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Simulated elephant-induced habitat changes can create dynamic landscapes of fear



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ABSTRACT

Landscapes of fear have become widely studied in the northern hemisphere, but are still largely understudied in the more complex, diverse carnivore-prey communities of Africa. Habitat changes brought about by a megaherbivore, the African elephant (*Loxodonta africana*), can modify the perceived landscape of fear by predation vulnerable prey species (impala *Aepyceros melampus* and warthog *Phacochoerus africanus*) in contrast with non-prey species (white rhinoceros *Ceratotherium simum*). We hypothesized that by opening up woody vegetation, elephants may modify perceived risk at a landscape-scale, but also at a fine scale by depositing escape impediments in the form of coarse woody debris. We experimentally tested this in Hluhluwe-iMfolozi Park, South Africa, by simulating elephant-induced habitat changes on patch scale (opening up woody vegetation) and within-patch scale (deposition of coarse woody debris) and monitoring the herbivore visitation using camera traps. We compared visitation on the edge of grazing lawns (in proximity of dense vegetation) and the centre (open, highly visible patches), either with or without coarse woody debris and with or without fresh predator scat. We found that mesoherbivore prey species showed contrasting responses, with warthog avoiding plots close to dense vegetation and plots with coarse woody debris. Impala reduced their visitation to dense vegetation patches only during risky times, at night, especially in the presence of predator scat, but did not clearly avoid plots with coarse woody debris. Our study indicates that, in African savannas, the perceived landscape of fear is a highly dynamic phenomenon varying in both space and time and being species-specific. Elephant induced habitat changes may shape landscapes of fear in complex and contrasting ways.

1. Introduction

Laundré et al. (2001) defined the term “landscape of fear”, following the earlier introduction of the “ecology of fear” by Brown et al. (1999). They suggested that prey perceive variation in predation risk across the landscape, driven principally by the space use by large carnivores and additionally by habitat features related to (perceived) predation risk, such as habitat openness and the presence of escape impediments (Moreno et al., 1996; Creel et al., 2005; Kuijper et al., 2015). Accordingly, prey spend more time in areas perceived as less risky. The resulting redistribution of prey over the landscape and their

subsequent impacts on lower trophic levels have become known as risk-mediated trophic cascades (Creel and Christianson, 2008; Ford and Goheen, 2015). This last decade, the literature on risk-mediated trophic cascades has boomed, yet stayed severely limited to a few northern hemisphere systems, focusing primarily on simple single predator – single prey systems (Kuijper et al., 2016). As a result, obvious complexities expected from more diverse carnivore-prey communities are largely unexplored. For example, in multi-species African savanna systems, mesograzers perceive a landscape of fear and concentrate on open habitat, while predation-insensitive megaherbivores (> 1000 kgs) use the landscape more evenly (le Roux et al., 2018), thus potentially

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counteracting the impacts of risk-sensitive species. Here, we want to extend this concept and explore whether megaherbivores, through their ability to structure landscapes, play a role in shaping the landscape of fear perceived by meso- and megaherbivores. We focus on the effects of the largest megaherbivore, the African elephant (*Loxodonta africana*).

Elephants have long been recognized as “ecosystem engineers” that may modify habitats for other species (Jones et al., 1997; Kerley and Landman, 2006). More specifically, they may influence tree-grass ratios and, together with fire, create and maintain open savanna (Sankaran et al., 2013) or even grassland habitats (Laws, 1970). Such engineering leads to higher habitat complexity on a landscape scale, creating a mosaic of closed and open patches (Jones et al., 1997; Wright and Jones, 2004; Guldemond et al., 2017). By increasing habitat heterogeneity in this way, elephants may both alter accessibility for predators (Tambling et al., 2013) and thus the landscape of fear as perceived by mesoherbivores (Underwood, 1982; Valeix et al., 2011). The direction of these elephant-mediated effects on predation risk depends on the anti-predator strategy of the prey species – while certain species take advantage of cover to avoid being detected by predators (Skinner and Chimimba, 2005), other species avoid dense vegetation and rely on early predator detection and flight (Valeix et al., 2009; Burkepile et al., 2013). By opening up vegetation, elephants may influence so-called “hider type” and “runner type” prey species in contrasting ways. For example, impala (*Aepyceros melampus*) and steenbok (*Raphicerus campestris*) perceived lower predation risk in habitats where elephant increased visibility (Valeix et al., 2011). In contrast, the fragmentation of thickets by elephant increased the predation risk for small “hider type” ungulates such as duiker and bushbuck (*Tragelaphus scriptus*) by allowing access to lion and hyena (Tambling et al., 2013). Moreover, prey responses to changes in habitat openness also depend strongly on the type of predator (ambush vs. coursing) to which the species are reacting (Thaker et al., 2011). Elephant-induced habitat changes can thus shape multi-species communities via complex effects on species-specific landscapes of fear.

What has been ignored up to now is that elephants may also affect perceived risk at a finer, within-patch scale. Elephants are sloppy feeders, and thus increase the amount of coarse woody debris (CWD) in the landscape (Kerley and Landman, 2006; Landman et al., 2019). Northern hemisphere studies have suggested that CWD may impede visibility or escape from predation for ungulates such as red deer (Halofsky and Ripple, 2008; Kuijper et al., 2013, 2015). This increases perceived risk as, for example, shown by increased vigilance levels in close vicinity to CWD (Kuijper et al., 2015). These fine-scale risk factors can strongly depend on landscape scale variation in predation risk and thus are scale-dependent (van Ginkel et al., 2019). We hypothesize that elephant-deposited CWD in savannas may similarly act as escape or visibility impediments. Thus, elephants are predicted to have a nested and scale-dependent influence on the perceived landscape of fear, depositing coarse woody debris at small scales while opening-up woody vegetation at larger scales. Elephant-deposited CWD could potentially create “patches of fear” (sensu Kuijper et al., 2015) even in low-risk habitat, and hereby counteract, or enforce, the effects of elephant on larger (i.e. patch) scale risk.

We tested these contrasting impacts of elephant by experimentally simulating elephant impact at the “patch” and “within-patch” scale in Hluhluwe-iMfolozi Park (HiP), South Africa. We measured the response of three savanna ungulates (warthog, impala and rhino) to factors modifying perceived risk at the patch scale (high versus low woody density) and within-patch scale (with and without CWD). CWD may not only increase predation risk, but also simply work as a physical barrier that reduces access to foraging patches (Smit et al., 2005). Thus, to account for this, we introduced another risk cue, and added carnivore scat (from wild dog (*Lycaon pictus*)) to intensify the perceived risk. Carnivore scat has been shown to increase perceived predation risk by a range of prey species (e.g. Shrader et al., 2008; Favreau et al., 2013; Kuijper et al., 2014). Moreover, many predators are active at night

(Cozzi et al., 2012) and prey may thus also respond to temporal variation in predation risk (Creel et al., 2008; Kohl et al., 2018). As such, we also tested how prey's response to the risk factors differed between day and night. We hypothesized the following:

1. Prey species (“runner type” in our case impala and warthog, (Estes, 1991)) will visit plots with dense woody cover less frequently and/or spend a shorter amount of time there compared to open plots, while non-prey species (in our case white rhino) will show no preference for open or dense plots.
2. Prey species (“runner type”) will visit plots with CWD less frequently and/or spend a shorter amount of time there than in plots without CWD, while non-prey species will show no preference.
3. Prey responses will be strongest during the riskiest times i.e. during night time (when predators are active) and/or when wild dog presence is simulated by placing fresh wild dog scat.

2. Methods

2.1. Study area

HiP is a ~900 km² protected area in KwaZulu-Natal, South Africa. Habitats range from woodland savanna and thickets to open grassland and scarp forest on the hilltops (see Cromsigt et al. (2017) for detailed description of HiP). Rainfall is highly seasonal, with a distinct wet season (October–March), and varies from about 550 mm per year in the lower-lying southwestern part of the park to around 1000 mm per year in the northern, higher, parts. The elephant population was estimated to number about 700 individuals in 2014 (Druce et al., 2017). Elephant impact varies across the park but can be locally extensive, including opening up of mature woodlands of certain acacia species (Druce et al., 2017). HiP hosts populations of all megaherbivores, most of the native ungulate species (le Roux et al., 2017) and a complete set of native large carnivores (Somers et al., 2017).

We used natural grazing lawns (short stoloniferous, high-quality grasslands, highly preferred by grazers (Cromsigt and Olf, 2008)) as our experimental sites to ensure high visitation by ungulates and to standardize food availability (grass quality and quantity) among sites. In HiP, grazing lawns occur as small patches (mostly < 8 ha) in a taller bunch-grass matrix (Archibald et al., 2005). Between mid-April and mid-August 2014, we set up an experiment using 11 grazing lawn sites distributed across the southwestern corner of HiP. These replicate sites were clustered in four regions, mostly for logistical reasons (Fig. 1). Each site was within 50 m from a road, within 100 m of water and dominated by the same lawn grass species (*Sporobolus nitens* and *Urochloa mosambicensis*). The distance between sites was at least 500 m.

2.2. Experimental design

Within each of the 11 sites, we set up five plots of 5 × 5 m, each with a different simulation of elephant impact. We set up two closed plots by placing them at the grazing lawn edge (in the proximity of dense woody vegetation of low visibility) and three open plots placed in the grazing lawn centre (open area of high visibility). These plots served as simulations of patch scale elephant impact which has been shown to be able to remove woody vegetation and open up closed habitats (e.g. Guldemond et al., 2017). We then placed CWD (approximate dimensions: 50 cm high, 50 cm wide, 100 cm long; following Halofsky and Ripple, 2008; Kuijper et al., 2013), which consisted of branches, bark and smaller logs found in the proximity of the site, in three corners of one open and one closed plot. We standardized debris size to avoid introducing additional variation to our experimental design such as variation in response of herbivores to variation in debris size. This size of CWD used falls into the true variation of debris deposited by elephant in the park (Fig. A.1, Fig. A.2). Thus we had one closed plot with and one closed plot without escape impediments and

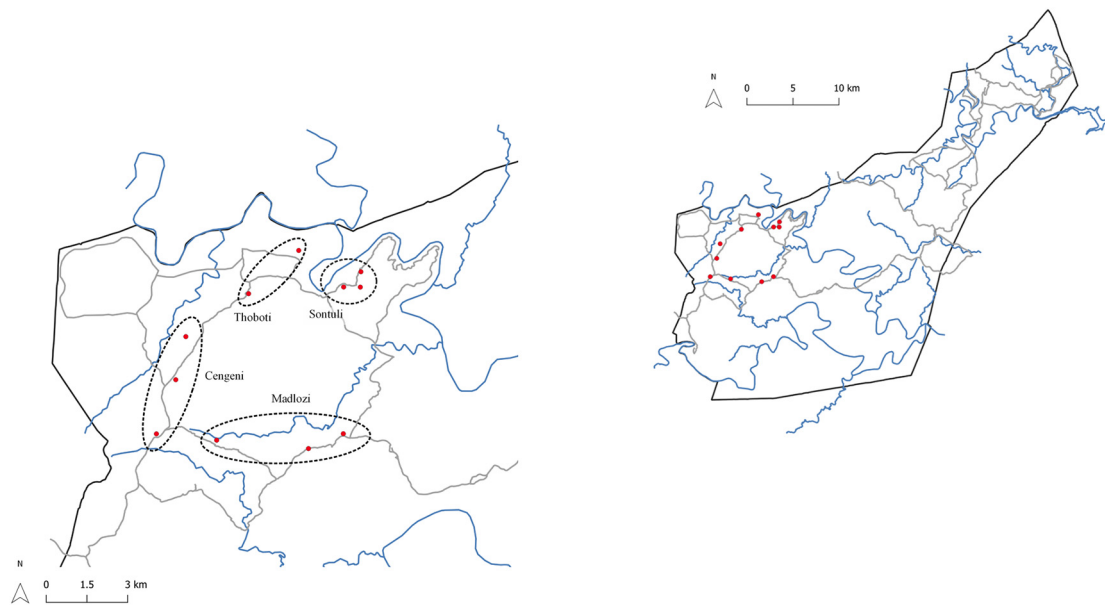


Fig. 1. The locations of our 11 experimental sites (red points) in Hluhluwe-iMfolozi Park (right), and the four regions (dashed ellipsoids) we assigned the sites to (left).

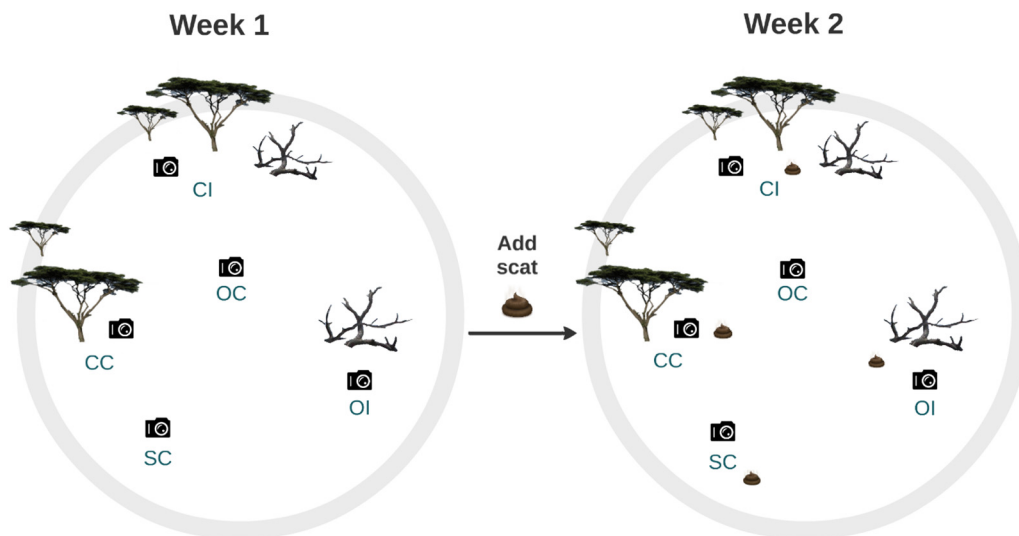


Fig. 2. Schematic overview of the experimental set up with the two circles representing one, and the same, experimental site (grazing lawn) which we ran over a course of 2 weeks. In Week 1, we simulated elephant-induced habitat changes by placing plots in open areas and close to woody vegetation (simulating elephants opening-up vegetation) and by adding coarse woody debris (CWD) as potential escape impediments. This led to five experimental treatment plots: Open without CWD (Open-Control, OC), Open with CWD (Open-Impediment, OI), Closed without CWD (Closed-Control, CC), Closed with CWD (Closed-Impediment, CI) and an Open plot without CWD but with scat in week 2 (Scat-Control, SC). In Week 2, we increased perceived risk by adding wild dog scat to all except the open-control plot. We measured herbivore visitation to plots with camera traps. We replicated this set-up across the 11 sites highlighted in Fig. 1.

one open plot with and two open plots without escape impediments (Fig. A.3). We ran these plots for one week and at the start of the second week we added a handful of fresh wild dog scat to all plots except one of the duplicate open plots without escape impediments, which served as a scat control (see Fig. 2). We will refer to these different plots as; closed-control, closed-impediment, open-impediment, open control, and scat-control plot, respectively. We used fresh scat as it is recognized as an olfactory cue for the prey, indicating recent predator presence, hence acting as an imminent threat (Apfelbach et al., 2005; Kuijper et al., 2014). Fresh wild dog scat was collected from translocation enclosures by park personnel (max. 10 h after defecation) and kept frozen until use. During the first week we tested how simulated elephant-mediated habitat changes (habitat openness and CWD) influence perceived risk without an immediate risk cue and during the second week we investigated if effects were amplified with an immediate risk cue. Hence, during the first week, the scat-control plot was functionally a replicate

control plot.

All plots within each site were spaced at least 10 m but not > 80 m apart, so that individual animals could easily choose among different plots. We avoided features that could attract ungulates to the plot, e.g. an active waterhole, well used trail, a tree providing good shade or scratching posts. For pragmatic reasons we could not run all sites simultaneously. To limit the duration of the study, we ran two sites simultaneously yet out of sequence i.e. one in week 1 and another in week 2 (Fig. A.4).

In summary, below, where we refer to sites, we refer to our 11 grazing lawns and where we refer to plots we refer to the 5 × 5 meter plots with our different experimental treatments, which we placed within each of the 11 sites. These experimental treatments included simulated elephant impact (plots with CWD present versus CWD absent and high versus low visibility plots), and addition of wild dog scat (plots with scat present versus scat absent). These treatments were set-out in a

full-factorial design with plots with all treatment combinations (see Fig. 2).

2.3. Animal visitation

We recorded animal visitation to each plot using Bushnell Trophy Cam HD camera traps, equipped with motion-activated passive infrared day/night sensors. At each plot, we placed a camera trap approximately 1 m from the plot corner facing southwest to avoid receiving direct sunlight onto the camera lenses. Cameras were secured to a pole or a tree trunk, approximately 30 cm above the ground. The corners of all plots were visibly marked (with small stones or sticks) to delineate the plot borders on the recorded images. Special care was taken to only select small stones or sticks, of a much smaller size than the CWD. Markings were necessary to ensure we standardize the size of the area monitored and only recorded animals within plots. The cameras were set to collect 30 s videos with a 1 s time-lapse between successive recordings. In total, the cameras recorded 1118 videos of animals within experimental plots. Moreover, although 24 different species visited our sites, only three ungulate species visited all sites frequently enough to include in the analyses: impala, white rhinoceros (henceforth rhino) and warthog (*Phacochoerus africanus*) (Table A.1). Impala and rhino visited sites during day and night, while warthog were almost completely absent from the sites during the night. Thus, we analysed warthog responses to experimental treatments using daylight data only. The combination of species also enabled us to differentiate between the response of vulnerable (impala and warthog) and invulnerable (rhino) prey species.

2.4. Plant cover and visibility

Plant cover within each plot was estimated as the cover of each grass species in 16 0.5×0.5 m quadrants per plot. Grass greenness was estimated according to the Walker (1976) 8-point scale of 0, 1–10, 11–25, 26–50, 51–75, 76–90, 91–99 and 100% greenness. The experiment ran during the early and late dry season and grass height was very short (≤ 7 cm.) throughout the study period and across all sites.

We measured habitat visibility surrounding each plot in the 8 cardinal and inter-cardinal directions (N, NE, NW, S, SE, SW, E, W) using a Nudds density board (Nudds, 1977). We estimated the distance at which approximately 50% of the 40–60 cm height section was no longer visible, up to a distance of 20 m from the centre of the plot. This height of 40–60 cm was chosen because it reflects the height of an approaching predator such as a wild dog or a stalking/crouching lion. The estimates were taken at 3 different “eye-height” levels representing warthog (50 cm), impala (100 cm) and white rhino (150 cm). All visibility measurements were undertaken by the same observer.

2.5. Data analyses

2.5.1. Vegetation and visibility

Grass species cover and greenness data were non-normally distributed and could not be transformed, so we performed non-parametric Kruskal-Wallis tests to determine differences in cover of the prevailing lawn grass species (*S. nitens* and *U. mosambicensis*) and greenness among plots. We ran a factorial analysis of variance (ANOVA) to determine differences in visibility between different plots for the different “eye-height” levels.

2.5.2. Herd visitation and visitation duration

We used two main response variables to measure the response of prey species to our experimental treatments. Herd visitation was defined as the total number of herds for which individuals were inside the plot boundaries, per species per experimental treatment per site per day/night. We used herd as a sample unit, rather than individuals, because all of the focal species are gregarious and the behaviour of

individuals within these herds is highly synchronized (Hunter and Skinner, 1998; Caro, 2005). Individuals would thus not be suitable as independent samples. All videos of the same species appearing within a time span of 15 min were still defined as the same herd. We considered a time lapse of 15 min or more between videos of the same species to denote a new visitation event, thereby capturing both visits by new herds and return visits by the same herd. In our analyses, we used sites as the independent replicates ($N = 11$; see next section on statistical approach). These sites were far enough apart to assume that they were largely visited by different individuals, ensuring that return visits by the same herd did not create pseudoreplication issues. We defined “day” as spanning from an hour before sunrise to an hour after sunset, and “night” as the converse. We measured the time that each herd spent on a plot and averaged to obtain visitation duration per herd, per species per experimental treatment per site per day/night. We rounded to the nearest second.

We used species-specific zero-inflated generalized linear mixed effect models to model 1) herd visitation and 2) herd visitation duration. We modelled both response variables as a function of simulated elephant impact (CWD addition and visibility), scat addition, time of day and the two way interactions between simulated elephant impact and time of day, between simulated elephant impact and scat addition, and between scat addition and time of day (R package: glmmTMB; Brooks et al., 2017). Here, simulated elephant impact consisted of five treatment levels (open plot with CWD, open plot without CWD plus scat in week 2, open plot without CWD minus scat in week 2, closed plot with CWD, closed plot without CWD) while scat addition (scat present, scat absent) and time of day (night, day) each had two treatment levels. Herd visitation was modelled using a Poisson family and visitation duration was modelled using a negative binomial family to resolve overdispersion. To account for the repeated measures and the hierarchical experimental design, we nested plot identity within site as random effects. However, failure to converge forced us to simplify this random structure to plot identity nested within region (see Fig. 1 for delineation of regions). To correct for variation in filming effort, we defined the log of the number of days each camera was recording as an offset term. We limited the camera trapping effort to a minimum of three days. We categorized the extent of zero-inflation per site, per day/night category as high ($\geq 60\%$ zeros) and low ($< 60\%$ zeros) and applied a separate zero-inflation parameter to each (Brooks et al., 2017). We attempted to include a spatial correlation structure, yet this resulted in the models not converging. Thus, we were forced to omit the spatial correlation and trust that at least some of the spatial correlation would have been dealt with by having the within-plot and within-region correlation defined in the random component. Such a random component allows for a compound correlation between observations from the same plot (Zuur et al., 2009). Where interactions and main terms were not significant, we simplified the model through AIC-based, step-wise backward selection, each time removing the least significant term until only significant ($P < 0.05$) variables remained. Where interactions remained within the best adequate model (Table A.2), we compared effect means through pair-wise Tukey post hoc tests (R package: lsmeans; Lenth, 2016).

3. Results

3.1. Vegetation and visibility

The cover of the dominant lawn grass species (*S. nitens* and *U. mosambicensis*) did not differ among plots ($\chi^2 = 5.12$, $p = 0.276$ for *S. nitens* and $\chi^2 = 1.71$, $p = 0.789$ for *U. mosambicensis*) and neither did greenness. ($\chi^2 = 4.00$, $p = 0.406$). Visibility differed significantly between different sight-levels at which it was measured and depending on the openness of the plot. Visibility at warthog level was lower than at impala and rhino sight-level (Table A.3), but visibility did not differ between impala and rhino sight-levels. The closed plots had the lowest

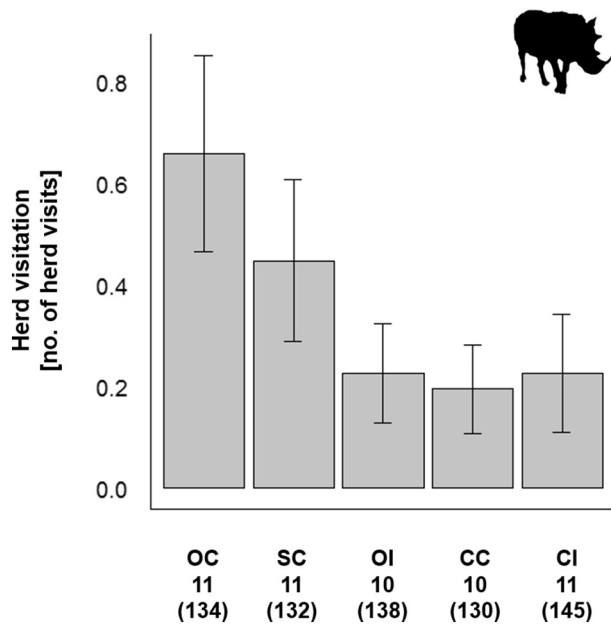


Fig. 3. Average visitation (number of herd visits; \pm SE) during the day for Open-Control (OC), Scat-Control (SC), Open-Impediment (OI), Closed-Control (CC) and Closed-Impediment (CI) plots. Values indicate the number of sites for which data were available with the cumulative number of monitoring days in parenthesis (added across all sites and weeks).

visibility of all plots. Open plots with CWD had lower visibility than open plots without CWD, but much higher visibility than the closed plots. There was no difference in visibility between the open plots without versus without scat or between the closed plots with versus without scat.

3.2. Herd visitation and herd visitation duration

Warthog only visited sites during the day and visited closed plots and plots with CWD less frequently than open plots without CWD, independent of predator scat presence (Fig. 3, Table A.4). During the week without predator scat, impala visitation did not differ among plots during the day (Fig. 4A, Table A.4). However, during the night, they significantly reduced their visitation to the low visibility plots without CWD (closed-control plots), relative to the other plots (Fig. 4A, Table A.4). Once we added scat, impala significantly decreased their visitation to all plots during the night (Fig. 4B, Table A.4). We did not find effects of simulated elephant impact or scat addition on the duration of visits for both warthog and impala. White rhino visited plots of lower visibility (with and without the addition of escape impediments) less often than open plots (Fig. 5A, Table A.4). They also spent less time on these low visibility plots (Fig. 5B, Table A.5). In addition, rhino visited all plots less often during the night than during the day (Fig. 5C, Table A.4).

4. Discussion

Prey species, vulnerable to predation, i.e. warthog and impala, responded to habitat openness, CWD addition and addition of predator scat in different ways. Warthog avoided low visibility and CWD plots, relative to control plots, whether scat was present or not. Moreover, they visited our sites only during the day. Impala only reduced their visitation to the low visibility plots during the night, especially after we added predator scat. Contrary to our predictions, white rhino (the non-prey species) also visited areas of low visibility less frequently than open plots. Moreover, they spent less time in these low visibility plots and visited all plots less frequently during the night than during the

day. We show that elephant-induced habitat changes may modify the perceived risk by improving visibility through the removal of vegetation at larger scales (e.g., in our study impala at night), but also by creating small-scale risky patches by adding CWD (e.g., warthog during the day). The degree to which this has an impact on species' behaviour varies largely among species. As such, our results suggest that mega-herbivores, such as elephant, may influence the landscapes of fear perceived by smaller ungulates but that responses are species-specific and can be dynamic and complex (le Roux et al., 2018).

4.1. Response of ungulate species to patch scale risk effects

In line with our first hypothesis, warthog generally avoided lawn edges where visibility was low. However, contrary to our prediction, impala did not. Warthog and impala avoid predation through early detection and flight (“runner type”), thus from a predator avoidance perspective both species should prefer open habitat (White, 2010; Riginos and Grace, 2008). Yet here, only warthog consistently avoided the lawn edges of low visibility, while impala only avoided these risky areas during the night time, when predator activity is generally higher. Like the impala in our study, Kohl et al. (2018) also found that elk (*Cervus elaphus*) did not avoid risky places entirely, but utilized these places during times when it was safe to do so, i.e. during the lull in predator activity. Impala are mixed feeders and switch to browse during dry season months (Scheel, 1993; du Toit and Yetman, 2005). Our study stretched from the beginning to the middle of the dry season, during a particularly dry period, and thus impala would have been very dependent on browse. By design, the plots with the low visibility occurred at the edge of the grazing lawn where dense woody vegetation limited visibility but also provided forage. Hence, forage requirements likely compelled impala to accept higher risk during the limiting season. Such a trade-off between foraging opportunities and predation risk (see Lima and Bednekoff, 1999) has been demonstrated elsewhere, where nutritionally stressed animals venture into more risky areas that they would have avoided under more favourable conditions (Sinclair, 1985; Brown and Kotler, 2004; Riginos, 2015; Owen-Smith, 2019). Warthog, on the other hand, do not browse and had no incentive to forage close to the lawn edges, and therefore avoided the dense vegetation throughout. Thus species that differ in functional type may respond very differently to the risk of predation, as also shown by Creel et al. (2019), and a diverse ungulate community might display many limitations on the ways in which they can respond to risk.

Contrary to prediction, white rhino (expected to be invulnerable to predation) also visited plots with dense woody vegetation and lower visibility less often. We cannot fully explain this result. In fact, recent work based on the distribution of dung suggests white rhino use dense woody habitats more than open habitat (le Roux et al., 2018). Perhaps the response in our study is driven by the very low grass availability in our plots during our time of study (see Fig. A.3), making the open plots less attractive for foraging than the closed plots with higher biomass. Even though there was no statistical difference in food availability among plots, the edge of the grazing lawn may have presented a feeding impediment to rhino offering too little biomass. Rhino also visited plots less at night. This is in line with observations from Jordaan (2010) and Patton et al. (2011), who showed that rhinos spend more time resting during the night in the dry season. We are thus inclined not to explain this as a response to perceived risk. Regardless, we cannot fully confirm our first hypothesis that vulnerable herbivores would visit closed habitat less often than non-vulnerable ones.

4.2. Response of ungulates to within patch risk effects (CWD)

Impact of coarse woody debris (CWD) on perceived predation risk has already been described in studies from temperate systems, recognizing red deer avoidance of CWD as a response to fine scale predation risk (Halofsky and Ripple, 2008; Kuijper et al., 2013). These

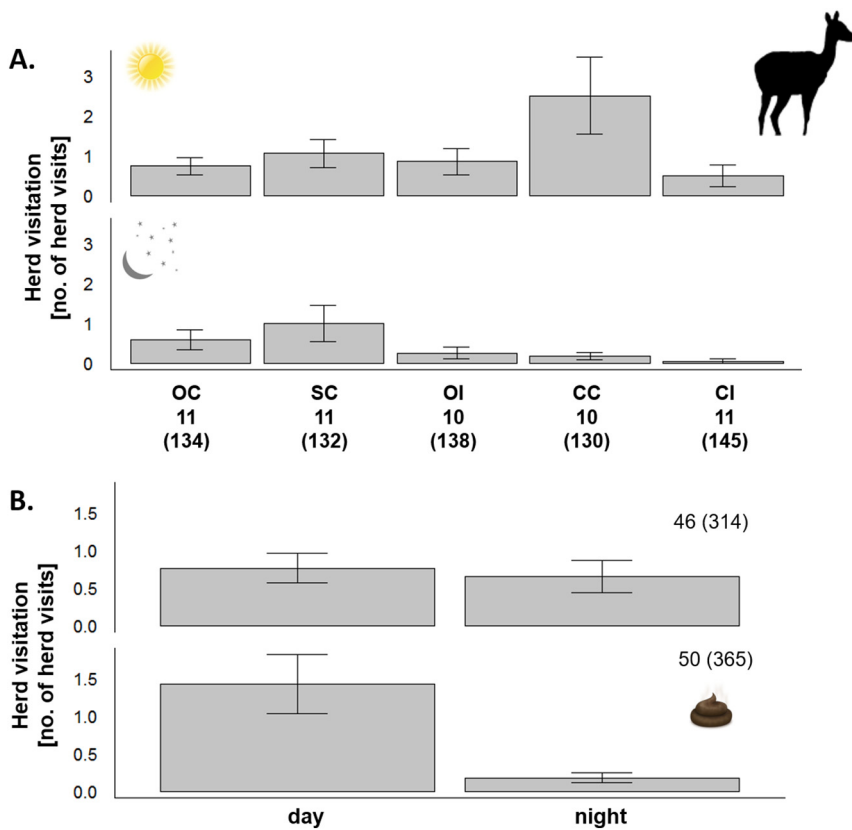


Fig. 4. A) Average visitation (number of herd visits; \pm SE) during the day (upper row of bars) and during the night (lower row of bars) for Open-Control (OC), Scat-Control (SC), Open-Impediment (OI), Closed-Control (CC) and Closed-Impediment (CI) plots. Values indicate the number of sites for which data were available with the cumulative number of monitoring days in parenthesis (added across all sites and weeks). B) Average visitation (\pm SE) separated between day and night, during the week without predator scat (upper row of bars) and the week with predator scat added (lower row of bars). Values in each panel indicate the number of plots for which data were available with the cumulative number of monitoring days in parenthesis (added across all sites and weeks).

effects of fine-scale habitat features are predicted to be especially pronounced with carnivores that use an ambush-style of hunting their prey (Schmitz and Suttle, 2001; Preisser et al., 2007 but see Kuijper et al., 2015). In our study system, lions and leopards are the main ambush predators for ungulates (Somers et al., 2017), and objects that block the view or prevent escape possibilities are expected to be avoided by ungulate prey species, as posed in hypothesis 2. Surprisingly, we found that the two common prey species (Somers et al., 2017) in our study

responded in opposite ways. Whereas impala did not respond to escape impediments, warthog did. A potential explanation for this difference is that warthogs are less agile than other savanna ungulates, as described by Estes (1999) and Skinner and Chimimba (2005). If indeed warthog are less manoeuvrable than impala, escape impediments may present more of a challenge to warthog than to impala and would be more strongly avoided. The dimensions of CWD (c. 50 \times 50 \times 100 cm) that were used in the current study are relatively small and may not have

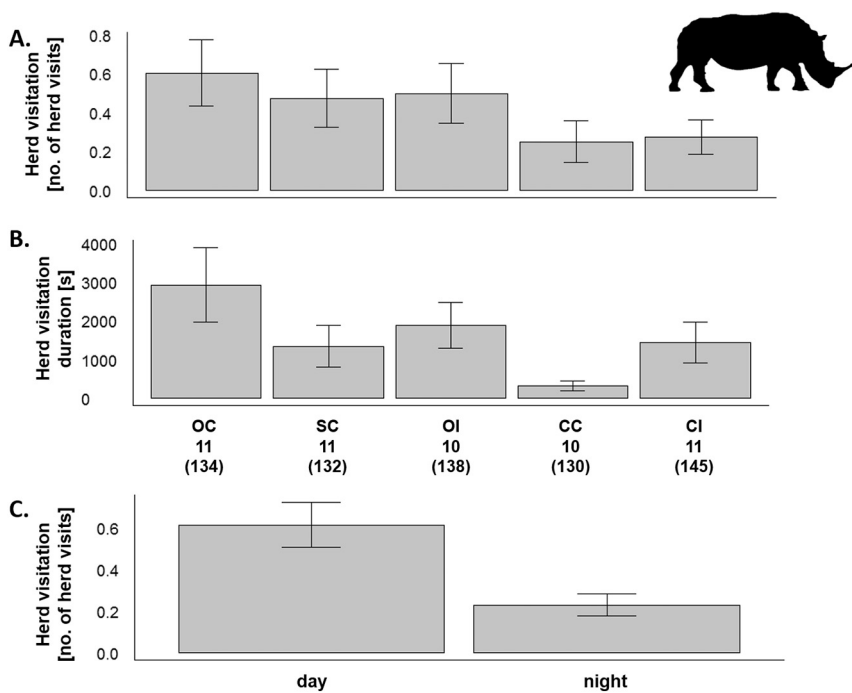


Fig. 5. A) Average visitation (number of herd visits; \pm SE) and B) average visitation duration (measured in seconds; \pm SE) for Open-Control (OC), Scat-Control (SC), Open-Impediment (OI), Closed-Control (CC) and Closed-Impediment (CI) plots, both averaged across day and night. C) Average visitation (\pm SE) separated between day and night. Values indicate the number of sites for which data were available with the cumulative number of monitoring days in parenthesis (added across all sites and weeks; applicable to panel A and B).

posed a very serious obstacle for agile jumpers as impala, however they do impede predator detection by lowering visibility. Rhino on the other hand did not respond to the addition of CWD (except when in combination with the dense vegetation at the edge of the grazing lawn). These results suggest that, in line with our second hypothesis, elephant-induced CWD is not perceived as risky by non-prey herbivores, such as white rhino, but can increase fine-scale predation risk for some vulnerable prey species such as warthog, while impala could be insensitive or could require larger dimensions of CWD to be perceived as an escape impediment. Again, we should note that our study was undertaken during a time of resource scarcity and the response of impala to CWD might be different during the growing season when food is widely available.

4.3. Temporal variation in predation risk

Both prey species showed a clear response to the temporal variation in predation risk. Warthog avoided plots entirely during the night (a time during which they retreat to their burrows). Without predator scat, impala avoided the low visibility plots at night. With wild dog scat, they avoided all plots at night relative to the day. Several studies have used predator scat (alone or in combination with predator urine) to simulate predator presence and demonstrated increased perceived risk by prey species (Shrader et al., 2008; Chamaillé-Jammes et al., 2014; Kuijper et al., 2014) but also that different prey species might recognize the predator species and accordingly adjust their behavioural response (Wikens et al., 2015). In addition, night time can be considered as the most risky time for both warthog and impala since two of their main predators, lion and leopard, are most active at night (Hayward and Slotow, 2009; Somers et al., 2017). Prey species might thus have responded to their presence and avoiding night visits, in addition to wild dog scat. The increased perceived risk by impala of all plots when we added wild dog scats can be explained by the importance of wild dogs as an important predator. Similarly, this may explain why warthog did not respond to the presence of wild dog scat. In HIP, impala make up about 50% of wild dog diet whereas warthog comprises only 2% (Somers et al., 2017). Wild dog are generally described as diurnal or crepuscular, but have in some places been shown to spend about 25% of the total activity budget at night, particularly on moonlit nights (Cozzi et al., 2012).

4.4. The potential role of elephant in engineering landscapes of fear for smaller ungulates

We showed that both warthog and impala, to varying extents, avoided areas of dense vegetation and low visibility. If elephant open up vegetation and create clearings within otherwise dense habitat (as suggested in the literature, Dublin et al., 1990; Conybeare, 2004; Skarpe et al., 2004), prey species such as impala and warthog may benefit and use these as refuges from predation. At a finer spatial scale, patches of fear caused by CWD (as described earlier for temperate forest by Kuijper et al. (2015), can affect the distribution of some, possibly

less nimble, species. The CWD that is characteristic of elephant feeding may obstruct movement and in this crucial moment of attack, tip the balance in favour of the predator. In this way, the effect of elephants on habitat structure could make habitats more accessible to smaller species at broad scales by opening up the vegetation, yet at finer scales create an intricate patchwork of risk and safety which prey must navigate.

With the majority of studies on predator-prey interaction being conducted in northern hemisphere systems (generally much more species poor), it is seldom possible to explicitly include multiple prey species of varying vulnerability in the same study (Montgomery et al., 2019). In contrast, our study not only plays off in a system where prey has to respond to a diverse predator assemblage, but it explicitly includes prey species that vary greatly in their vulnerability to predation and in their capacity to respond to predation risk (e.g. with nutritional requirement compelling impala to use risky places and with warthog being able to retreat to burrows during the night). Moreover, our study is one of the few that simultaneously incorporates spatial and temporal variation in predation risk as has recently been described for northern hemisphere systems (Kohl et al., 2018). Incorporating these components confirmed that the landscape of fear perceived by prey species is often highly dynamic. Our study adds to this knowledge that in savanna ecosystems, megaherbivores may play a considerable role in inducing habitat changes that create these dynamic and complex landscapes of fear that vary in space and time and are scale-dependent (see also van Ginkel et al., 2019).

Role of the funding source

There has been no influence of the study sponsors on the interpretation of data; in the writing of the report; and in the decision to submit the paper for publication.

Declaration of Competing Interest

The authors have no competing interests to declare.

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Appendix A

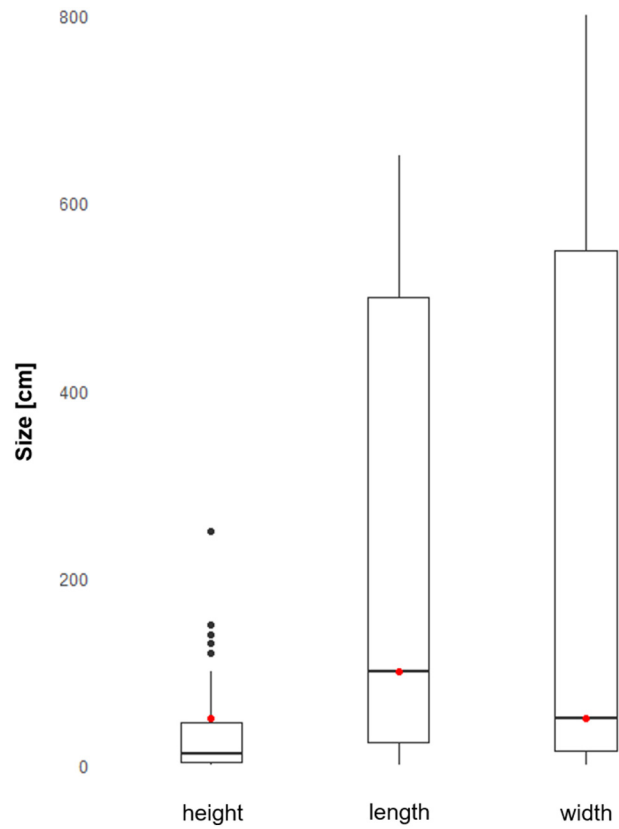


Fig. A.1. Natural variation in coarse woody debris (CWD) deposited by elephants at five grazing lawns in Hluhluwe-iMfolozi Park (data extracted from Prinsloo, 2017). The red points represent the sizes of our experimentally created debris, indicating its comparability to natural elephant-created debris



Fig. A.2. Natural coarse woody debris deposited by elephants at a grazing lawn in an area with high elephant impact in Hluhluwe-iMfolozi Park.



Fig. A.3. Photos of experimental plots, open control (OC) or scat control (SC) plot (a), open plot with escape impediments (OI) (b), closed (CC) plot (c), closed plot with escape impediments (CI) (d).

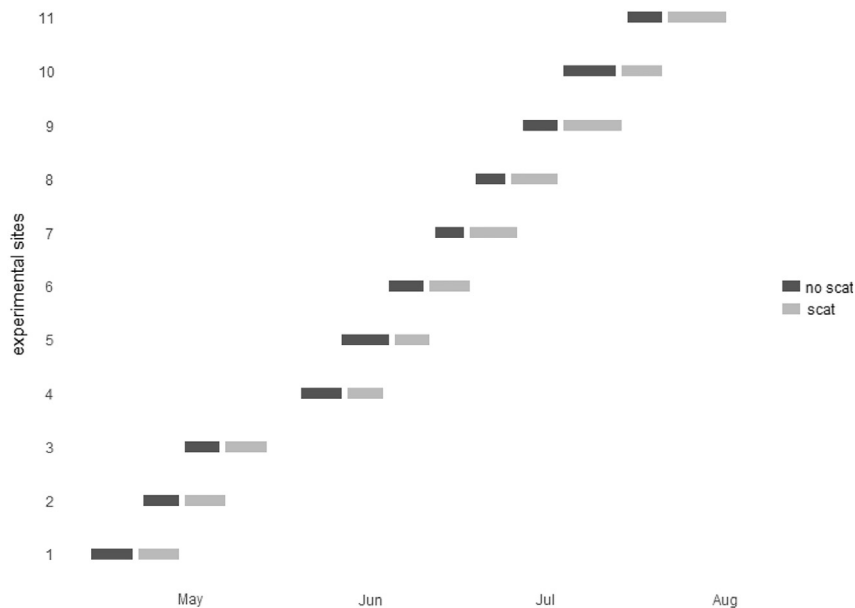


Fig. A.4. The duration of the study, showing camera trapping days per experimental site in presence or absence of wild dog scat.

Table A.1

Summarized data from camera trapping; the total number of different herds, or groups, and total number of records for 24 species that visited our sites.

Common name	Scientific name	No. of herds	No. of records
Impala	<i>Aepyceros melampus</i>	166	811
White rhinoceros	<i>Ceratotherium simum</i>	86	286
Common warthog	<i>Phacochoerus africanus</i>	70	175
Birds	<i>Aves</i>	64	81
Genet	<i>Genetta spp.</i>	37	39
White tailed mongoose	<i>Ichneumia albicauda</i>	36	41
Blue wildebeest	<i>Connochaetes taurinus</i>	28	101
Scrub hare	<i>Lepus saxatilis</i>	27	33
Black rhinoceros	<i>Diceros bicomis</i>	17	58
Giraffe	<i>Giraffa camelopardalis</i>	11	23

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Table A.1 (continued)

Common name	Scientific name	No. of herds	No. of records
African elephant	<i>Loxodonta africana</i>	9	21
Aardvark	<i>Orycteropus afer</i>	9	12
Hyena	<i>Crocuta crocuta</i>	9	11
Greater kudu	<i>Tragelaphus strepsiceros</i>	8	22
Plain's zebra	<i>Equus quagga</i>	7	15
Chacma baboon	<i>Papio ursinus</i>	5	13
African buffalo	<i>Syncerus caffer</i>	5	10
Blue duiker	<i>Cephalophus monticola</i>	4	4
Vervet monkey	<i>Chlorocebus pygerythrus</i>	4	4
Common duiker	<i>Sylvicapra grimmia</i>	3	3
Lion	<i>Panthera leo</i>	3	3
Slender mongoose	<i>Galerella sanguinea</i>	3	3
Cape porcupine	<i>Hystrix africaeustralis</i>	2	2
Nyala	<i>Tragelaphus angasii</i>	1	2
Cheetah	<i>Acinonyx jubatus</i>	1	1

Table A.2

Best adequate models for impala, rhino and warthog herd visitation and visitation duration.

Species	Response variable	Model parameters
Impala	Herd visitation	Simulated elephant impact + Scat Addition + Time of day + Simulated elephant impact : Time of day + Scat Addition : Time of day
	Herd visitation duration	Null model
Rhino	Herd visitation	Simulated elephant impact + Time of day
	Herd visitation duration	Simulated elephant impact
Warthog	Herd visitation	Simulated elephant impact
	Herd visitation duration	Null model

Table A.3

Multiple comparisons of visibility at different sight-line levels and plots with confidence intervals. Significant (alpha = 0.05) differences in observed means are annotated in bold.

		diff (means)	CI (lwr)	CI (upr)
Sight-line level	Impala-warthog	0.980	0.330	1.629
	Rhino-warthog	1.134	0.484	1.784
	Rhino-impala	0.155	-0.495	0.804
Plots	Open-impediment vs open-control	-2.008	-2.986	-1.029
	Scat-control vs open-control	-0.470	-1.448	0.509
	Closed-control vs open-control	-6.739	-7.717	-5.760
	Closed-impediment vs open-control	-6.750	-7.728	-5.772
	Scat-control vs open-impediment	1.538	0.560	2.516
	Closed-control vs open-impediment	-4.731	-5.709	-3.753
	Closed-impediment vs open-impediment	-4.742	-5.721	-3.764
	Closed-control vs scat-control	-6.269	-7.247	-5.291
	Closed-impediment vs scat-control	-6.280	-7.259	-5.302
	Closed-impediment vs closed-control	-0.011	-0.990	0.967

Table A.4

Parameter estimates with standard errors and p values of impala, warthog and white rhino visitation at different experimental plots, during different time of day and with or without presence of wild dog scat.

	IMPALA			RHINO			WARTHOG		
	Visitation			Visitation			Visitation		
	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
Open-control, day × open-impediment, day	-1.100	0.797	0.168	-0.198	0.389	0.610	-1.211	0.525	0.021
Open-control, day × scat-control, day	0.270	0.639	0.672	-0.540	0.395	0.172	-0.702	0.439	0.110
Open-control, day × closed-control, day	0.184	0.665	0.782	-0.911	0.492	0.064	-1.461	0.545	0.007
Open-control, day × closed-impediment, day	-0.688	0.814	0.398	-1.008	0.441	0.022	-1.220	0.488	0.012
Open-control, day × open-control, night	0.228	0.588	0.698	-0.916	0.289	0.002			
Open-impediment, day × open-impediment, night	0.589	0.642	0.996						
Scat-control, day × scat-control, night	0.247	0.382	1.000						
Closed-control, day × closed-control, night	2.094	0.658	0.047						
Closed-impediment, day × closed-impediment, night	2.045	1.128	0.727						

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Table A.4 (continued)

	IMPALA			RHINO			WARTHOG		
	Visitation			Visitation			Visitation		
	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
Open-control, night × open-impediment, night	0.547	0.710	0.999						
Open-control, night × scat-control, night	−0.299	0.536	1.000						
Open-control, night × closed-control, night	1.153	0.791	0.909						
Open-control, night × closed-impediment, night	2.293	1.137	0.587						
Open-control, no scat × open-impediment, no scat	1.205	0.641	0.683						
Open-control, no scat × scat-control, no scat	−0.337	0.484	1.000						
Open-control, no scat × closed-control, no scat	0.673	0.614	0.985						
Open-control, no scat × closed-impediment, no scat	1.520	0.780	0.635						
Open-control, no scat × open-control, scat	0.097	0.573	0.866	−0.107	0.258	0.679	−0.380	0.268	0.156
Open-impediment, no scat × open-impediment, scat	−1.015	0.606	0.809						
Scat-control, no scat × scat-control, scat	0.718	0.454	0.857						
Closed-control, no scat × closed-control, scat	−0.244	0.422	1.000						
Closed-impediment, no scat × closed-impediment, scat	0.392	0.741	1.000						
Open-control, scat × open-impediment, scat	−0.321	0.594	1.000						
Open-control, scat × scat-control, scat	−0.129	0.566	1.000						
Open-control, scat × closed-control, scat	−0.081	0.571	1.000						
Open-control, scat × closed-impediment, scat	1.402	0.788	0.750						
No scat, day × scat, day	−0.535	0.272	0.200						
No scat, day × no scat, night	0.463	0.390	0.634						
Scat, day × scat, night	1.679	0.456	0.001						
No scat, night × scat, night	0.680	0.483	0.494						

Table A.5

Parameter estimates with standard errors and p values of impala, warthog and white rhino visitation duration at different experimental plots, during different time of day and with or without presence of wild dog scat.

	IMPALA			RHINO			WARTHOG		
	Visitation duration			Visitation duration			Visitation duration		
	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
Open-control, day × open-impediment, day	−0.393	0.536	0.463	−0.877	0.457	0.055	−0.323	0.668	0.629
Open-control, day × scat-control, day	−0.875	0.451	0.052	−1.349	0.470	0.004	−0.214	0.609	0.725
Open-control, day × closed-control, day	0.503	0.446	0.259	−1.581	0.644	0.014	−0.846	0.726	0.244
Open-control, day × closed-impediment, day	0.505	0.605	0.404	−1.000	0.523	0.056	−1.063	0.712	0.135
Open-control, day × open-control, night	−1.027	0.599	0.086	−0.779	0.373	0.037			
Open-impediment, day × open-impediment, night	−0.016	0.754	1.000	−0.464	0.376	0.967			
Scat-control, day × scat-control, night	−0.688	0.454	0.886	0.589	0.514	0.980			
Closed-control, day × closed-control, night	0.104	0.639	1.000	0.163	0.523	1.000			
Closed-impediment, day × closed-impediment, night	0.779	1.084	0.999	0.382	0.471	0.999			
Open-control, night × open-impediment, night	−0.650	0.769	0.998	−0.388	0.501	0.999			
Open-control, night × scat-control, night	−0.840	0.579	0.911	1.496	0.661	0.413			
Open-control, night × closed-control, night	−1.425	0.776	0.712	1.368	0.507	0.174			
Open-control, night × closed-impediment, night	−0.753	1.085	1.000	0.243	0.544	1.000			
Open-control, no scat × open-control, scat				0.374	0.442	0.998			
Open-control, no scat × scat-control, no scat				1.372	0.456	0.078			
Open-control, no scat × closed-control, no scat				1.391	0.562	0.281			
Open-control, no scat × closed-impediment, no scat				0.920	0.545	0.802			
Open-control, no scat × open-control, scat	0.234	0.295	0.428	−0.713	0.326	0.029	−0.343	0.503	0.495
Open-impediment, no scat × open-impediment, scat				−0.042	0.370	1.000			
Scat-control, no scat × scat-control, scat				0.678	0.440	0.875			
Closed-control, no scat × closed-control, scat				0.809	0.497	0.835			
Closed-impediment, no scat × closed-impediment, scat				−0.716	0.479	0.895			
Open-control, scat × open-impediment, scat				−0.145	0.459	1.000			
Open-control, scat × scat-control, scat				1.573	0.574	0.157			
Open-control, scat × closed-control, scat				1.724	0.516	0.029			
Open-control, scat × closed-impediment, scat				−0.273	0.447	1.000			
No scat, day × scat, day				0.478	0.214	0.113			
No scat, day × no scat, night				0.479	0.254	0.235			
Scat, day × scat, night				0.005	0.299	1.000			
No scat, night × scat, night				0.005	0.335	1.000			

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