

THESIS

FEAR OF HUMANS DRIVES COMPLEX CHANGES IN PREDATORS AND PREY IN SOUTH
AFRICA

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ABSTRACT

FEAR OF HUMANS DRIVES COMPLEX CHANGES IN PREDATORS AND PREY IN SOUTH AFRICA

Wildlife responses to human presence vary greatly; species can be fearful of humans or habituate to human presence. Using experimental and observational methods, I investigated how South African wildlife altered species-specific behavior and predator-prey co-occurrence in response to simulated and actual human presence. I used camera traps to capture wildlife responses to human voice playbacks in areas with and without tourists, and found that wildlife variably altered space use, temporal activity, and fleeing behavior in response to human voice playbacks and tourism, which further altered predator-prey co-occurrence within the system. Human-induced fear elicited a different response from wildlife than predator-induced fear, suggesting that not all species treat humans as they would their natural predators. Furthermore, prey responded to human voice playbacks and tourists similarly, while predators had different responses to human playbacks than how they responded to tourists. Prey species may be using humans as a shield against predation regardless of the amount of time humans have been present within the system, while predators may be more fearful of a novel human stimulus but appeared to be habituated to long-occurring human presence. The eventual habituation to humans by predators reverted the initial decrease in predator-prey co-occurrence to that observed in the control sites, suggesting that eventual habituation of predators to humans may help re-establish prey access to predators in disturbed systems. However, habituation may also lead to future human-predator conflict that can impact species conservation. Finally, I conclude by providing future research directions for studying how humans can impact predator-prey interactions.

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FEAR OF HUMANS DRIVES COMPLEX CHANGES IN PREDATORS AND PREY IN SOUTH AFRICA

1. INTRODUCTION

Interactions between species can shape ecological communities and their underlying systems through top-down processes (Ford and Goheen 2015; Schmitz et al. 2010; Suraci et al. 2019), making species interactions vital to ecosystem health. For example, loss of apex predators can lead to degraded predator-prey interactions and further alterations in natural communities (Belgrad and Griffen 2016; Wang et al. 2015). In Serengeti, Tanzania, local extirpation of African lions (*Panthera leo*) led to dramatic increases in abundance for three small ungulates, leading to overgrazing of the community's available vegetation (Estes et al. 2011). The Green World Hypothesis states that predators reduce herbivore densities through consumption (density-mediated, direct interactions - Hairston et al. 1960; Lima 1998a; Lima and Dill 1990), rather than through 'donor', or bottom-up control, which is also a major determinant of community structure (Power 1992). Predators can also alter herbivore behavior non-consumptively via trait-mediated, indirect interactions (Griffin et al. 2011; Lima 1998a; Lima and Dill 1990; Trussell et al. 2006; Valeix et al. 2009). Predator presence itself can induce fear (defined as the perceived predation risk) in prey, which can be powerful enough to drive behavioral changes in lower trophic levels (Churski et al. 2021; Clinchy et al. 2016; Suraci et al. 2016; Suraci et al. 2019).

Predator-induced fear can have equivalent, or even greater, effects on animal behavior compared to direct predation (Berger et al. 2001; Bleicher 2017; Caravantes 2020; Kohl et al. 2018). Prey species must navigate through space and time with respect to the tradeoff between avoiding predation and gaining sufficient resources (Palmer et al. 2017; Riginos 2015). To deal with this tradeoff, prey will alter behavior to avoid apex predators, such as changes in activity patterns, habitat selection, spatial distributions, vigilance, and grouping behavior (Iranzo et al. 2020; Montgomery et al. 2020; Palmer et al. 2017).

However, responses to predator-induced fear vary between species, across time, and over landscapes. In Africa, predation risk for (and, correspondingly, fear responses of) African ungulates are

correlated with body size (Jarman 1974; Riginos 2015; Riginos and Grace 2008; Sinclair et al. 2003; Thaker et al. 2011). Ungulates in the Serengeti that are above a threshold body size of 150 kg have fewer natural predators, making them less likely to respond fearfully to predators (Sinclair et al. 2003; Thaker et al. 2011). African elephants (*Loxodonta africana*, average body size ~6,000 kg), for example, are known to favor habitats with many trees, while other herbivores favor sites with high visibility due to the risk of predation (Riginos 2015). Diet also appears to influence prey's fear of predators. In a study by Valeix et al. (2009), browsing species (defined as species that feed on high-growing vegetation, like trees and shrubs) distributions were altered by high risk of lion predation, but the distributions of grazing species (defined as species that feed on low-growing vegetation, like grasses) were not altered. Temporal variation also appears to be an extremely important factor in fear responses, which can otherwise appear “temporally flattened” if space use over time is not considered (Kohl et al. 2018; Lima and Bednekoff 1999; Palmer et al. 2017). For example, Palmer et al. (2017) found that Thomson's gazelle (*Eudorcas thomsonii*), common wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus quagga*) all decreased nighttime activity when moonlight - and thus, visibility - was low in order to minimize predation threat.

When responses to predator-induced fear vary across the landscape, ecosystem structure and functioning can be altered (Clinchy et al. 2016; Trussell et al. 2006). Grazers in Africa avoid habitats with low visibility (e.g., tall vegetation) in order to decrease risk of predation from stalking predators that use vegetation to hunt (Riginos and Grace 2008). These “dangerous” areas for herbivores provide “safe havens” for plant species (Iranzo et al. 2020; Pringle 2018). For example, it is common for prey species in African savannas to avoid woodlands where carnivores are more likely to hunt, and herbivores will instead use open grasslands that possess higher visibility (Anderson et al. 2010; Ford et al. 2014; Riginos 2015; Riginos and Grace 2008; Thaker et al. 2011; Valeix et al. 2009).

Although much evidence suggests that apex predators can play a strong role in shaping prey behavior, the assumption that apex predators maintain ecological roles at the top of food webs is being challenged. Humans consume animals at rates as much as nine times higher than natural predators (Darimont et al. 2015; Montgomery et al. 2020; Smith et al. 2017; Suraci et al. 2019). Therefore, humans

are now thought to inhabit a trophic level above apex predators as the human ‘apex predator’ (Darimont et al. 2015; Montgomery et al. 2020), and may push large, natural apex predators into the functional role of mid-level predators (Williams et al. 2020). In line with this hypothesis, several studies suggest that wildlife respond fearfully to human activity similarly to how they would respond to vocalizations of natural predators (Suraci et al. 2019). For example, apex predators such as African lions (Mills and Harris 2020), African wild dogs (*Lycaon pictus*; Rasmussen and Macdonald 2012), spotted hyenas (*Crocuta crocuta*; Boydston et al. 2003), pumas (*Puma concolor*; Wang et al. 2015), bobcats (*Lynx rufus*; Wang et al. 2015), and coyotes (*Canis latrans*; Wang et al. 2015) have all shown spatial or temporal avoidance of humans, similarly to how mid-level predators avoid apex predators in other instances (Gigliotti et al. 2020; Jachowski et al. 2020; Suraci et al. 2019; Wang et al. 2015). Humans can also induce fear further down the food web, not only altering behavior of natural predators but their prey as well (Clinchy et al. 2016; Mills and Harris 2020; Suraci et al. 2019). For example, Mills and Harris (2020) found that increased human presence led to both predators and prey species increasing vigilance behavior and nocturnal activity in order to avoid humans.

In addition to inducing fear, human presence can also act as a refuge for prey, a phenomenon known as the human shield effect (Berger 2007; Suraci et al. 2019). When predators avoid humans, prey may take advantage of ‘predator-free’ spaces or times to decrease risk of predation. For example, mule deer (*Odocoileus hemionus*) living near urban environments will specifically seek out areas with elevated light levels to avoid puma predation (Ditmer et al. 2020). As with fear responses, however, not all prey species use humans as a shield. In West Africa, access to some prey species increased in response to human presence, but human presence also led to a decrease in overall prey availability for African lions and spotted hyenas, providing experimental evidence that humans may shield some species from predation in African wildlife communities while making other species more at risk (Mills and Harris 2020).

Whether a species responds to human presence via human shields or human-induced fear exemplifies the complexity of wildlife responses to human presence (Mills and Harris 2020; Suraci et al.

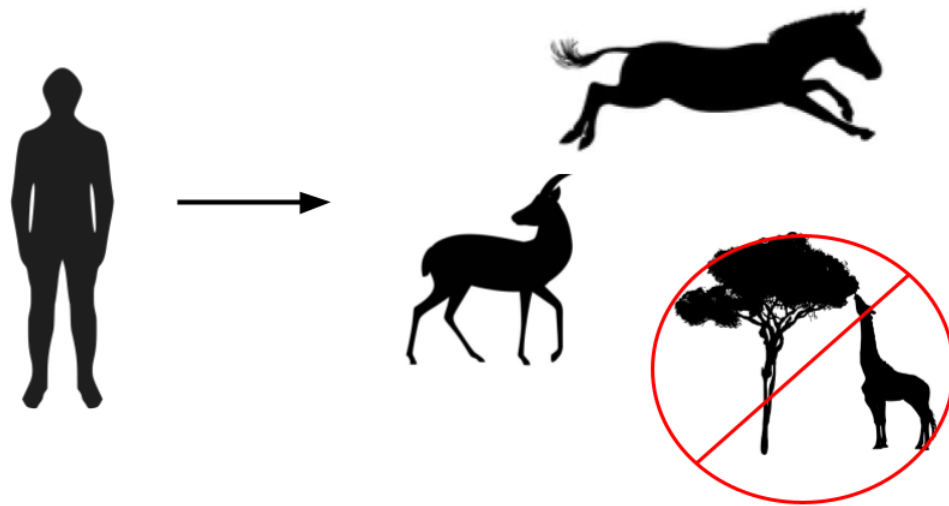
2019; Wang et al. 2015). Humans can induce fear in predators, prey, or both, or act as a shield for some species and not others (Crawford et al. 2022; Ditmer et al. 2020; Mills and Harris 2020; Suraci et al. 2019). In the southeastern United States, wildlife responded differently to recreation (i.e., humans hiking on trails) than they do to hunting pressure, with some species altering space use to both and others not responding to either disturbance type (Kays et al. 2017). Some species that have frequent, non-lethal contact with humans can also habituate to human presence (Bateman and Fleming 2017), which can help facilitate use of areas with high human disturbance (Thompson and Henderson 1998). Such variable reactions to human presence can lead to complex, unpredictable changes in predator-prey interactions (Suraci et al. 2019), such as changes in predation pressure for different prey species (Mills and Harris 2020).

As human-induced changes in wildlife behavior and interactions become more prevalent in consort with increasing human populations, it will be important to understand causes of variability in human-induced behavioral modifications of wildlife (Wang et al. 2015; Williams et al. 2020), such as the amount and type of anthropogenic exposure. It is unclear whether patterns found in the few experimental studies analyzing human-induced changes in wildlife interactions will hold true in more complicated food webs (Montgomery et al. 2020; Sinclair et al. 2003), and diverse assemblages of mammalian herbivores and carnivores - such as those found in Africa - are a pivotal testing ground for human-induced changes in wildlife behavior and interactions. Therefore, I investigated how human presence impacts species-specific behavior and predator-prey co-occurrence in South Africa and analyzed how these alterations corresponded with variation in tourism pressure. This study addresses 1) how simulated human presence alters species-specific behaviors, 2) how simulated human presence impacts spatiotemporal co-occurrence between predators and prey, and 3) how tourism pressure impacts these responses to a novel human disturbance. Ecotourism in South Africa is vital to the country's economy, with biodiversity-related tourism generating ZAR 31 billion (\$2.4 billion USD, 0.4% of the country's GDP) in 2015 alone (Snyman et al. 2021). As ecotourism increases in South Africa and across the globe, it will be important to understand how it impacts wildlife responses to human presence, and if these differentiated responses

also change species interactions. This study will enhance the body of knowledge documenting how human-induced fear can reshape species behavior and predator-prey co-occurrence within a complex and biodiverse mammal assemblage.

To address my research questions, I conducted a playback experiment in Kruger National Park, South Africa in areas with and without tourist access. I used recordings of a native bird, native predators, and human voices to simulate presence of these species across research sites. Though Kruger National Park does not allow legal hunting of wildlife, other authors have found that, even in areas without hunting, wildlife will show fear-associated behaviors towards humans (Baker et al. 2013; Hayward and Hayward 2009). Therefore, I predicted that all species would decrease foraging activity and be more likely to flee 1) from human and predator playbacks compared to bird playbacks and 2) in tourist areas compared to non-tourist areas (Figure 1). I also predicted that 1) simulated presence of humans and native predators and 2) tourist presence would increase nighttime activity and/or decrease spatial occurrence of all species, and correspondingly increase spatiotemporal (i.e., across space and time) co-occurrence between predators and prey (Figure 1).

Prediction 1: Humans will increase fear-associated (running, vigilance) behaviors & decrease foraging behavior.



Prediction 2: Simulated human presence and tourists will increase predator-prey co-occurrence.

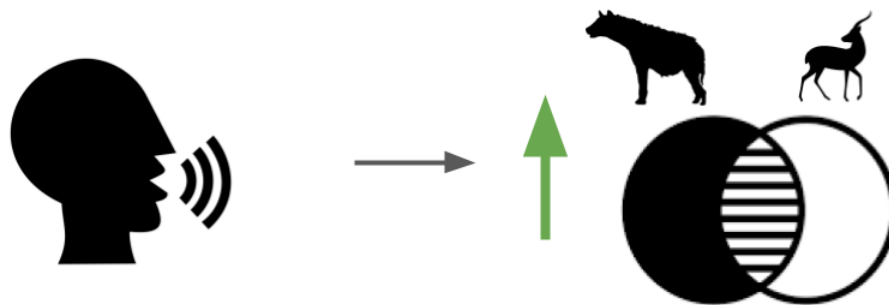


Figure 1. I predicted that humans (i.e., both simulated human presence and tourists) will increase fear-associated (running, vigilance) behaviors and decrease foraging behavior. I also predicted that humans would increase spatiotemporal co-occurrence between predators and prey.

2. METHODS

2.1. Study site

This study was conducted in Kruger National Park (KNP), South Africa (23°51'27.1"S 31°34'18.1"E) in July - August 2021. The park's area is 19,633 km² and is in the northeast region of South Africa in the Limpopo and Mpumalanga Provinces along the Mozambique border (Gertenbach 1983). KNP was first established in 1926 with the merging of Sabie and Shingwedzi Game Reserves, and the first roads were built in 1927 (Gertenbach 1983). My study site is in the central region of the park in mostly mopane-dominated woodlands with intermixed bushwillow and *acacia* species (Figure 2; Gertenbach 1983). Winters (May - September) tend to be warm and mild with little rainfall in this region (KNP 2006). Average monthly rainfall in July and August is 6-7 mm, and the average temperature in winter is 17.8 °C (KNP 2006).

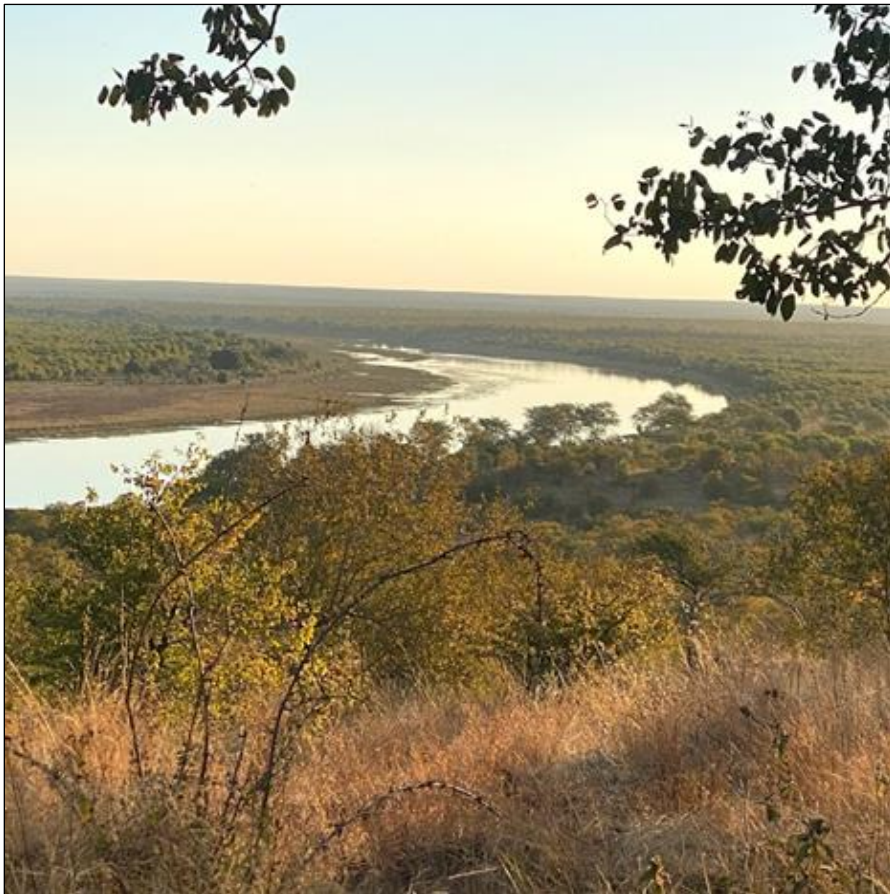


Figure 2. This study was conducted in the central region of Kruger National Park, South Africa, in mopane-dominated woodlands.

2.2. Study species

Though camera traps captured videos of most large vertebrates in the study area, I used four species of interest to analyze how predator-prey co-occurrence is affected by human-induced fear: spotted hyenas (*C. crocuta*; onwards referred to as hyena), impala (*Aepyceros melampus*), Burchell's zebra (*E. q. burchellii*; onwards referred to as zebra), and southern giraffe (*Giraffa giraffa*; onwards referred to as giraffe). Because rare species would not provide sufficient data, study species were chosen based on their prevalence within the study region. Approximate species prevalence in the park was estimated using camera trap data from Snapshot Safari (SS), a large-scale collaborative network aimed at monitoring African biodiversity (Pardo et al. 2021).

Hyenas are a native South African apex predator (Boydston et al. 2003) known to avoid human vocalizations spatially and temporally (Boydston et al. 2003), making them likely to respond to the human voice playbacks in this experiment. Hyenas are credited with inducing anti-predator behaviors in African herbivores (Boydston et al. 2003; Watts and Holekamp 2007). This apex predator's propensity to avoid humans and impact the behavior of indigenous herbivores makes hyenas preferable for studying human-induced changes in predator-prey interactions.

Impala, zebra, and giraffe represent the prey trophic level in this study. All three of these species are predated upon by hyenas (Boydston et al. 2003; Sinclair et al. 2003; Thaker et al. 2011; Watts and Holekamp 2007). I chose prey species that cover an array of body sizes and diets, as these factors impact how herbivores respond to predation pressure (Sinclair et al. 2003; Thaker et al. 2011).

2.3. Experimental framework

I broadcasted human voice playbacks as a simulated risk cue to test spatiotemporal wildlife responses to human presence (Smith et al. 2020). I had 30 study sites total: ten sites used human voice playbacks, ten sites had predator call playbacks, and ten control sites had native bird call playbacks (call types described in detail below). Playbacks were broadcasted using automated behavioral response units called 'Boomboxes' (from this point onwards referred to as playback units; Palmer et al. 2022). The BoomBox is programmed using Arduino Integrated Development Environment (Arduino LLC,

Scarmagno, Italy) and includes a specialized circuit board, two speakers, three AA batteries, connecting cable, IP65 enclosure, and USB programming dongle (Palmer et al. 2022).

I played multiple cue types in stratified random order to minimize the effects of animal habituation to sound playbacks and to enable robust conclusions of wildlife responding to a class of sounds (Clinchy et al. 2016; Smith et al. 2020). Human voices speaking in conversational tones were used for the treatment site, with a male and female voice from each of the three dominant local languages: Shangaan/Tsonga (downloaded from Wikitongues Youtube page), Afrikaans (recorded by collaborators in South Africa), and English (recorded by myself), leading to six voices total (Caravantes 2020). Though human voices are not novel to wildlife by themselves, the location of human voices away from roads and unassociated with vehicles produces a novel stimulus to test wildlife fear of humans. Predator playbacks included three call types from African lions and three from spotted hyenas, also resulting in six individual recordings. Based on Snapshot Safari's data, both African lions and spotted hyenas are present in the study site, and both species predate upon and/or induce fear in the herbivores of interest in this study (Holekamp et al. 1997; Mills and Harris 2020; Owen-Smith and Mills 2008; Sinclair et al. 2003; Thaker et al. 2011; Valeix et al. 2009; Watts and Holekamp 2007). The use of these predator's call playbacks in ten of the sites helped distinguish between human and natural predator effects on wildlife behavior. For control sites, I used playbacks of a non-threatening, crepuscular native bird species, the fiery-necked nightjar (*Caprimulgus pectoralis* - Caravantes 2020; Smith et al. 2017; Suraci et al. 2017).

One of the six possible playbacks from each camera was broadcasted once for 10 seconds before the playback unit underwent a one-minute delay, after which the 10-second playback would be broadcasted again if the animal re-triggered the camera. Peak amplitudes, duration, and perceived loudness of all playback calls were normalized to -1.0 dB, 10 seconds, and -23.0 LUFS, respectively (using Audacity Version 2.4.2; Clinchy et al. 2016). Playbacks were broadcasted at 80 dB at 1m² (Caravantes 2020; Clinchy et al. 2016; Suraci et al. 2017), except for two units that were unable to play up to 80 dB and were played at their maximum capacity of 70 dB.

2.4. Field methods

Study sites were placed at least 1 km apart, were close to access roads, covered a gradient of vegetation cover (i.e., predation risk), and had similar access to water. To test if wildlife's responses varied with tourism pressure, half (n=15) of the research sites were marked as “non-tourist”, defined as being in an area in which tourists were unable to access (due to lack of access roads; all non-tourist sites were 1 - 13 km away from a tourist road). The other half (n=15) were within areas of the park accessible to tourists (Figure 3).

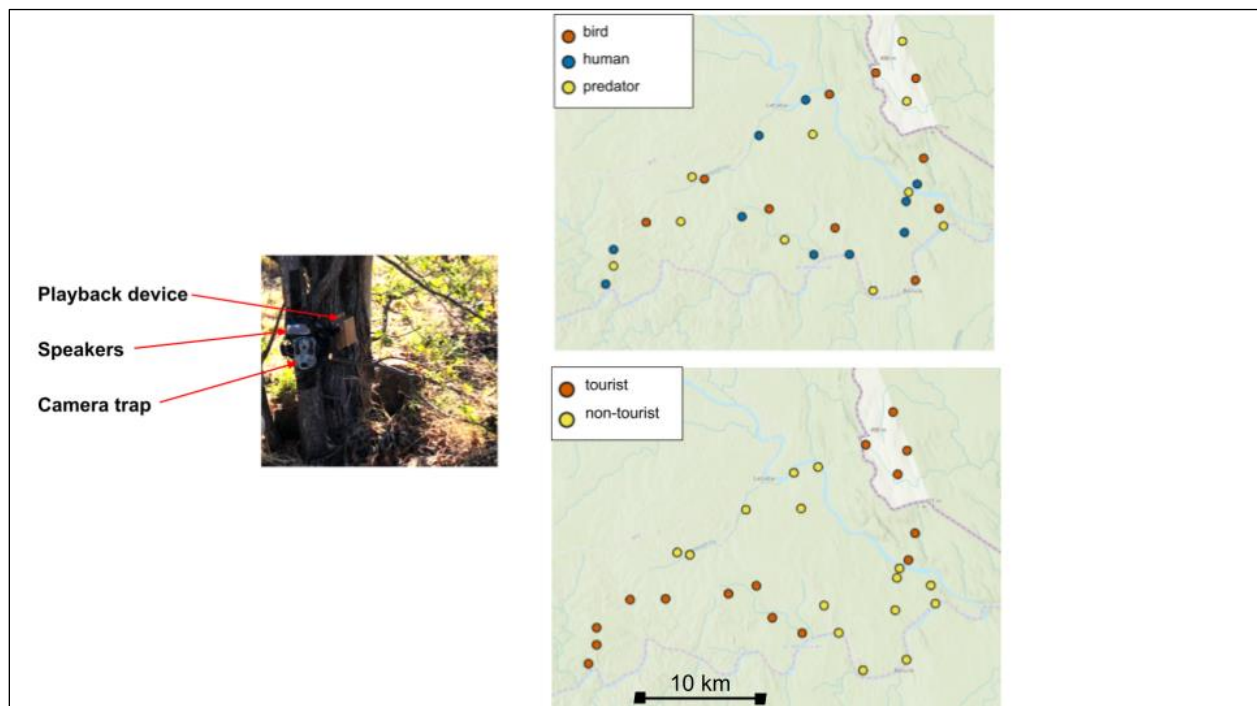


Figure 3. Location of experimental units for this study. Each site/unit had a speaker, playback unit, and camera trap placed on a tree approximately 50cm above ground level. The top graph indicates treatment type (bird, human, or predator playbacks), while the bottom graph indicates which sites were in tourist or non-tourist areas.

Heat- and motion-sensitive SpyPoint Dark Force cameras were placed 50 cm above the ground (best to capture medium- to large-sized vertebrates) on trees (Figure 3; Pardo et al. 2021). Cameras were set to normal or low sensitivity depending on the presence of savanna grass (grass produced frequent false triggers, so cameras set in grassy areas were programmed to low sensitivity to increase battery life). Camera detection distance varied between 8-22m, with an average detection distance of 13.86m. Trigger rate was set to the fastest possible (0.71s), and cameras were set to ‘no glow’ night mode (Henrich et al.

2020). When triggered, cameras were programmed to take a 30-second video, defined as one capture event (Pardo et al. 2021). I also included an off delay of one minute (i.e., once triggered, the camera could not be triggered again for one minute) to decrease the number of repeated detections of the same individual (Suraci et al. 2017). The speakers were set directly above the camera trap so that wildlife would look at the camera when triggered (Figure 3; Meredith Palmer, personal communication).

Playback units were placed next to or above camera traps depending on tree structure (Figure 3) and programmed to broadcast playbacks whenever an animal triggered the camera's sensor. Playbacks were delayed for one second after cameras were triggered, followed by a 10-second playback (Suraci et al. 2017). The playback unit was camouflaged with brown paint to avoid wildlife damage. I removed human scent from all equipment using scent-removal spray (Scent-A-Way Spray, Odorless, manufactured by Hunters Specialties).

All units were placed for 85 days in KNP between July 27 and October 20, 2021. Of the 30 experimental units originally set, data from 16 cameras were used in this study. Deployment dates and lengths varied for each camera within the study period (see A2 for exact deployment dates for each camera). Dates of usable data varied because of incorrect date and time stamps on 14 of the cameras' videos, information which was required to conduct my analyses. The videos used in this study from the 16 cameras with correct date and time stamps provided an even distribution of data across treatments and tourism, which allowed for statistically robust analyses.

2.5. Statistical analyses

I identified wildlife species observed in each 30-second video captured on the study's 30 camera traps, and scored behaviors displayed by each animal in response to sound playbacks (see 'Behavior analysis' section below for more details on behavior scoring). The number of individuals of each species and the amount of time each species remained in the camera's view were also recorded. I collected date, time, and temperature from each video observation as well. Videos were viewed individually with DropBox's video preview capability, and video metadata was recorded in Google Sheets. To reduce pseudoreplication, I did not include videos of individual animals from the same species that occurred

within 30 minutes of a previous video of that species if captured from the same camera (Palmer et al. 2017).

I conducted three analyses to explore changes to species-specific responses and predator-prey co-occurrence across treatments and tourism pressure: detection frequency, temporal activity, and species-specific behavioral responses. For models of detection frequency and for models of behavior responses, I used generalized linear mixed models (GLMM) with Poisson regression and a logarithmic link (Bowkett et al. 2008). In order to extend GLMMs for zero-inflated data common to camera trap results, I used the package glmmTMB (version 1.1.3; Brooks et al. 2017) and assigned zero-inflation for the ‘component’ argument. In other words, the glmmTMB package requires that a one-sided formula combining fixed and random effects is provided for zero-inflation, and I set the zero-inflation formula to be identical to the model formula (Brooks et al. 2017). All GLMMs were fitted using maximum likelihood estimation through the Template Model Builder in glmmTMB (Brooks et al. 2017). I used study site location as a Gaussian random effect in all models to account for spatial autocorrelation among sites (Brooks et al. 2017). I chose the most parsimonious models among candidate models based on Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2004). Any top models ($\Delta\text{AICc} < 2$) that did not converge were excluded from candidate models. Model estimates and standard errors are provided for all top-performing models. I also provide z-statistics and two-tailed p-values from model summary outputs for moderately or strongly ($p < 0.05$) supported predictors, which were compared across categories (such as across treatments or tourism pressure) using pairwise comparisons of estimated marginal means (emmeans, using package emmeans; Lenth 2022). For all analyses in this study, I used program R version 4.0.3 (2020-10-10; R Core Team 2020).

2.5.1. Analyzing detection frequency and species co-occurrence

I used GLMMs to contrast ‘detection frequency’ of wildlife to treatment, tourism pressure, other species’ detection frequencies, and land cover. Detection frequency is defined here as the number of observations per day of each species, which was calculated for every day each camera trap was deployed. Photographic capture rates of wildlife are comparatively simple relative abundance indices that can yield

results that correlate strongly with independent estimates of abundance for large mammals (Freeman et al. 2022; Palmer et al. 2018). Treatment, tourism pressure ('tourism' from this point onwards), and land cover were provided as categorical variables in each model as a function of each camera location. Specifically, land cover was identified as either 'closed' (forested areas - from the 2018 South Africa's National Land Cover Dataset; Thompson 2019) or 'open' (grasslands, shrublands, or arid land; Thompson 2019) since habitat visibility is known to influence both herbivore and carnivore spatial activity (Mills and Harris 2020; Valeix et al. 2009). Treatment was categorized as 'bird' (sites with playbacks of bird calls), 'predator' (sites with playbacks of lion and hyena calls), or 'human' (sites with human voice playbacks). Tourism was either present or absent for each site. See A3 for the top-performing ($\Delta AICc < 2$) detection frequency models. Detection frequency by each herbivore species (impala, zebra, and giraffe) was predicted using hyena detection frequency, and hyena detection frequency was predicted using each herbivore's detection frequency (i.e., impala, giraffe, and zebra detection frequencies; Freeman et al. 2022).

It is important to note that treatment was only used as a predictor in models for hyenas, zebra, and impala detection frequency, and not for giraffe detection frequency. This is because no observations of giraffes occurred in the human treatment, and, thus, models using treatment as a predictor for giraffe detection frequency would not converge. Therefore, giraffe detection frequency was predicted using land cover, tourism, and camera location.

2.5.2. *Temporal species overlap*

I produced non-parametric kernel density estimates using timestamps on camera observations to create diel activity curves using the procedure described by Ridout and Linkie (2009). With the R package 'overlap' (version 0.3.4; Ridout and Linkie 2009), I created each species' probability density distribution of activity across the 24-hour cycle, then calculated the overlap term Δ_i^* (used for small sample sizes; Ridout and Linkie 2009) for each predator-prey species pair for each treatment and tourism type. Finally, I evaluated how human presence altered the amount of spatiotemporal overlap (percent area under the diel curve) between each predator-prey pair for each site using 95% confidence intervals for

estimates from 10,000 bootstrap samples (Ridout and Linkie 2009). All graphs produced were created using the overlap (version 0.3.4) package's built-in graphing functions (Ridout and Linkie 2009).

2.5.3. Behavior analysis

I scored animal behaviors in each camera trap video in which an animal was present. The behavior observed for most of the video's length was assigned to the occasion. For example, if an impala displayed foraging behavior for 20 seconds of a 30 second video, then foraging behavior was assigned to that individual for that video. If there was more than one individual present, behavior was recorded for each individual animal separately. For behavior analyses, the behavior of the first-observed individual or individual closest to the center of the camera trap's frame within each video was used.

Behaviors were assigned to the following categories (adapted from Caravantes 2020): head up, looking at camera, scanning, approaching, running, retreating, threatening/posturing, walking, standing, defecating, foraging, recumbent, head down, head horizontal, other, N/A, or unknown. See Appendix 1 (A1) for behavior definitions. I used the following behaviors to analyze wildlife responses to playback treatments: foraging, looking at camera, scanning, and running. I decided to use these four behaviors as representations of immediate responses to treatments since 1) these behaviors were displayed by the species of interest, and thus 2) could be compared across species. Importantly, these behaviors have also been successfully used in previous studies to indicate fear and/or vigilance behavior (Caravantes 2020; Clinchy et al. 2016; Suraci et al. 2017). Foraging was defined as the animal standing or walking and grazing or chewing at the same time (for herbivore species only - foraging behavior was not observed from hyenas). 'Looking at camera' was defined as the animal standing or walking with its head raised above the horizontal and looking directly at the camera with both eyes visible. Scanning was defined as the animal standing or walking with its head at or above the horizontal while scanning with its ears. Finally, running was defined as an animal taking more than three consecutive steps in a single direction away from the camera at a speed greater than walking.

For each GLMM, I calculated the number of observations of each behavior for each species, per day and per camera trap, and used this as my response variable. For example, I calculated the number of

observances in which impala displayed foraging behavior for each day camera SD03 was deployed and repeated this process for all study sites. GLMMs were created for each of the following behaviors for herbivores: foraging, looking at camera, running, and scanning. Hyenas did not display any foraging behavior and did not display scanning behavior frequently enough for models to converge, so only ‘looking at camera’ and ‘running’ behaviors were analyzed for hyenas. See A4 for top-performing behavior models.

3. RESULTS

I collected 713 camera trap nights, 622 of which resulted in wildlife observations. Cameras at bird playback sites collected 242 trap nights, predator sites 306, and human playback sites 165 trap nights. I collected 362 camera trap nights from tourist areas and 351 trap nights from non-tourist areas. From these data, I received 1,231 observations of at least 38 species of wildlife, including 331 observations of impala, 133 giraffe observations, 126 zebra observations, and 56 hyena observations.

3.1. Impacts of predator or prey detection frequencies on species-level detection frequency

I originally predicted that predator-prey spatial overlap would increase with the simulated human presence treatment and in areas with tourists. However, I found that treatment was not an important predictor for any of the species of interest’s detection frequencies, and tourism was only associated with impala ($\beta = -1.190$, $SE = 0.6500$) and giraffe ($\beta = 0.1126$, $SE = 0.4371$) detection frequencies (Figure 4). Hyena detection frequency predicted herbivore (zebra, impala, giraffe) detection frequency, but herbivore detection frequency was not associated with hyena detection frequency (Figure 4). Specifically, giraffe detection frequency was very strongly ($z = 9.194$, $p < 2e-16$), positively correlated with hyena detection frequency ($\beta = 51.88$, $SE = 5.642$), while zebra detection frequency was strongly ($z = -3.120$, $p = 0.00181$), negatively correlated with hyena detection frequency ($\beta = -18.16$, $SE = 18.17$; Figure 4). Top models for impala detection frequency included hyena detection frequency ($\beta = -2.846$, $SE = 10.02$), though this association was very weak (Figure 4).

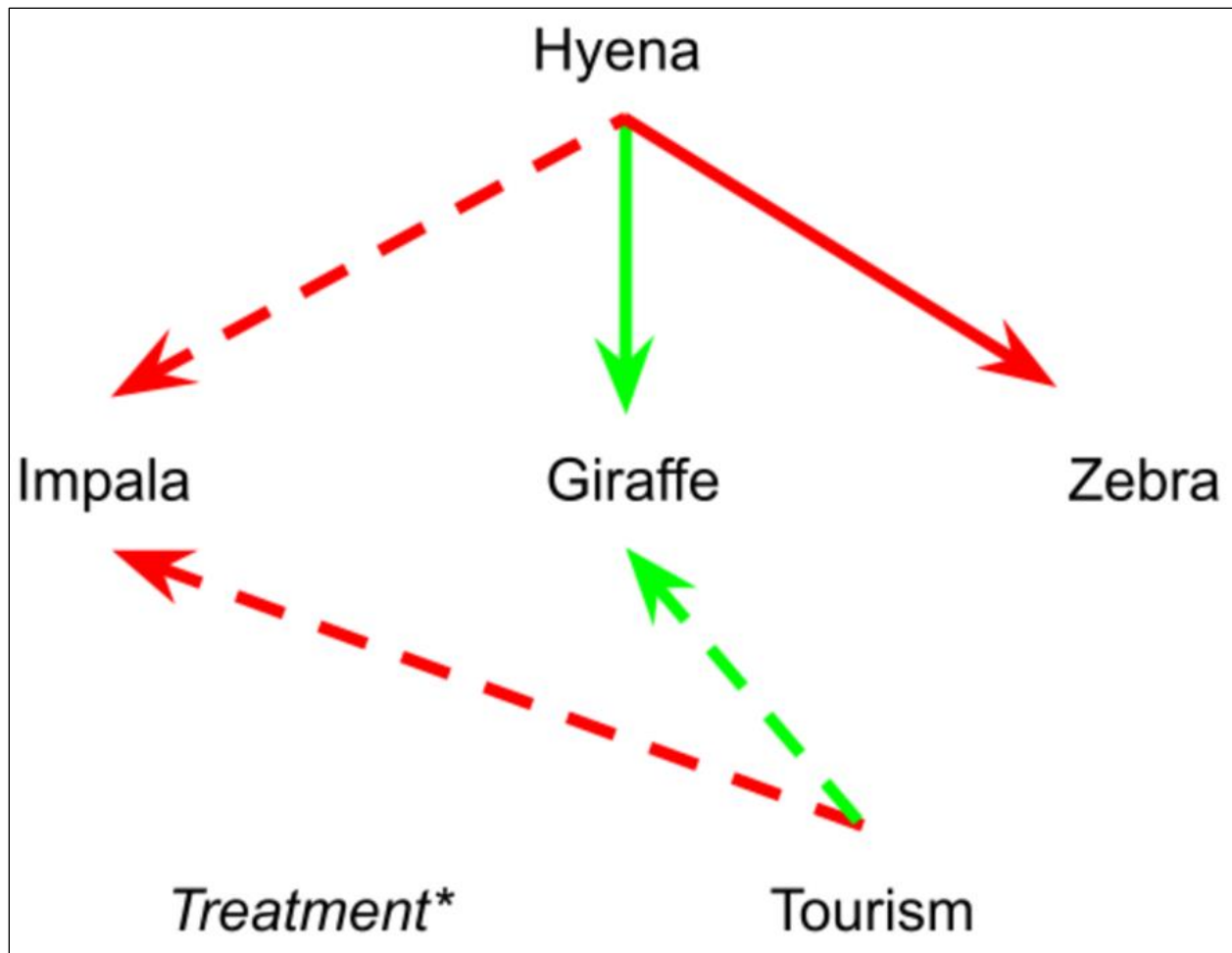


Figure 4. Variables affecting impala, giraffe, zebra, and hyena detection frequencies in this study. Red arrows indicate negative associations and green arrows indicate positive associations. Solid arrows show strong associations, and dashed arrows show weak associations. Hyena detection frequency was negatively associated with impala and zebra detection frequencies, and hyena detection frequency had a strong, positive association with giraffe detection frequency. Tourism had a weak, positive association with impala and giraffe detection frequency, but did not impact zebra or hyena detection frequency. *Treatment did not greatly impact any species' detection frequencies.

Land cover is a known predictor of wildlife detection frequencies in Africa (Iranzo et al. 2020; Pringle 2018), and was an important predictor for all species' detection frequencies in this study. Land cover was strongly associated with giraffe detection frequency ($z = -2.855$, $p = 0.0043$; $\beta = -0.6940$, $SE = 0.2431$). Giraffes used open habitat sites ($emmean = 3.005$, $SE = 0.5770$) nearly twice more frequently compared to sites with closed habitats ($emmean = 1.501$, $SE = 0.2887$). Land cover was included in the top models for impala ($\beta = 1.051$, $SE = 0.6642$), zebra ($\beta = -0.2598$, $SE = 0.7909$), and hyena ($\beta = 1.898$, $SE = 0.7627$) detection frequencies, though its association was weak in these models (Figure 4).

3.2. Species temporal activity overlap from kernel density estimation

My original prediction was that predator-prey temporal overlap would be highest in the simulated human presence treatment and in areas with tourists. When I analyzed wildlife activity across the 24-hour cycle, I found that, on average, treatment had a negative association with temporal overlap between predators and prey, but predator-prey overlap did not differ greatly across tourism pressure. Specifically, I found that overlap between hyenas and either zebra or impala were lower at human compared to predator or bird treatment sites (Table 1). Across tourism pressure, giraffes and impala both had slightly more overlap with hyena activity in tourist compared to non-tourist areas (7.4% and 4.1% more overlap with hyenas for giraffe and impala, respectively; Table 2). Zebras, however, appeared to have slightly less overlap in activity with hyenas in tourist areas compared to non-tourist areas (6.2% less overlap in tourist areas; Table 2).

Table 1. Averages and standard deviations for activity overlaps between prey and predators across treatments. Difference in predator-prey overlap between predator and human playback sites as well as bird and human playback sites for each species pair is also included.

Species Pair*	Bird (mean± SD)	Predator (mean± SD)	Human (mean± SD)	Difference (Predator - Human)	Difference (Bird - Human)
Impala & Hyena	0.3532 ± 0.2334	0.333 ± 0.1761	0.1381 ± 0.1418	0.1949	0.2151
Zebra & Hyena	0.4031 ± 0.2266	0.3806 ± 0.1982	0.1426 ± 0.1575	0.2380	0.2605

*Giraffe activity across treatment was not included since giraffes were never observed in the human treatment.

Table 2. Averages and standard deviations of overlap between each predator-prey pair in areas with and without tourism, and differences between overlap in tourist and non-tourist areas.

Species Pair	Tourist Areas (mean± SD)	Non-Tourist Areas (mean± SD)	Difference (Tourist - Non-tourist)
Giraffe and Hyena	0.2507 ± 0.1728	0.1772 ± 0.1545	0.0735
Impala and Hyena	0.3218 ± 0.1691	0.2807 ± 0.1989	0.0411
Zebra and Hyena	0.3075 ± 0.1789	0.3693 ± 0.1704	-0.0618

When assessing predator-prey activity overlap across each hour of the day, I found that hyena overlap with impala and zebras occurred across much of the day from dawn to dusk at the bird playback sites (Figure 5a,d), but overlap was limited to crepuscular and nighttime hours at predator playback sites (Figure 5b,e), likely due to hyenas drastically limiting daytime activity at predator playback sites. Overlap between hyenas and impala or zebra was even more restricted at human playback sites (Figure 5c,f) since 1) hyenas did not display daytime activity and 2) impala and zebra decreased midday and nighttime activity at the human playback sites.

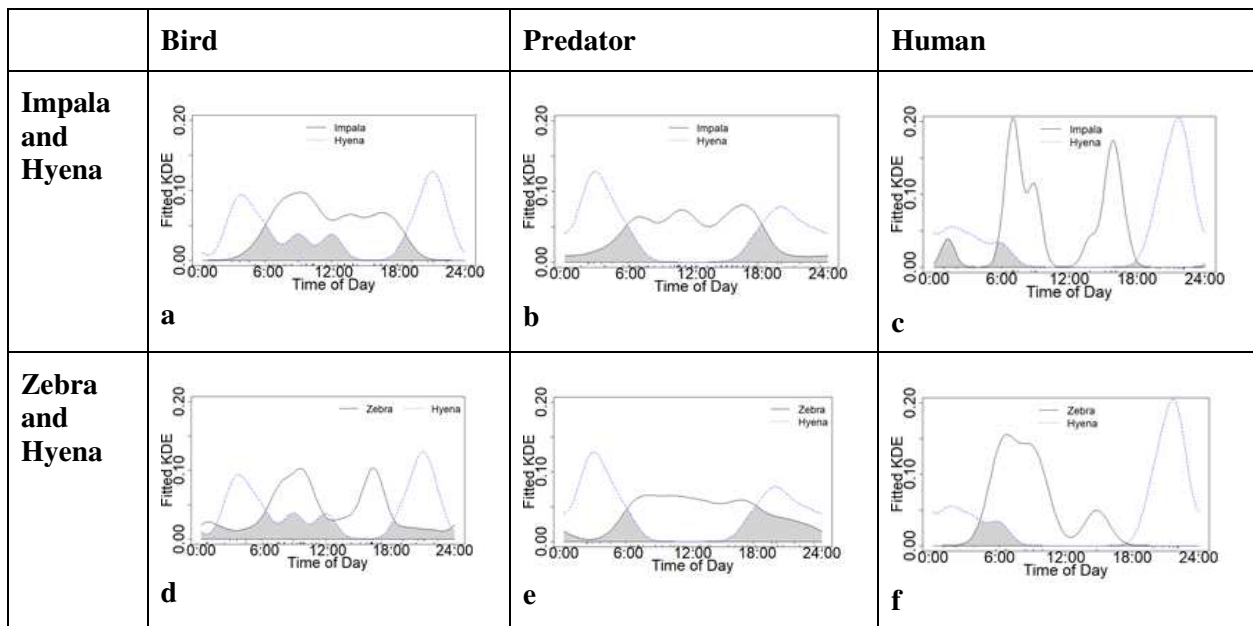


Figure 5. Kernel density estimates (fitted KDE) of daily activity patterns for predator-prey pairs across time of day (0:00 - 24:00h). Activity of predator-prey pairs was graphed for observations in bird (column 1), predator (column 2), and human (column 3) treatments. Overlap in activity between the predator and prey (i.e., times when both predators and prey were active) is shaded in gray. Giraffe activity across treatment was not included since giraffes were never observed in the human treatment.

Though the total amount of overlap between hyenas and their prey did not notably differ between tourist and non-tourist sites, I found that the times during which hyenas overlapped with their prey changed across tourism pressure. Activity overlap between hyenas and all prey species (giraffe, zebra, and impala) were observed during crepuscular and nighttime hours in non-tourist areas (Figure 6b,d,f) since hyenas did not display diurnal activity in non-tourist areas. However, in tourist areas, hyenas did

display diurnal activity, and thus overlap between hyenas and all prey species became notably more diurnal (Figure 6a,c,e).

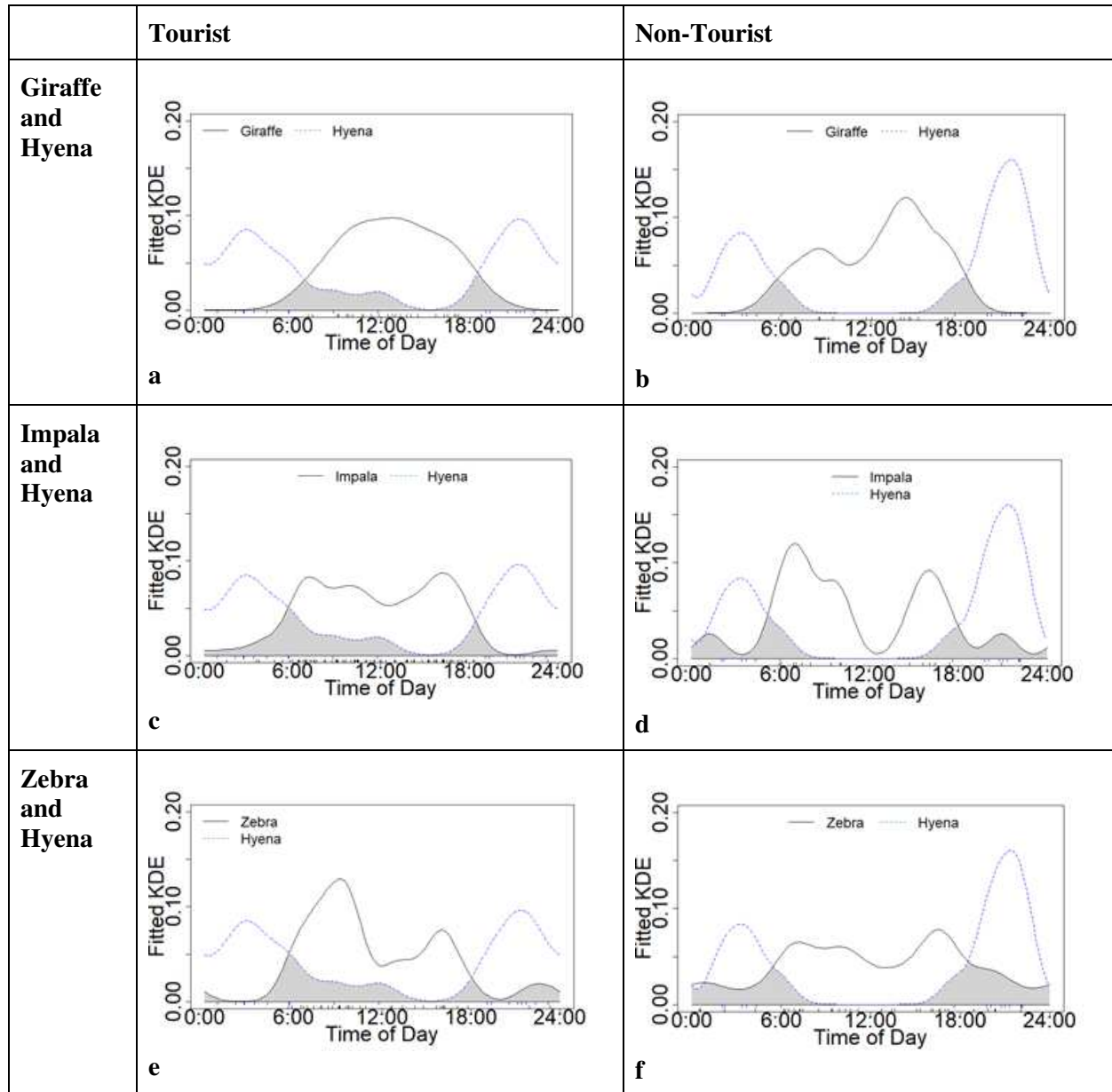


Figure 6. Kernel density estimates (fitted KDE) of daily activity patterns for predator-prey pairs across time of day (0:00 – 24:00 h). Activity of predator-prey pairs was graphed for observations at tourist (column 1) and non-tourist (column 2) sites. Overlap in activity between the predator and prey is shaded in gray.

3.3. Species behavioral responses to playbacks

I initially predicted that all species of interest would decrease foraging activity and be more likely to flee, be vigilant, or look at cameras when in sites with 1) human or predator playbacks (compared to

bird playbacks) and 2) tourists (compared to sites without tourists). This hypothesis is partially supported by my results, as zebras and impala were more likely to flee from human or predator playbacks (Figure 7a). However, hyenas were more likely to look at cameras in non-tourist areas than in tourist areas (Figure 7b), which opposes my original hypothesis.

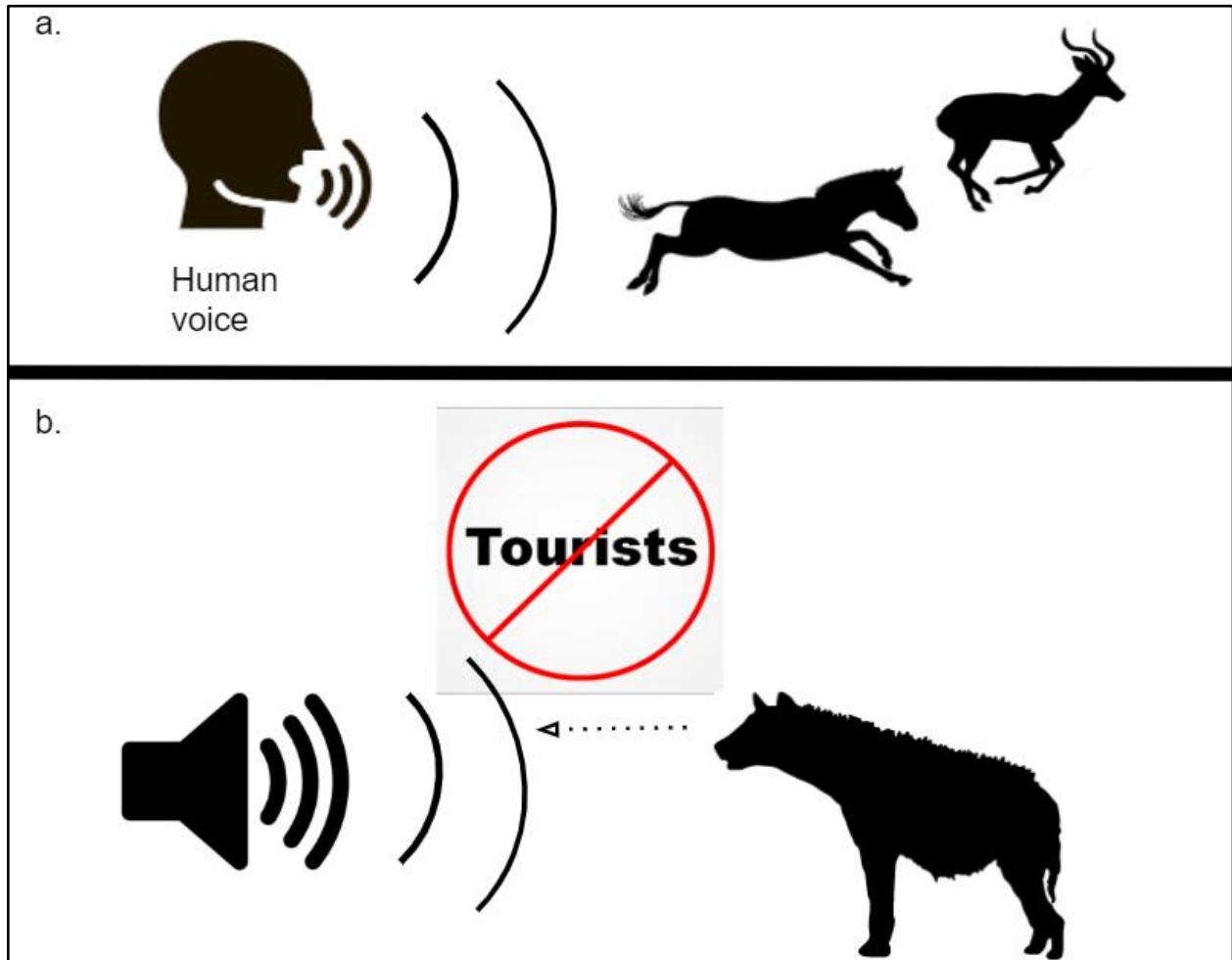


Figure 7. (a) Impala and zebra were more likely to run from human voices than from predator or bird calls. (b) Hyenas were more likely to look at the camera in non-tourist areas compared to hyenas in tourist areas, regardless of playback treatment.

Treatment was moderately associated with impala foraging behavior ($z = -2.440$, $p = 0.0150$; $\beta = -2.428$, $SE = 1.029$), impala running behavior ($z = 2.443$, $p = 0.0146$; $\beta = 1.910$, $SE = 0.7817$), and zebra running behavior ($z = 2.407$, $p = 0.0160$; $\beta = 2.197$, $SE = 0.9129$). The frequency of foraging behavior displayed by impala was considerably lower in the human (emmean = 0.0520, $SE = 0.0533$) compared to bird (emmean = 0.6440, $SE = 0.1968$) or predator (emmean = 0.4999, $SE = 0.1655$) treatments. Both

zebra and impala were more likely to run in human (emmean for frequency of impala running behavior at human treatments = 0.6429 ± 0.2143 ; zebra running emmean = 0.6000 ± 0.3464) compared to bird (impala = 0.0952 ± 0.0673 ; zebra = 0.0667 ± 0.0471) or predator (impala = 0.1600 ± 0.0800 ; zebra = 0.3043 ± 0.1150) treatments (Figure 7a). Treatment was weakly associated with impala scanning behavior ($\beta = -0.2341$, SE = 1.4279), zebra foraging behavior ($\beta = -1.0641$, SE = 1.0395), zebra looking at camera behavior ($\beta = 1.9566$, SE = 1.1028), zebra scanning behavior ($\beta = 1.7918$, SE = 1.0), and hyena looking at camera behavior ($\beta = 1.2417$, SE = 0.7817).

Tourism pressure had a moderate association with hyena looking at camera behavior ($\beta = -1.5488$, SE = 0.7746; $z = -2.0$, $p = 0.0456$). Hyenas were more than four times as likely to look at camera traps in non-tourist areas (emmean = 0.5882, SE = 0.1860) than in tourist areas (emmean = 0.1250, SE = 0.0884; Figure 7b). Tourist pressure was also included in the top models for impala foraging behavior ($\beta = 0.8000$, SE = 0.5349), impala scanning behavior ($\beta = 1.034$, SE = 1.428), giraffe foraging behavior ($\beta = 0.3878$, SE = 1.225), giraffe looking at camera behavior ($\beta = 0.7932$, SE = 1.155), zebra foraging behavior ($\beta = 0.2914$, SE = 0.4970), zebra looking at camera behavior ($\beta = 0.5257$, SE = 0.8219), zebra running behavior ($\beta = -0.7554$, SE = 0.6687), zebra scanning behavior ($\beta = 1.054$, SE = 0.8367), and hyena running behavior ($\beta = 1.159$, SE = 1.150), though associations with tourism pressure were weak in these models.

Finally, I found no top models (i.e., no models in the set of candidate models with a $\Delta AIC_c < 2$) for impala looking at camera behavior, and all giraffe behaviors (foraging, looking at camera, scanning, and running) were best predicted by null models ($y \sim 1$).

4. DISCUSSION

My results provide experimental evidence that reduced predator-prey co-occurrence caused by predator's fear of humans may re-establish over time as predators habituate to prolonged, consistent human disturbance. I initially predicted that simulated human presence and tourists would increase predator-prey co-occurrence (Table 3). However, I found that simulated human presence led to a 20%

reduction in hyena-zebra and hyena-impala temporal overlap, and hyena-prey overlap did not differ greatly across tourism pressure (Table 3).

Table 3. Comparing results found to initial predictions.

Prediction	Result
Simulated human presence and tourists will increase predator-prey co-occurrence.	No support: Simulated human presence led to a 20% <u>reduction</u> in hyena-zebra/impala temporal overlap (compared to control), while hyena-prey temporal overlap was similar across tourist and non-tourist areas (difference < 8%).
Simulated human presence and tourists will lead to more fear-associated behaviors displayed by wildlife.	Partial support: Behavioral responses to human presence was species dependent. Specifically, zebras and impala were more likely to run from human voices, but giraffes did not have any notable changes in fear-associated behaviors across tourism pressure or playback type. Hyenas were more likely to look at cameras in non-tourist than in tourist sites, which opposes the original hypothesis.

At control (i.e., bird call playback) sites, hyenas co-occurred with their prey frequently throughout the day, as both hyenas and their prey displayed frequent daytime activity. However, at predator playback sites, hyena-prey overlap was restricted to crepuscular and nighttime hours (i.e., hyenas did not display daytime activity). Prey species, on the other hand, did not differ much in temporal activity patterns between control and predator playback sites. Hyenas becoming more nocturnal at predator playbacks is likely due to hyenas avoiding potential competition or conflict with other predators (Barker et al. 2022) by restricting activity across the day. Though prey did not change daily activity patterns between control and predator treatments, impala and zebra did display spatial avoidance of hyenas across sites. These prey species may be more inclined to alter spatial rather than temporal activity patterns to avoid predation by hyenas. However, both impala and zebra decreased midday and nighttime activity when human voices were broadcasted at a research site. This suggests that impala and zebras may respond to humans differently than they do to natural predators, avoiding natural predators spatially but avoiding humans temporally. Wildlife can and will respond to risks differently depending on the situation (e.g., Bates et al. 2007). Though many authors have suggested that humans can act as an apex predator in wildlife communities (Darimont et al. 2015; Montgomery et al. 2020; Williams et al. 2020), this finding

suggests that some species may consider humans a different risk than that brought about by natural predators, which could lead to complex changes in wildlife behavior and interactions.

Both impala and zebras limited their temporal activity to crepuscular hours at human playback sites, which is also when predators are most active (Hayward and Hayward 2007). Avoiding predator playback sites and selecting for human playback sites during the most ‘dangerous’ times of day indicates that zebras and impala may be using humans as a shield against natural predation. Human shields are common throughout Africa (Mills and Harris 2020) and other areas around the world (Berger 2007; Suraci et al. 2019) and can decrease availability of prey to predators (Berger 2007; Mills and Harris 2020). The drastic decrease in predator-prey co-occurrence seen at the human playback sites suggests that human presence may decrease prey access for hyenas, which has the capacity to alter hyena survival within the system.

Unlike the differences seen in predator-prey co-occurrence across treatments, hyena-prey co-occurrence was similar in tourist and non-tourist sites. At non-tourist sites, hyena daytime activity was extremely limited, which led to a restriction in hyena-prey overlap to crepuscular and nighttime hours. Hyenas had higher daytime activity at tourist sites, allowing for a similar activity pattern at tourist sites as what was observed at control sites. Hyenas will alter temporal activity in response to their main competitor, African lions (Barker et al. 2022), and are also known to avoid humans (Boydston et al. 2003). For example, hyenas will use diurnal activity to reduce the risk of pup predation by lions (Kolowski et al. 2007) and responded similarly to human presence in this study by avoiding human activity (i.e., diurnal activity). However, hyenas increase activity during times when tourists are also most active in tourist areas, providing evidence that hyenas may be habituated to tourist presence. Tourists have been present in Kruger National Park for decades, and any wildlife currently present in the park are likely to frequently encounter tourists. Therefore, hyenas may be responding to human voices as a novel stimulus but are habituated to the long-term presence of tourists (see Bateman and Fleming 2017).

Hyena habituation to tourists indicates that human-induced fear might no longer deter certain predators from encroaching on human settlements, potentially increasing human-predator conflict in areas

with long-established human presence. Habituation of predators to humans can negatively impact the livelihoods of people, such as through livestock depredation (Butler 2000). Habituation can also negatively impact wildlife, since unavoidable human-wildlife conflicts can deter the public from attempting to conserve or protect a problem species (Thavarajah 2008), and habituated individuals can also become less responsive to the very real threat of poaching (Kasereka et al. 2006). Tourism, often used as motivation for wildlife conservation, may therefore lead to more frequent human-wildlife conflict and negatively impact humans and wildlife alike.

Though the total amount of predator-prey temporal overlap was consistent across tourism pressure, the times during which predators and prey overlapped differed. Hyenas co-occurred with impala and zebra during the daytime in tourist areas but co-occurred with impala and zebra during crepuscular and nighttime hours in non-tourist areas. In other words, the presence of tourists changed when predators and prey co-occurred across the day. Increasing co-occurrence between hyenas and their prey during daylight hours may cause hyenas to shift from primarily hunting during crepuscular and nighttime hours (as they do currently – Kolowski et al. 2007) to hunting more frequently during the day. Daylight provides a higher likelihood of predator detection by prey, and daytime hunting can have a lower probability of success than nighttime hunting (Ford and Goheen 2015; Palmer et al. 2017). Therefore, if prey and their predators shift activity to the day, predator hunting success rate may be negatively impacted by consistent, prolonged human presence.

It is important to note that the presence of tourists differs from the experimental human voice playback in that tourists in KNP are usually in vehicles and are restricted to tourist-approved roads, while the human voice playbacks were broadcasted away from roads and not in proximity to vehicles. Compared to tourists, human voice playbacks provided a novel ‘type’ of human presence that is dissimilar to the context wildlife usually associate with human voices (i.e., away from roads, not in vehicles). Context of human disturbance can impact how wildlife perceive human-associated risks; for example, African elephants in Kenya are more fearful of humans wearing garments associated with the Maasai than those wearing clothing associated with the Kamba people (Bates et al. 2007). Wildlife in the current study

may be responding differently to tourists compared to how they respond to the experimental human playback due to the differences in presentation. Though human voice playbacks were a novel stimuli compared to tourists, differences in these stimuli's contexts may have also impacted how species in this study perceived human presence.

Finally, I also found some experimental evidence for my hypothesis that human voice playbacks and tourists would lead to an increase in fleeing behavior and decrease in foraging behavior (Table 3). My results show that 1) impala and zebras were more likely to run and 2) impala were less likely to forage in response to human voice playbacks compared to the other treatments. Impala and zebras also displayed restricted activity (i.e., limited overall activity to early morning and mid-afternoon) in response to human voice playbacks. Giraffes did not greatly change their behavior in response to human playbacks. Giraffes may have been less responsive to human-induced fear than zebras or impala because they are a larger-bodied species, making them less vulnerable to predation risk (Sinclair et al. 2003). Other studies have found that smaller species (e.g., zebras/impala) are more likely to respond to predator-induced fear than larger species (e.g., giraffe - Jarman 1974; Riginos 2015; Riginos and Grace 2008; Sinclair et al. 2003; Thaker et al. 2011; Valeix et al. 2009). Like predator-induced fear, human-induced fear may also have a greater impact on smaller-bodied compared to larger-bodied species. In other words, large-bodied species that are not responsive to predator-induced fear may also not respond to human-induced fear, and thus may be less affected by human presence than smaller-bodied species. Predator-induced fear can increase stress (Lima 1998b) and decrease foraging efficacy (Creel et al. 2009) in prey, which can alter individual fitness by lowering reproductive success (Creel et al. 2009; Lima 1998b). Some evidence suggests that human-induced fear can also cause similar changes in species fitness (Ciuti et al. 2012), and human-induced fear may act as an additional stressor, compounding negative impacts of pre-existing predator-induced fear (see Schmitz and Trussell 2016). Since 1) species that already respond to predator-induced fear appear also more likely to respond to human-induced fear and 2) predator- and human-induced fear may have compounding effects on species fitness, efforts to limit the impacts of human presence on wildlife should concentrate on already-fearful species.

5. STUDY LIMITATIONS

Though this study provides novel insights into how predators and prey co-occur across the South African landscape, it is important to note that predator-prey co-occurrence is not synonymous with predator-prey interactions, and this study does not provide any support as to whether changes in co-occurrence will lead to alterations in species-level demographics. Furthermore, land cover category (i.e., open or closed) is not a perfect measure for habitat use or resource selection, and more research should be conducted as to how land cover may alter wildlife behavior in response to human disturbance. Because this study analyzed the effects of simulated human presence and tourism separately, interactions between these variables were not observed or drawn upon. Finally, the data included in this study are limited to one season (July – August) and only include one predator and three prey species that are part of a much more complex predator-prey assemblage in South Africa. Therefore, future research should analyze how seasonality and multiple predator-prey pairs may impact anthropogenic changes in wildlife behavior and interactions.

6. CONCLUSION

My work provides strong evidence that, while novel human presence restricts predator-prey co-occurrence, long-established human presence may not have lasting impacts on the amount of predator-prey co-occurrence. Because changes in predator-prey co-occurrence can lead to changes in species interactions (which, in turn, drive ecosystem functioning - Clinchy et al. 2016; Trussell et al. 2006), predator-prey interactions may not be as negatively impacted by human presence as previously suggested. I propose six potential research directions to further investigate how human-induced fear may impact predator-prey interactions:

1. How long does it take for a predator to habituate to human presence, if habituation ever occurs?
What species-specific traits or contexts affect this time requirement?
2. Is predator-prey co-occurrence in human-disturbed areas functionally equivalent to co-occurrence found in non-disturbed systems? In other words, does predator-prey co-occurrence have similar impacts on predator-prey interactions in disturbed and non-disturbed areas?

3. How might individual-level differences (sex, age, personality, etc.) impact fear responses to humans?
4. Can the evidence found in this study be replicated in a study within other savanna habitat types? For example, will ecological implications found in mopane woodlands (current study habitat) be the same as those that could be found in the open savannas of southern Kruger National Park?
5. How do other southern African species respond to human presence, and does this knowledge change current perceptions of human-wildlife interactions in this system? For example, how might occurrence of lions in response to human-induced fear impact the species relationships observed in this study?
6. How might other types of human disturbance impact wildlife behavior and community dynamics? For example, do tourists on foot elicit a similar response from wildlife to tourists in vehicles? How might responses wildlife have to walking tourists compare to responses to human voice playbacks?

Human-altered landscapes now dominate the world, yet research on how humans may reshape wildlife interactions is lacking (Clinchy et al. 2016). The insights into how experimental and real human presence can reshape predator-prey co-occurrence across space and time can be used to lead to optimal management of South Africa's nature-based tourism industry. This study has provided a critical foundation for future investigations into the consequences of human-induced fear for large, complex predator-prey assemblages.

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APPENDIX 1. BEHAVIOR DEFINITIONS

Table A1. All potential behaviors used in the behavior portion of this study. Behaviors were assigned for each video in which an animal was present. Behaviors of interest for this study displayed in **bold**. These definitions have been adapted from Caravantes 2020.

Behavior	Definition
Head up	The animal was standing with its head above the horizontal. The head could move for scanning.
Looking at camera	The animal was standing or walking with its head raised up above their knee and looking directly at the camera with both eyes visible
Scanning	The animal is standing or walking with its head at or above the horizontal while scanning with its ears.
Approaching	The animal took more than three consecutive steps towards the camera with its head also turned towards the camera.
Running	The animal took more than three consecutive steps in a single direction away from the camera at speed greater than walking.
Retreating	The animal took more than three consecutive steps backwards. Left and right legs alternate.
Threatening/ Posturing	The animal displaying threatening or posturing behavior towards the camera; indicators for this behavior are species dependent. For prey, head bowing and pawing while facing the camera were used as indicators of threatening behavior. Predators were defined as showing threatening behavior when showing teeth or raising hackles.
Walking	The animal took more than three consecutive steps in a single direction with its head not towards the camera.
Standing	The animal is in an upright position and is remaining in one location. The animal can make three or less steps in any direction to scan
Defecating	Also includes peeing
Foraging	The animal was standing or walking and grazing or chewing at the same time.
Recumbent	The animal is lying down with limited attention to its surroundings.
Head down	The animal was standing or walking with its head below horizontal
Head horizontal	The animal was standing with its head completely horizontal with the rest of its body.
Other	Any other behavior not listed here.

N/A	No behavior because no animal or unknown animal.
Unknown	The animal is present but could not observe behavior.

APPENDIX 2. STUDY SITE NAMES AND ASSOCIATED START AND END DATES FOR DATA
USED IN THIS STUDY.

Table A2. Start and end dates of data collection for each camera trap unit set in Kruger National Park, South Africa. Data from 16 camera traps were used in this study, with deployments ranging from 7/27-10/20, 2021.

Study Site	Data Start Date	Data End Date
SD01	7/27/2021	10/12/2021
SD02	7/30/2021	9/13/2021
SD03	9/18/2021	10/19/2021
SD05	7/28/2021	8/12/2021
SD09	7/30/2021	9/22/2021
SD10	8/2/2021	9/5/2021
SD12	7/29/2021	9/4/2021
SD13	7/28/2021	10/2/2021
SD15	7/30/2021	9/22/2021
SD20	7/31/2021	9/19/2021
SD21	7/28/2021	9/18/2021
SD23	7/27/2021	9/18/2021
SD24	8/6/2021	8/12/2021
SD26	7/29/2021	9/27/2021
SD27	8/6/2021	10/20/2021
SD29	9/23/2021	9/27/2021

APPENDIX 3. TOP SPECIES DETECTION FREQUENCY MODELS AND ASSOCIATED OUTPUTS

Table A3.1. Variable key and descriptions for A3 and A4.

Variable	Definition
i.obs	number of impala observations by day; dependent variable
g.obs	number of giraffe observations by day
z.obs	number of zebra observations by day
h.obs	number of hyena observations by day
idf	impala detection frequency (number of impala observations per day per each camera trap)
zdf	zebra detection frequency (number of zebra observations per day per each camera trap)
gdf	giraffe detection frequency (number of giraffe observations per day per each camera trap)
hdf	hyena detection frequency (number of hyena observations per day per each camera trap)
lc	binary indicator of land cover for open (0) or closed (1) habitats
tr	camera treatment / playback type (bird, predator, human)
to	binary indicator of whether camera site was in tourist (1) or non-tourist (0) areas
forage	foraging behavior (# foraging behavior observations / # total species observations, per day)
look	‘looking at camera’ behavior (# behavior observations / # total species observations, per day)
run	running behavior (# behavior observations / # total species observations, per day)
scan	scanning behavior (# behavior observations / # total species observations, per day)

Table A3.2. Top species detection frequency models conducted and associated outputs. Ordered first by species of interest then by AICc values. *NOTE: All models also include a random effect of camera trap location [+ (1|location)]. See Table A3.1 for variable key and descriptions.

Species of Interest	Model*	AICc	ΔAICc	AICc weight	log Likelihood	# params	df
Impala	i.obs ~ hdf + lc + to	873.0563	0.0000	0.5177	-426.3750	3	10
Impala	i.obs ~ hdf + to	874.6452	1.5888	0.2339	-429.2226	2	8
Giraffe	g.obs ~ hdf + lc	418.7916	0.0000	0.5772	-205.368	2	4
Giraffe	g.obs ~ hdf + lc + to	420.7546	1.9630	0.2163	-205.336	3	5
Zebra	z.obs ~ hdf + lc	602.7413	0.0000	0.5159	-293.2707	2	8
Zebra	z.obs ~ hdf	604.1241	1.3828	0.2584	-296.0039	1	6
Hyena	h.obs ~ lc	240.2467	0.0000	0.4973	-114.065	1	6
Hyena	h.obs ~ 1	242.0896	1.8429	0.1979	-117.017	0	4

APPENDIX 4. TOP MODEL OUTPUTS FOR BEHAVIOR MODELS

Table A4. Top ($\Delta\text{AICc} < 2$) model outputs for behavior models. Ordered first by species of interest then by AICc values. See Table A3.1 for variable key and descriptions.

Species of Interest	Model	AICc	ΔAICc	AICc weight	log Likelihood	# params	df
Impala	forage ~ tr + to	132.7312	0.0000	0.5433	-62.0019	2	4
Impala	forage ~ tr	133.1526	0.4214	0.4401	-63.3620	1	3
Impala	look ~ tr + to	57.4034	0.0000	0.3090	-24.3381	2	4
Impala	look ~ 1	57.9042	0.5007	0.2406	-27.9176	0	1
Impala	look ~ to	57.9527	0.5493	0.2348	-26.8711	1	2
Impala	look ~ tr	58.1228	0.7193	0.2157	-25.8471	1	3
Impala	run ~ tr	71.2203	0.0000	0.6928	-32.3959	1	3
Impala	scan ~ tr + to	48.85033	1.3170	0.1450	-20.061527	2	4
Impala	scan ~ 1	47.5333	0.9824	0.2801	-22.7322	0	1
Giraffe	forage ~ 1	31.0000	0.0000	0.108	-14.435	0	1
Giraffe	forage ~ to	32.1000	1.1000	0.061	-13.872	1	2
Giraffe	look ~ 1	28.3970	0.0000	0.0657	-13.1340	0	1
Giraffe	look ~ to	30.1393	1.7423	0.0275	-12.8697	1	2
Giraffe	run ~ 1	11.1220	0.0000	0.3691	-4.4965	0	1
Giraffe	scan ~ 1	23.9000	0.0000	0.146	-10.887	0	1
Zebra	forage ~ tr	66.5514	0.0000	0.7266	-30.0535	1	3
Zebra	forage ~ tr + to	68.5136	1.9622	0.2724	-29.8794	2	4
Zebra	look ~ tr	40.5074	0.0000	0.4360	-17.0315	1	3
Zebra	look ~ 1	41.2956	0.7882	0.2940	-19.6121	0	1
Zebra	look ~ tr + to	42.4132	1.9058	0.1681	-16.8292	2	4
Zebra	run ~ tr	60.9958	0.0000	0.5050	-27.2757	1	3
Zebra	run ~ tr + to	61.9521	0.9563	0.3131	-26.5987	2	4

Zebra	scan ~ 1	45.6749	0.0000	0.3867	-21.8017	0	1
Zebra	scan ~ to	46.0455	0.3706	0.3213	-20.9137	1	2
Zebra	scan ~ tr	47.1631	1.4882	0.1837	-20.3593	1	3
Hyena	run ~ 1	27.0107	0.0000	0.5675	-12.4409	0	1
Hyena	run ~ to	28.1103	1.0995	0.3275	-11.8551	1	2
Hyena	look ~ to	47.3303	0.0000	0.4524	-21.4652	1	2
Hyena	look ~ tr	48.4896	1.1592	0.2534	-20.8310	1	3
Hyena	look ~ tr + to	48.9925	1.6622	0.1971	-19.7820	2	4