southern African savanna biome and hosts vegetation types ranging from open grasslands to closed Acacia and broad-leaved woodlands (Whateley and Porter 1983). The mean annual rainfall depends on altitude, ranging from 985 mm in the high altitude regions to 650 mm in the lower areas and mainly falls between October and March. Daily maximum temperatures range from 13°C to 35°C. HiP's landscape is characterized by highly heterogeneous grasslands, in which tall bunch grass (tussock forming) communities of *Sporobolus pyramidalis*, *Eragrostis curvula* and *Themeda triandra* are interspersed with short lawnforming (stoloniferous) communities of *Digitaria longiflora*, *Urochloa mosambicensis*, *Dactyloctenium australe* and *Sporobolus nitens*. One of Africa's oldest conservation areas, the park hosts a diverse and complete set of indigenous large herbivores. Most notably, it is with Kruger National Park the stronghold of the white rhinoceros (*Ceratotherium simum*). As of 2016, the park hosts an estimated 5249 African buffaloes (*Syncerus caffer*), 700 African elephants (*Loxodonta africana*), 367 giraffes (*Giraffa cameleopardis*), 14019 impala (*Aepyceros melampus*), 648 greater kudu (*Tragelaphus strepsiceros*), 3297 nyala (*Tragelaphus angasii*), 885 common warthogs (*Phacochoerus africanus*), 598 wildebeest (*Connochaetes taurinus*) and 896 plains zebra (*Equus quagga*). HiP is also home to the 5 large African mammalian predators, with latest estimates indicating 300 spotted hyenas (*Crocuta crocuta*) 130 lions (*Panthera leo*), 54 to 125 leopards (*Panthera pardus*), 40 to 106

African wild dogs (*Lycaon pictus*) and probably less than 15 cheetahs (*Acynonix jubatus*) (Earthwatch 2016 annual field report, Le Roux et al. 2017, Somers et al. 2017).
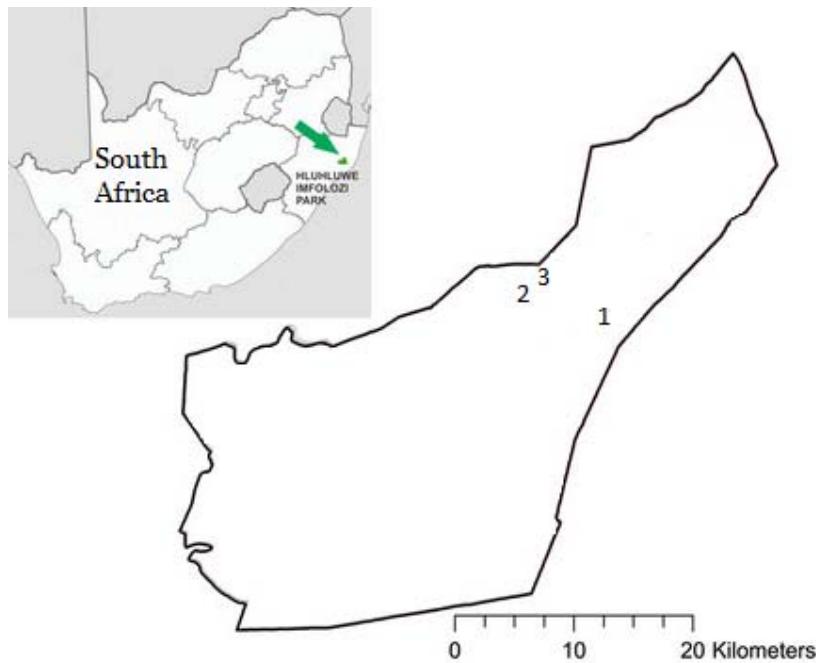

Figure 1
Location of the three Sites in Hluhluwe-iMfolozi Park. Site 1: Mnqabatheki, Site 2: Shooting Range, Site 3: Seme.

Experimental design

Camera traps
Each plot was equipped with a camera trap (Bushnell) attached to a wooden pole in the corner of the 10x10m central plot to capture all animals visiting it. The cameras recorded video clips of 30 seconds with 1 second intervals (if triggered again). Technical defaults and damage caused by wild animals (mainly white rhinoceros) greatly reduced the amount of available footage. As a rule of thumb, I chose to only use material with at least the first 3 days of consecutive footage.

Risky place
In 2013, a long-term experiment was set-up with the aim of looking at the effect of woody cover (as proxy for perceived predation risk) and resources on the behaviour and patch use of mammalian herbivores. Three sites in the central part of the park (figure 1) were selected, and in each of these, four 40 x 40m plots were delineated (i.e. 12 plots in total). In the centre of each 40 x 40m plot, a further 10 x 10m subplot was delineated, which served as the focal sampling plot throughout the study. The

perception of risk was manipulated by removing the entire woody component from two randomly selected plots of the four 40 × 40m plots in each of the three sites with the purpose of improving visibility. The woody cover of the remaining two plots was left intact. However, to enable comparisons among the four plots, the woody component from the centre 10 × 10m subplots was cleared, such that the only risk-related differences between the plots were in the visibility surrounding the central subplot. All further manipulations and measurements were taken from these central subplots.

The plot size of 40 x 40m was based on a study performed by Elliott et al. (1977) on hunting success of female lion, wherein the probability of escape with a flight distance of 20 m was calculated at 75% for blue wildebeest and zebra and 100% for Thomson's gazelle. The distance among plots varies from 60 - 350 m, and the distance among sites from 1.5 - 6 km.

Every week, I maintained the structural differences of the plots by cutting whatever woody plant that started growing (from the entire 40 x 40 m area in the "open" plots and from the 10 x 10m area in the "closed" plots). I did not cut any grass in order not to influence the forage availability for grazers, except for the patches directly in front of the cameras to prevent them being triggered by waving grass.

Risky time
I simulated the immediate, short-term risk of carnivore presence by adding scats of lions and African wild dogs to the plots. The treatment period started on January 20 and ended on March 27, 2017 (figure 2). During a specific treatment week, carnivore scats were added to one of the two closed plots and one of the two open plots (chosen randomly) of all three sites, the two other plots in each site remaining without scats. During any week, scats of only one carnivore species were added. I applied the carnivore scats in the centre of the 10*10 subplot and removed them after one week. Week 1, 2, 5 and 9 were control weeks with no scat on any of the 12 plots. Overall, the experiment was made of 4 lion scat weeks, 3 wild dog scat weeks and 4 control weeks. Most of the scats were obtained in bomas (enclosures) located in the park where lions and wild dogs were temporarily kept with the objective of being released in the wild later. For wild dogs, I also acquired scats of free-ranging animals I or other people encountered randomly, and which defecated on the road in front of me/them. I also obtained fresh scats of free-ranging lions from the park. Overall, I made sure that none of the scats sampled were older than 24 hours and had not been impacted by rain. The samples were stored in a freezer upon application on the plots.

Week	Application period	Scat treatment	N selected plots
1	06.01-13.01	Control	9
2	13.01 - 20.01	Control	9
3	20.01 - 26.01	Wild dog	9
4	26.01 - 03.02	Lion	8
5	03.02 - 10.02	Control	8
6	10.02 - 20.02	Lion	8
7	20.02 - 27.02	Wild dog	7
8	27.02 - 06.03	Lion	9
9	06.03 - 13.03	Control	6
10	13.03 - 20.03	Wild dog	5
11	20.03 - 27.03	Lion	8

Figure 2
Schedule of the scat application design. Application periods for each treatment week are shown, along with the number of plots that produced at least 3 days of footage and were hence included in the analysis.

Visibility

Even though "open" and "closed" plots were experimentally created, vegetation cover and hence visibility among plots of the same category still varied due to pre-existing variation in woody cover. In the beginning on March 2017, I conducted visibility measurements on all 12 plots to assess and compare the perceived predation risk by herbivores in response to the covariate visibility. I measured visibility with the help of a 160 cm long wooden board divided in 8 sections of 20 cm each (20, 40, 60, 80, 100, 120, 160). I remained in the centre of the subplot while another person was walking away from it in one of the 8 cardinal directions (N, NE, E, SE, S, SW, W, NW). Every time 50% of one of the sections was invisible due to vegetation cover, I wrote down how many meters had been walked up to that point. I recorded the visibility at three different heights (60 cm, 90 cm and 140 cm), respectively the standard heights of warthog, impala and wildebeest. I repeated the same procedure for all cardinal directions. For each measurement level, I obtained a mean value for every direction. I then averaged these means to obtain 3 standard visibility values for each measurement level. Warthogs and grey duikers were assigned the 60cm visibility values, while other species of size class 1 (impala, nyala) were assigned the 90 cm values. All other ungulates were assigned the 140cm values. In the analyses, I decided not to consider the measurement sections above 100 cm as they are not relevant when considering a hunting carnivore.

Measurement of vegetation biomass

In order to control for possible bottom-up effects, I measured the vegetation biomass in every subplot plot at the beginning of March 2017. This was done by putting a grid within the subplot of 1000 by 1000 cm, divided into 100 cells of 10 by 10 cm. I recorded the biomass in every cell using a Disc Pasture Meter (DPM). All 100 values were then averaged to obtain a single biomass value for every plot.

Experimental units

Size classes
Following Hopcraft et al. (2010), I divided ungulates into 4 size classes because of the importance of body mass in determining the relative strength of bottom-up and top-down effects in population regulation. Size class 1 (20 - 150 kg) included (ranked after abundance) impala, common warthog, nyala and grey duiker. Size class 2 (175 - 400 kg) included plains zebra, blue wildebeest and greater kudu. Size class 3 (500 – 1000 kg) was solely represented by the African buffalo. Size class 4 (>1000 kg) comprised white rhinoceros, giraffe, African elephant and black rhinoceros.

Ungulate Species
I also looked at 6 species (impala, zebra, wildebeest, buffalo, giraffe and white rhinoceros) in more detail. These were not only the most abundant but also represented all size classes. While impala, zebra, buffalo and white rhinoceros were relatively well represented across all three sites, wildebeest were almost exclusively present in Seme (n=3 in Mnqabatheki and n=1 in Shooting range), so I excluded Mnqabatheki and Shooting Range from the wildebeest analysis. Giraffes only very rarely visited Shooting Range (n=4), so I excluded this site from the giraffe analysis. This only concerned the "number of visits" analysis, since other analyses only considered visited plots (no zero values). When analysing the proportion of time spent being vigilant, I only looked at impala, zebra, buffalo and white rhinoceros.

Footage and data analysis

Presence and number of animals
I processed the videos using the program JWatcher. For every video clip, I recorded which species and how many individuals of them were present in the subplot, as well as outside of it.

Behavioural analysis
For impala, plains zebra, African buffalo, and white rhinoceros, I recorded the proportion of time spent being vigilant while foraging on the subplot. Behaviour outside the subplot was not recorded. I used vigilance in a wider sense, including both routine as well as intense vigilance (Periquet et al., 2012). Vigilant behaviour was recorded when the animal had its head raised above shoulder level and scanning its environment. It could be chewing or walking a few steps. Behaviours that were not linked to foraging (e.g. walking through the plot with no purpose of feeding, fighting,

resting, mating etc.) were excluded from the analysis. When more than one individual were present on the subplot on the same video clip, I only looked at the behaviour of one single individual. This individual was selected as follows: 1) of all individuals, the selected animal was the one that was present on the subplot for the highest amount of time. 2) If many animals were present for an equally long time on the plot, I recorded the behaviour of the animal that was most centrally located with respect to its conspecifics (e.g. in the middle of the group) as these animals will tend to show vigilance levels comparatively lower than the rest of the group, and can thus be more accurately compared with each other (Krause 1994)

Number of visits
For each size class and for the 6 selected species, I recorded the number of visits of groups (or single animals) per plot per week. While it is impossible to completely differentiate between individual animals or groups of animals, I only recorded visitation events with a time interval of at least 30 minutes between videos. This strongly reduces multiple recordings of the same individuals and can be considered a time interval long enough to consider that plot visits are independent events (Rovero, Jones, & Sanderson, 2005; Tambling et al., 2012). For plots with less than 7 days of observation, I multiplied the number of visits by the following coefficient: *7/n* (*n*=days of observation) in order to compensate for missing data.

Group size
For each size class and selected species, I recorded the average group size per plot per week by averaging the number of individuals per video for every plot per week. Since I was only interested in the group sizes of animals if they visited the plot, I did not include plots with zero visits per week in the analysis. Here too, I only recorded visitation events with a time interval of at least 30 minutes in order to not record the same group of animals multiple times.

Total time spent on plots
For each size class and selected species, I recorded the total time spent on each plot by summing up all 30 s video clips per plot per week. As for the "group size" variable, I did not include plots with zero visits per week because I was only interested in the amount of time spent by animals that visited the plot.

Statistical Analysis

To test my predictions, I used IBM SPSS Statistics v24. I used Generalized Linear Mixed Models in order to allow for repeated measurements of each plot. This was done by creating a random effect structure made of repeated measurements (successive weeks) nested within a specific plot. For vigilance analyses, I added a second layer of repeated measurements nested within "weeks", namely the different animal units of which I obtained vigilance proportion values. I also ran a more simple vigilance model with only one repeated measurements layer in which I just considered the vigilance proportions of animal units averaged per plot per week. Results of both models were similar and I showed those obtained with 2 layers of repeated measurements since they

better reflect reality by taking into account the number of measured animal units per plot per week.

Even though the variables "number of visits", "group size" and "time spent on plots" are count data, I used linear models when the residuals fitted a normal distribution, and only used Poisson and negative binomial (NB) models when the data was not normally distributed. When I had to choose between Poisson and NB models, I used 1) the model that was statistically more significant 2) if both models were equally significant, I used a NB model as they give a better fit than Poisson models (Ismail & Zamani, 2013). The use of linear models for "group size" and "time spent on plot" was often made possible by the fact that these two variables have no "zero" values. For "number of visits" , however, I used NB models for all analyses except for size class 2 (linear model following square root transformation). For "time spent on plot", I used Poisson models for zebra, as well as NB models for size classes 1 and 2. For the proportional data of the vigilance analysis, I used linear models and – for zebra and white rhinoceros – NB tests following transformation of the continuous data into count data. Except for white rhinoceros, all "group size" analyses were run using linear models. I used a first-order autoregressive covariance structure, with homogeneous variances and correlations that decline exponentially with distance. Unfortunately, I could not control for site as a random factor because it would have overparameterized the models. When sample sizes were large enough, I ran a second set of analyses in which I only looked at the first three days following the scat application (or the changing of cameras in the case of control weeks), with the aim of obtaining a stronger effect from the scat treatment.

Number of visits

$$y = \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2 + \beta_4 x_3 + Uz$$

With y being the number of visits of a specific species or size class per plot per week, β_1 the effect of the scat treatment, β_2 the effect of visibility, β_3 the interaction effect between the scat treatment and visibility, β_4 the effect of the vegetation biomass and U the random effect of repeated measurements within the same plot.

Group size

$$y = \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2 + \beta_4 x_3 + Uz$$

With y being the group size of a specific species or size class per plot per week, β_1 the effect of the scat treatment, β_2 the effect of visibility, β_3 the interaction effect between the scat treatment and visibility, β_4 the effect of the vegetation biomass and U the random effect of repeated measurements within the same plot.

Time spent on plot

$$y = \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2 + \beta_4 x_3 + Uz$$

With y being the time spent by a specific species or size class per plot per week, β1 the effect of the scat treatment, β2 the effect of visibility, β3 the interaction effect between the scat treatment and visibility, β4 the effect of the vegetation biomass, and U the random effect of repeated measurements within the same plot.

Proportion of vigilance time

$$y = \beta 1x1 + \beta 2x2 + \beta 3x1x2 + \beta 4x3 + UVz$$

With y being the proportion of time spent being vigilant while foraging of a specific species or size class per plot per week, β1 the effect of the scat treatment, β2 the effect of visibility, β3 the interaction effect between the scat treatment and visibility, β4 the effect of the vegetation biomass, U the random effect of repeated measurements within the same plot and V the random effect of repeated behavioural measurements on different animals units on a specific plot during a specific week.

RESULTS

Number of visits per plot

When lion scats were present, animals of size class 2 selected for plots with higher visibility (Figure 3 ; p=0.050, t= 1.998). Impalas selected for plots with high visibility (p= 0.019 t= 2.4) and low vegetation biomass levels (p= 0.036 t= -2.139). Size class 1 (p=0.05 , t= -1.997) and size class 2 (p=0.005, t= -2.873) animals selected plots with lower vegetation biomass levels. The number of visits of species heavier than 500 kg was not influenced by any of the variables.
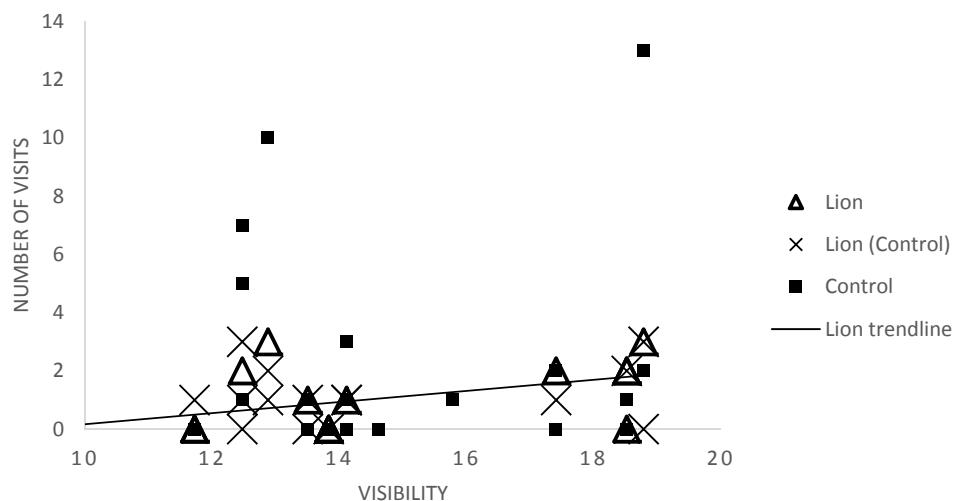
Figure 3

The relationship between visibility and number of visits of size class 2 animals for plots without any carnivore scat on the whole site (Control), plots with lion scats (Lion) and control plots without scat during the lion scat week (Lion Control). Only the interaction effect with Lion was significant.

Group size

Group sizes of wildebeest (p=0.013 t=-2.779) and buffalo (p=0.016 t= -1.965) were significantly larger on plots with lion scats than on plots with no scat across the whole site (figure 4). Group sizes of size class 2 animals were higher on plots with wild dog scats than on plots during the control week with no scat (p=0.049 t=0.466) and on no scat control plots during the wild dog scat week (p=0.005 t= 1.055; figure 5). When lion scats were present, impala increased their group size with decreasing visibility (p=0.05 t= -2.063 ; figure 6).

Group sizes of impala (p=0.005 t= 3.069) and buffalo (p=0.015 t=2.929) increased with increasing vegetation biomass.
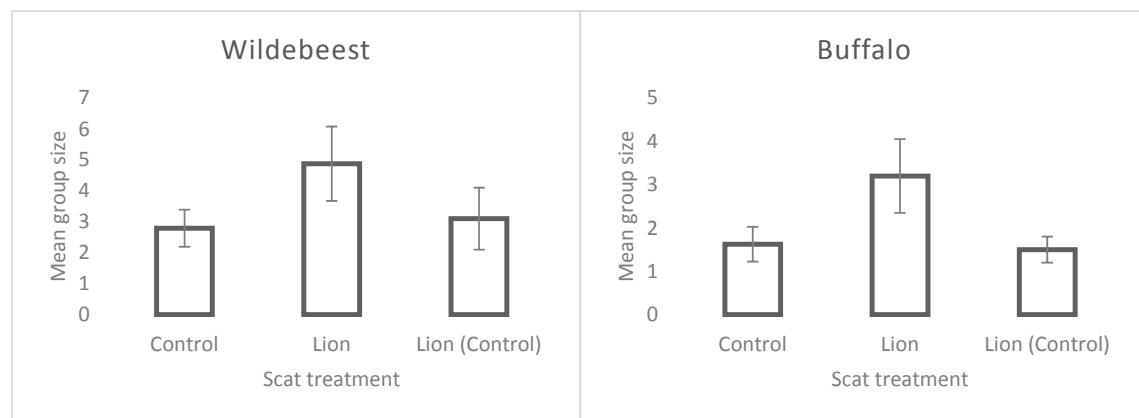
Figure 4

Differences in mean wildebeest and buffalo (size class 3) group size between plots without any carnivore scat on the whole site (Control), plots with lion scats (Lion) and control plots without scat during the lion scat week (Lion Control). Plots with wild dogs site on the site were excluded from the analysis because of low sample size. For both species, only the difference between "Control" and "Lion" was significant. Simple means per treatment are shown, with standard error bars.
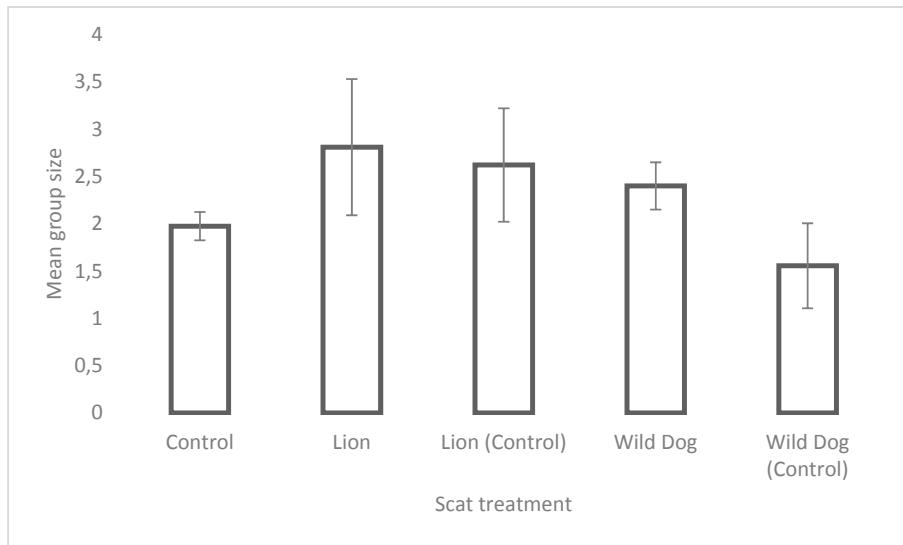
Figure 5

Differences in mean group size of size class 2 animals between plots without any carnivore scat on the whole site (Control), plots with lion scats (Lion), control plots without scat during the lion scat week (Lion Control), plots with wild dog scats (Wild Dog) and control plots without scat during the wild dog scat week (Wild Dog Control). Only "Wild Dog"-"Wild Dog (Control)" and "Wild Dog"-"Control" differences ware significant. Bars show the means per treatment, with standard error bars.
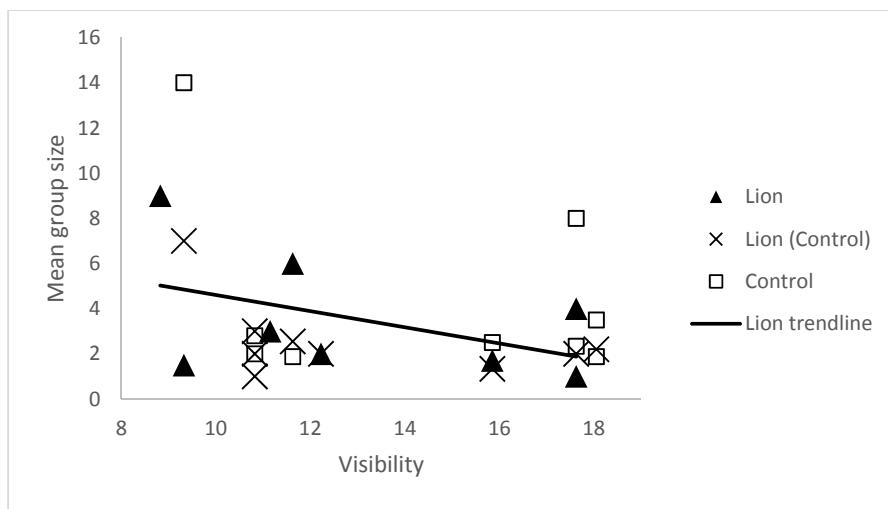
Figure 6

The relationship between visibility and mean Impala group size on plots without any carnivore scat on the whole site (Control), plots with lion scats (Lion) and control plots without scat during the lion scat week (Lion Control). Only the interaction effect with "Lion" was significant.

Time spent on plot

When looking only at data from the first 3 days, animals of size class 1 spent more time on plots with lion scats than on no scat control plots during the lion scat weeks (p=0.02, t=5.386), and spent also more time on plots with wild dog scats than on no scat control plots during wild dog scat weeks (p= 0.037 t= 2.274; figure 7). Buffalos (size class 3) spent more time on plots with lion scats than on plots with no scat across the whole site (p=0.018 t= -0.566; figure 7) There was a negative interaction effect (p=0.035 t= -2.441) between plots with lion scats and visibility for buffalos (figure 8). Similarly, giraffes spent more time on plots with lion scats than no scat control plots during the lion scat weeks (p=0.015 t=13.705 ; figure 9). Animals of size class 2 spent significantly less time on plots with higher vegetation biomass.
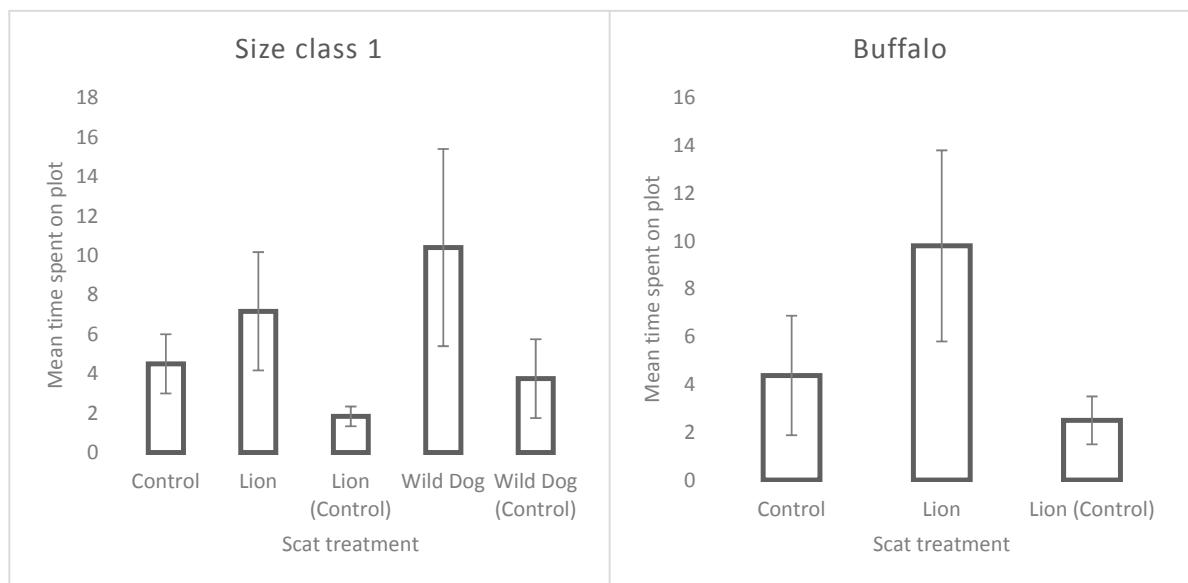

Figure 7
Differences during the first 3 days of observation in the time spent on plots for size class 1 animals and buffalos (size class 3) between plots without any carnivore scat on the whole site (Control), plots with lion scats (Lion), control plots without scat during the lion scat week (Lion Control), plots with wild dog scats (Wild Dog) and control plots without scat during the wild dog scat week (Wild Dog Control). For size class 1 animals Only "Wild Dog"-"Wild Dog (Control)" and "Lion"-"Lion (Control)" differences are significant. For buffalos, only the difference between "Control" and "Lion" is significant. Simple means per treatment are shown, with standard error bars. For buffalos, wild dog weeks were excluded because of low sample size.
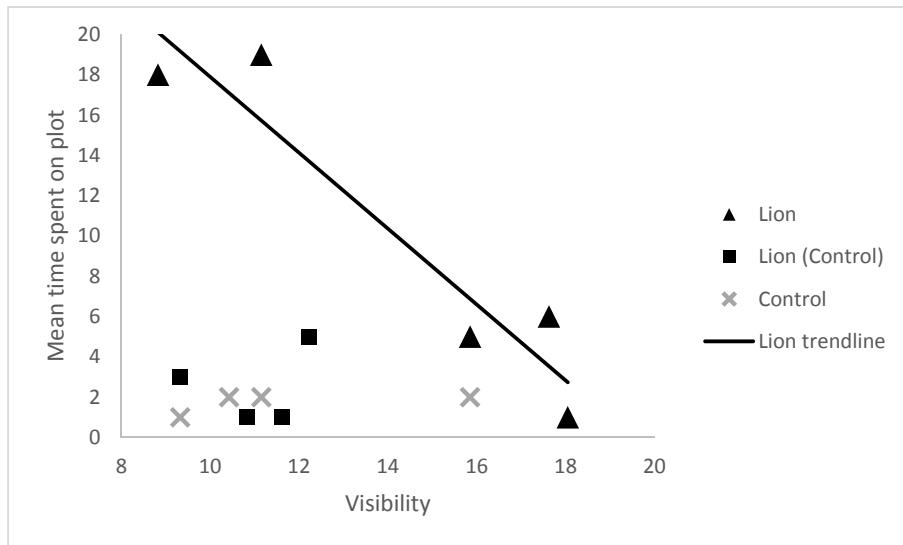
Figure 8

The relationship between visibility and mean time spent by buffalos on plots without any carnivore scat on the whole site (Control), plots with lion scats (Lion) and control plots without scat during the lion scat week (Lion Control). Only the interaction effect with "Lion" was significant.
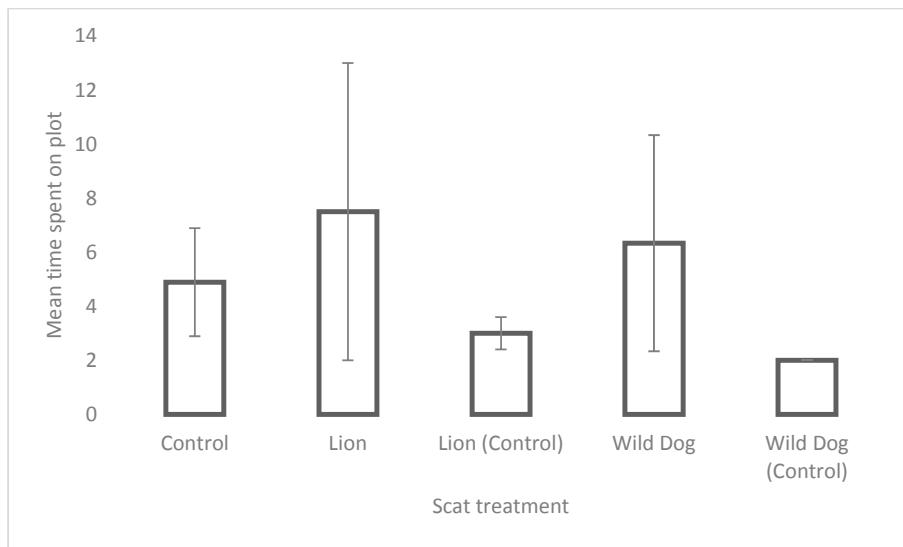

Figure 9

Differences in the time spent on plots by giraffes between plots without any carnivore scat on the whole site (Control), plots with lion scats (Lion), control plots without scat during the lion scat week (Lion Control), plots with wild dog scats (Wild Dog) and control plots without scat during the wild dog scat week (Wild Dog Control). Only "Lion"-"Lion (Control)" differences were significant. Simple means per treatment are shown, with standard error bars.

Vigilance

Zebras were more vigilant on plots with lion scats than on no scat control plots during lion scat weeks (p=0.005 t= 43.891). The difference in vigilance level between plots with lion scats and plots with no scats across the whole site was not significant. The difference between plots with wild dog scats and plots with no scats across the whole site, although large, was not significant (figure 10). Impalas were more vigilant on plots with lion scats than on no scat control plots during lion scat weeks (p=0.049 t= 2.004) and were also significantly more vigilant on plots with wild dog scats than on no scat control plots during wild dog scat weeks (p=0.034 t= 2.163 ; figure 10). Vigilance levels of buffalos and megaherbivores were not influenced by any variable.
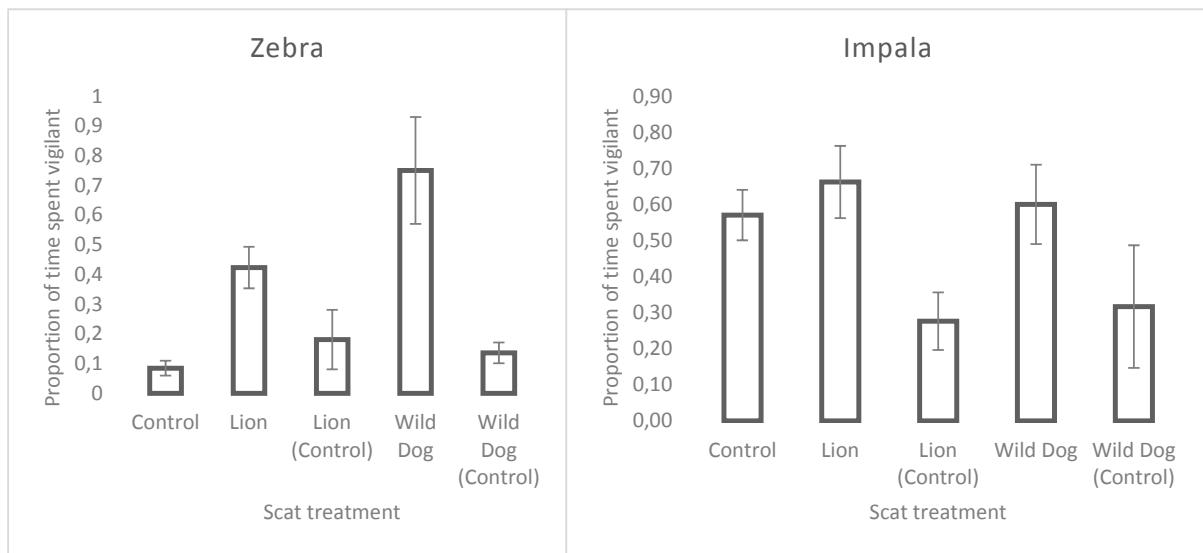

Figure 10
Differences in the proportion of time impala (size class 1) and zebra (size class 2) spent vigilant while foraging between plots without any carnivore scat on the whole site (Control), plots with lion scats (Lion), control plots without scat during the lion scat week (Lion Control), plots with wild dog scats (Wild Dog) and control plots without scat during the wild dog scat week (Wild Dog Control). For impala, only "Lion"-"Lion (Control)" and "Wild Dog"-"Wild Dog (Control)" differences are significant. For zebra, only the difference "Lion" and "Control" is significant. Simple means per treatment are shown, with standard error bars.

DISCUSSION

The results suggest the existence of size dependent differences in perceived risk and associated antipredator behaviour among ungulates. While predation risk appeared to strongly influence behaviour of small and intermediate-sized ungulates, it only moderately impacted large ungulates (African buffalo). Although the number of effects decreased with increasing body mass, the effects of carnivore scats and

visibility on the four response variables did not systematically decrease linearly with increasing body mass, which suggests the existence of species-specific antipredator behaviours independent from body mass. As predicted, megaherbivores did not react to or did not perceive any predation risk.

While, apart from impalas, ungulates responded much more to risky times than to risky places, responses to risky times tended to be stronger at risky places. By selecting for plots with high visibility, impala, by far the most abundant species of size class 1, was the only ungulate to respond to risky places in all circumstances, thus confirming the findings of Rogers (2016) but also of Valeix et al. (2009 (b)) and Thaker (2011) who found that impalas avoided areas with long-term predation risk by lions. Confirming findings of Périquet et al. (2012), impalas also exhibited higher levels of vigilance and increased their group size with decreasing visibility on plots with lion scats. However, the reaction of impalas and size class 1 animals to wild dog scats was less strong than expected, and only took place in the form of increased vigilance. Contrary to expected, wild dog scats did not lead impala to seek for woody cover, nor to aggregate in larger numbers or to increase their vigilance in more open habitat.

In the presence of lion scats, size class 2 animals selected for plots with high visibility. Surprisingly, size class 2 animals aggregated in larger numbers on plots with wild dog scats, while lion scats did not lead to significantly higher group sizes. However, wildebeest increased their group size in the presence of lion but not of wild dog scats. Zebras (size class 2) increased their vigilance on plots with lion scats – confirming findings by Périquet et al. (2012) –, but not wild dog scats. Ungulates of intermediate size constitute only a very small proportion of the diet of wild dogs in HiP. Out of 838 recorded wild dog kills in HiP, there were only two zebras and one wildebeest (Somers et al. 2017). The significant increase of group sizes in the presence of wild dog scats is hence surprising. Rather than a mean to better detect wild dogs, larger group sizes could perhaps be interpreted as a proactive attempt to better physically protect vulnerable foals from potential attacks. Buffalos (size class 3), the main prey of lion in HiP (25% of recorded kills between 1983 and 2010), responded to lion scats with larger group sizes, but showed no response in terms of patch selection and vigilance.

While impala avoided woody cover at any time, species predated upon by both lions and wild dogs enhanced their anti-predatory behaviour with increasing woody cover when lion scats where present. On the other hand, no species or size class enhanced its anti-predatory behaviour in open areas, with or without wild dog scats. This in line with most predator-prey studies conducted in African savannas, which indicate that ungulates usually select against, gather in larger groups and are more vigilant in areas with increased woody cover. To my knowledge, the only counterexample is brought by Périquet et al. (2012), who found that zebras increased their vigilance with increased distance from woody cover. This pattern could be explained by many factors. Lions are considered to be the "dominant" carnivore species of savanna ecosystems (Thaker et al., 2011). In HiP, they are also more abundant than wild dogs

(Somers et al. 2017). Moreover, the space use of sit-and-pursue predators tends to be more nested and predictable than that of cursorial predators (Thaker et al., 2011). Finally, the common perception of wild dogs relying on open landscapes and long chases to kill their prey has recently been challenged, with studies showing that the species can be quite efficient in killing prey in wooded areas, relying on short bursts of speed instead of stamina (Hubel et al., 2016). Similarly, cheetahs have been shown to be very able to hunt in thicket vegetation (Bissett & Bernard, 2007).

In terms of time spent on plots, ungulates behaved in a way diametrically opposed to what I expected. Indeed, size class 1 animals spent more time on plots with scats of wild dogs and lions than on control plots (first 3 days). Buffalos and giraffes also remained longer on plots with lion scats. Most surprisingly, in the presence of lion scats, buffalos spent more time on plots with higher woody cover. In Hwange National Park, ungulates spent more time approaching waterholes (except kudu) and drinking when the long-term risk of encountering lions increased (Valeix et al. 2009 (a)). While it could be speculated that ungulates increase their time spent on plots with carnivore cues in order to compensate for increased time spent vigilant, I did not find a significant correlation between time spent on plot and proportion time spent vigilant for any species.

Overall, scats of lions and wild dogs seem to be perceived as indicators of their potential presence by ungulates, and especially herbivores of small and intermediate size displayed enhanced antipredator behaviour in the presence of scats. This runs opposite to results of van der Meer et al. (2012) who found no effect of wild dog vocal and olfactory cues on the visitation rate, vigilance and time spent drinking of kudus and impalas around waterholes in Hwange National Park. Moreover, the aforementioned study found that visibility was negatively correlated to visitation rate in impalas, while I found the opposite. This might suggest that in Hwange, impalas consider woody cover more as a protection from predators than a potential ambush place. This however is contradicted by many studies conducted there (Périquet et al. 2012; Valeix et al. 2009 (a); Valeix et al. 2009 (b)). The findings of van der Meer et al. are even more surprising given the fact that they do not include any significant interaction effect between visibility and wild dog olfactory and vocal cues on vigilance. Our very low sample size for kudus (n=9) does not allow for any species-based comparison.

Several factors have to be taken into account when interpreting these results. Effects of carnivore scats (or of their absence) could be reduced by the presence of spotted hyenas, lions, wild dogs and leopards in the vicinity of the plots (cheetahs are very rare and restricted to the south of the park). Indeed, hyenas were recorded on 2 occasions crossing plots at a relatively high pace. Fortunately, this happened on a plot with wild dog scats (cursorial predator cue), and on a plot that was not included in the analysis because of insufficient footage. Other predators were not detected but could as well have been present. Another limitation of this study is the impact of weather on the experiment. Most importantly, rain washes away an important part of the organic content of scats responsible for the smell, which could lead species to consider

predation risk less acute. Rain was mostly an issue during the 7th week of the experiment, during which I applied wild dog scats (figure 2). Following this week, grass grew quickly, especially on some open plots, which reduced visibility. Fortunately, visibility measurements were taken in the middle of week 8, so that grass height was then higher than at week 1, but shorter than at week 11. Nevertheless, taking visibility and vegetation biomass measurements every week would have produced more accurate values. This, however, was impossible for logistic reasons. Finally, it cannot be ruled out that, at least in some cases, scats located on one plot also affected the behaviour of ungulates on control plots of the same site. The distance between plots (60 to 350 m) was comparable to that of similar experimental studies. For example, the minimal distance between experimental and control plots in the study of Kuijper et al. (2014) was 50 m.

Other interesting aspects of predation risk and associated research questions have not been covered in this study for time reasons. These include possible avoidance of risky places at night, when lions (but not wild dogs) are most active, as well as possible effects of different social groups within species (male, female, female with calf), and different diets (grazer, browsers, mixed feeders) on antipredator behaviour. In Hwange National Park, all ungulates avoided waterholes at night when lions were in the vicinity, and the long-term predation-risk by lions influenced the space use of browsers, but not of grazers (Valeix et al. 2009 (a); Valeix et al. 2009 (b)).

In conclusion, the results illustrate the complex interactions between structural, habitat-related risk and short-term variations in risk that determine behavioural responses of ungulates to perceived predatory risk. While taken independently, risky times seem to be more relevant in determining antipredator behaviour than risky places, triggering responses across all size classes (except for megaherbivores), the presence of a short-term risk appears to activate habitat-related risks. This interaction effect, however, only took place with scats of lions, not of wild dogs. Our results thus suggest that in African savannas, risky places are only associated with the space use of sit-and-pursue predators, whereas risk emanating from cursorial predators seems to be perceived by ungulates as independent from any landscape characteristic.

ACKNOWLEDGMENTS

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