**Breaking the human shield: Predator habituation may reduce human effects on predator-prey dynamics**

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**Statement of Authorship**

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**Data Accessibility Statement**

The authors confirm that, should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository (Dryad, Figshare, or Hal) and the data DOI will be included at the end of the article.

**ABSTRACT**

While many species are fearful of human presence, others may habituate after prolonged, non-lethal exposure. Highly persecuted carnivores often take longer to habituate than herbivores, which can lead to prey associating with humans to ‘shield’ themselves from predators. We conducted an experiment in a hyper-diverse African reserve to examine how an apex predator (spotted hyena) and two primary prey species partition spatiotemporal activity in response to 1) threatening human voice playbacks and 2) long-term, less-threatening tourism activity. Hyenas avoided areas with human voice playbacks during the day, allowing prey to use these areas diurnally to shield themselves from predation. Neither predator nor prey were deterred from sites with tourists. This apparent habituation by predators conserved co-occurrence between predators and their prey, ‘breaking’ the human shield. While use of human shields may be widespread among large mammalian predators and prey, these effects may lessen through time in the absence of predator persecution.

**1. INTRODUCTION**

Humans can induce strong fear-associated behaviors in wildlife, acting as ‘super-predators’ that reshape the behavior of both natural predators and their prey (Boydston et al. 2003; Mills and Harris 2020; Suraci et al. 2019; Wang et al. 2015). The nature of human presence in the landscape affects the type and strength of these behavioral responses; for example, many animals respond more strongly to hunting than to recreation (Kays et al. 2017). Human-induced fear can cause wildlife to modify their habitat use (Boydston et al. 2003; Ciuti et al. 2012; Clinchy et al. 2016; Darimont et al. 2015; Suraci et al. 2019) or temporal activity patterns (Darimont et al. 2015; Smith et al. 2017; Suraci et al. 2019; Wang et al. 2015), which, if extreme enough, can drive species to local extinction (Darimont et al. 2015; Gaynor et al. 2018; Suraci et al. 2019).

Though human-induced fear is common, some prey species associate closely with humans to avoid their natural predators, a phenomenon known as the ‘human shield effect’ (Berger 2007; Ditmer et al. 2020; Suraci et al. 2019). This has been documented in large mammalian systems, where large carnivores that have been highly persecuted by humans are often more averse to human presence than their herbivore prey (Darimont et al. 2015; Suraci et al. 2021). When prey take advantage of human shields, predator fitness may consequentially suffer (Berger 2007; Geffroy et al. 2015, Elton and Nicholson 1942; Pyke et al. 1977). The propensity of some species to habituate to - while others remain fearful of - benign human presence can alter species interactions, such as predator-prey dynamics, in complex ways (Mills and Harris 2020; Suraci et al. 2019; Wang et al. 2015).

Many studies of the human shield effect have been empirical in nature; few have experimentally evaluated how perceived human presence alters wildlife behavior and presence. Much research on the human shield effect has been conducted in habitats with relatively small assemblages of predators and prey (e.g., western North America; Berger 2007; Smith et al. 2017; Suraci et al. 2019). Given the additional sources of predation and competition that must be balanced when making behavioral decisions (i.e., prey experiencing competing demands to avoid multiple predators, heightened competition decreasing predator and/or prey ability to shift their activity in space and time; Montgomery et al. 2020; Sinclair et al. 2003), it is unclear whether the human shield hypothesis can be generalized to more complicated food webs. Species-rich assemblages of large herbivores and carnivores - such as those found across Africa - are therefore pivotal testing grounds to test the human shield hypothesis.

We conducted a remotely triggered audio playback experiment (Figure 1) in a South African system containing a diverse group of large herbivores (19 species >15kg) and carnivores [including leopards (*Panthera pardus)*, cheetahs (*Acinonyx jubatus*), spotted hyenas (*Crocuta crocuta*), and lions (*P. leo)*]. We investigated how simulated (triggered audio playbacks) and actual (tourist activity) human presence affected co-occurrence between a nocturnal predator (spotted hyena; hereafter hyena) and its primary diurnal prey (impala *Aepyceros melampus*; Burchell's zebra *Equus quagga burchellii*, hereafter zebra). As the human voice playbacks presented a novel, potentially more frightening stimulus, we included tourism activity to assess responses to human activity that these species had long (>100 years) exposure to and anticipated that there may have been some degree of habituation, particularly in the large herbivore species, towards tourist presence. We simulated the presence of native birds (negative controls), native predators (spotted hyena and lion - positive controls), and human voices (native speakers of English, Africaans, and Tsonga in conversational tones) with remotely triggered audio playbacks (Figure 1; Palmer et al. 2022; Suraci et al. 2017). Tourist spatial activity was assessed based on the presence of tourist-accessible park roads. The timing of human activity is largely restricted to between sunrise and sunset by controlling tourist entrance access (see: <https://www.sanparks.org/parks/kruger/>).

We predicted that all species may show adverse effects to human disturbance (avoiding tourists and playbacks in space and during times of human activity), but that these responses would be 1) stronger for predators than prey and 2) stronger in response to the playbacks than to tourism activity. We predicted that recordings of human voices and tourist presence would 1) cause a shift to nighttime activity in diurnal species and 2) result in spatial avoidance of human sites for all species. This compaction of spatial and temporal activity to avoid humans by both predator and prey was anticipated to 3) increase co-occurrence between predators and prey during times and in places without humans unless 4) prey habituate to humans, in which case a human shield would be formed against predators. With this study, we have improved upon understanding in the scientific literature on how the human shield may be impacted by temporal variation in human disturbances.

**2. MATERIALS AND 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 to October 2021. The park (19,633 km²) is in the northeast region of South Africa in the Limpopo and Mpumalanga Provinces along the Mozambique border (Gertenbach 1983). Our study was conducted in the central region of the park in mostly mopane-dominated woodlands with intermixed bushwillow and *Acacia* species (Gertenbach 1983). The winter season (May - September) tends to be warm and mild with little rainfall in this region (KNP 2006). Average monthly rainfall in winter is 6-7 mm, and the average temperature in winter is 17.8 ℃ (KNP 2006).

***2.2. Study species***

Though camera traps captured videos of most large vertebrates in the study area, we used three species of interest to analyze how predator-prey co-occurrence is affected by human-induced fear: hyenas, impala, and zebra. These species were chosen based on their prevalence within the study region and based on their frequency of observation in this experiment. Hyenas are native South African apex carnivores that predate upon the prey species in this study (Boydston et al. 2003; Sinclair et al. 2003; Thaker et al. 2011; Watts and Holekamp 2007).

***2.3. Experimental framework***

We used remotely triggered human voice playbacks to test spatiotemporal wildlife responses to human presence (Palmer et al. 2022; Suraci et al. 2017). Thirty study sites were set up: ten used human voice playbacks, ten had predator call playbacks, and ten control sites had native bird call playbacks (call types described in detail below). Half (n=15) of the sites were in tourist areas, and the other half in non-tourist areas. Random site selection within these parameters resulted in 10 sites being placed in open land cover and 20 sites being placed in closed land cover (see data analysis section for land cover category descriptions). Playbacks were remotely triggered using Automated Behavioral Response systems (‘BoomBoxes’, hereafter ‘playback units’; Palmer et al. 2022, Suraci et al. 2017), in which the playback and recording camera trap are both triggered by passing wildlife but are otherwise silent. The playback unit 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). Each playback unit was attached to a heat- and motion-sensitive SpyPoint Force-Dark Trail Camera.

We developed cue playlists of the same class (i.e., either human, bird, or predator calls; see below) 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 J.V.), and English (recorded by M.L.), leading to six voices total (Caravantes 2020). Predator playbacks included three call types from African lions and three from spotted hyenas, also resulting in six individual recordings. Both African lions and spotted hyenas are present in the study site, and both species predate upon and induce fear in the prey 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 or competitor effects on wildlife behavior. For control sites, we 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). All animal recordings were obtained from online, open-access YouTube videos of nearby but unrelated individuals in South Africa.

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, and had similar access to water (Figure 2). To test if wildlife’s responses varied with tourism pressure, half (n=15) of the research sites were placed 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 2).

Camera traps were placed 50 cm above the ground, a height best suited to capture medium- to large-sized vertebrates, on trees (Figure 1; 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 - 22 m, with an average detection distance of 13.86 m based on the camera’s built-in detection test with a human passing in front of the camera’s sensor. Trigger rate was set to the fastest possible speed (0.71 s), and cameras were set to ‘no glow’ night mode to minimize disturbance to wildlife (Henrich et al. 2020).

When triggered, two actions occurred: 1) the camera trap captured a 30 s video, defined as one capture event, and 2) playback units simultaneously broadcasted one of the six possible playbacks (see ‘Experimental framework’ above) for 10 s before the playback unit underwent a one-minute delay (to decrease the number of repeated detections of the same individual - see Suraci et al. 2017). After this quiet period, the 10-second playback would be broadcasted again if the animal re-triggered the camera. Playback units were placed next to or above camera traps depending on tree structure (Figure 1) and were camouflaged with brown paint to avoid wildlife damage. The speakers were set directly above the camera trap so that wildlife would look at the camera when triggered (Figure 1; Palmer et al. 2022). We removed human scent from all equipment left in the field using scent-removal spray (Scent-A-Way Spray, Odorless, manufactured by Hunters Specialties).

Units were deployed for 85 days in KNP between July 27 and October 20, 2021. Of the 30 experimental units set, 16 cameras had usable data and were thus used in this study (see A2 for deployment history of each camera). Dates and locations of usable camera data varied due to incorrect date and time stamps on some of the cameras’ videos, information which was required to conduct our analyses. Though some data was lost, 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 (see results section for details), which supported our analyses.

***2.5. Data analyses***

We identified wildlife species observed in each video captured on camera traps and collected date, time, and temperature from each video. To reduce pseudoreplication, we removed videos within 30 minutes of a previous video of the same species, if captured from the same camera (Palmer et al. 2017; Pardo et al. 2021). For all analyses in this study, we used program R version 4.0.3 (2020-10-10; R Core Team 2020).

*2.5.1. Analyzing spatial occurrence*

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). We used generalized linear mixed models with Poisson regression and a logarithmic link (Bowkett et al. 2008) to contrast ‘spatial occurrence’ of wildlife species to treatment, tourism pressure, other species’ spatial occurrences, and land cover using the package glmmTMB (version 1.1.3; Brooks et al. 2017). Spatial occurrence is defined here as the number of observations per day of each species, which was calculated for every day each camera trap was deployed. Land cover, treatment, and tourism 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) to correct for underlying differences in habitat preference. Treatment was categorized as ‘bird’ (sites with broadcasts of bird calls), ‘predator’ (sites with broadcasts of lion and hyena calls), or ‘human’ (sites with human voice broadcasts). Tourism was either present or absent for each site (see introduction for details). Note, this study analyzed the effects of simulated human presence and tourism separately and interactions between these variables were not observed or drawn upon due to small sample size of wildlife observations. Finally, we used study site location as a Gaussian random effect in all models to help account for spatial autocorrelation among sites (Brooks et al. 2017). We tested for the effect of distance to water and did not obtain any significant correlations with any of our variables of interest (see A4 for these results).

To provide insight into predator-prey spatial co-occurrence, spatial occurrence (number of observations of each species for each site, each day) of each prey species (impala and zebra) was predicted using hyena simultaneous spatial occurrence, and hyena spatial occurrence was predicted using each prey’s simultaneous spatial occurrence (i.e., impala and zebra spatial occurrences; Freeman et al. 2022). To extend models for zero-inflated data common to camera trap results, we assigned zero-inflation for the ‘component’ argument, a one-sided formula combining fixed and random effects, and we set the zero-inflation formula to be identical to the model formula (Brooks et al. 2017). All models were fitted using maximum likelihood estimation (Brooks et al. 2017). We chose the most parsimonious models among candidate models based on Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2004). Models that did not converge were excluded. We used pairwise comparisons of estimated marginal means (emmeans, using package emmeans; Lenth 2022) to compare spatial occurrence estimates across categories (such as across treatments or tourism pressure). See A3 for the top-performing (ΔAICc < 2) spatial occurrence models.

*2.5.2. Analyzing temporal activity*

We 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), we created each species’ probability density distribution of activity across the 24-hour cycle, then calculated the overlap term Δ̂4 (used for small sample sizes; Ridout and Linkie 2009) for each predator-prey species pair for each treatment and tourism type. Finally, we 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).

**3. RESULTS**

From July to October 2021, we gathered data from 713 camera trap nights from 16 research sites in Kruger National Park, South Africa, with 242 camera nights from bird playback sites, 306 at predator playback sites, and 165 at human playback sites. We collected 362 camera trap nights from tourist areas and 351 trap nights from non-tourist areas. In total, we received 1,231 observations of 41 species of wildlife, including 475 observations of impala, 170 zebra observations, and 56 hyena observations (see A1 for the number of observations for each species, per playback and tourist treatment).

***3.1. Predator-prey spatial co-occurrence***

We originally predicted that spatial co-occurrence between predators and prey would increase with simulated human presence and in areas with tourists. We found that neither human voice playbacks nor tourist presence influenced any of the focal species’ spatial occurrence (Figure 3a,c). While hyena spatial occurrence predicted prey (zebra and impala) spatial occurrence, the reverse was not true. Zebra were rarely (z = -3.1, p = 0.002) found in areas where hyenas were frequently detected (β = -18.2, SE = 18.2), and impala were slightly less likely to be found in areas where hyenas were frequently detected (β = -2.9, SE = 10.0).

Habitat type (land cover) was a weak predictor for all species’ spatial occurrences in this study (Figure 3b). Impala (β = 1.1, SE = 0.66) and hyena (β = 1.9, SE = 0.76) were slightly more likely to be found in closed habitats, while zebra (β = -0.26, SE = 0.79) were slightly more likely to be found in open habitats.

***3.2. Predator-prey temporal co-occurrence***

We originally predicted that diurnal focal species would increase nocturnal activity in response to human voice playbacks or tourists, thereby increasing predator-prey temporal co-occurrence at sites with human presence. Predator-prey temporal co-occurrence differed across playback treatments, but not between areas with and without tourists. Specifically, hyenas co-occurred with impala and zebras across much of the day from dawn to dusk at bird playback sites (Figure 4a,d). However, predator-prey co-occurrence was limited to crepuscular and nighttime hours at predator playback sites (Figure 4b,e) due to hyenas drastically limiting their daytime activity at predator playback sites. Overlap between hyenas and impala or zebra was even more restricted at human playback sites (Figure 4c,f) since 1) hyenas did not display daytime activity and 2) impala and zebra decreased midday and nighttime activity at the human playback sites compared to bird or predator playback sites.

Impala temporally co-occurred with hyenas slightly (4.1%) more frequently in tourist areas compared to non-tourist areas (Figure 5a,b) while zebras had slightly (6.2%) less co-occurrence with hyenas in tourist areas compared to non-tourist areas (Figure 5c,d). Though the total amount of temporal co-occurrence between hyenas and their prey did not notably differ between tourist and non-tourist sites, we found that the times during which hyenas co-occurred with their prey changed across tourism pressure. In non-tourist areas, hyenas did not display daytime activity and, as such, co-occurrence between hyenas and both prey species (zebra and impala) was only observed during crepuscular and nighttime hours (Figure 5b,d). However, in tourist areas, hyenas were increasingly diurnal, and thus daytime activity overlap between hyenas and both prey species became notably more frequent (Figure 5a,c).

**4. DISCUSSION**

We provide strong evidence that predators and prey alter their temporal activity in response to simulated threatening human presence, demonstrating that human presence can shape predator-prey activity patterns even in complex African food webs. While prey were expected to habituate to humans to shield themselves from predation (the ‘human shield effect’), we did not consider that the same processes can also work on predators in certain situations. For the human shield effect to work, only prey can habituate to human presence; however, as may be anticipated by the ‘evolutionary arms race’ (Abrams 2000), we found that predators have also apparently habituated to non-lethal human presence in this system, leading to a relaxation of the human shield effect (Figure 6).

Impala and zebras moderately or strongly avoided hyenas across sites, which likely reduces their risk of hyena predation (Boydston et al. 2003; Watts and Holekamp 2007). Hyenas did not alter spatial occurrence across sites, potentially due to the constraints in resources and niche space from the presence of numerous other predators in this complex system (Wang et al. 2015; Watts and Holekamp 2007). They were most active at night when observed at sites with human voice playbacks, which we suspect is due to human presence being associated with daytime activity and hyenas being predominantly nocturnal or crepuscular under natural circumstances (Boydston et al. 2003). Impala and zebras, on the other hand, were less active at night at human playback sites compared to other playback sites, potentially using human activity to reduce risk from natural predation. This dichotomous response to human voices by hyenas (increase nighttime activity) and their prey (decrease nighttime activity) led to a decrease in temporal co-occurrence between these species. On the other hand, when tourists were physically present, both hyenas and their prey were more active during the day compared to sites without tourists. Thus, while impala and zebras responded in the same way to human voice playbacks as they did to tourist presence (increasing daytime activity), hyenas responded differently to human voice playbacks (decrease daytime activity) than how they responded to tourists (increase daytime activity).

The different responses of predators and prey to human voices and tourists may be indicative of the differences between human voices and tourists as stimuli. Vehicle-bound tourists have been present in the area for decades (Carruthers 1995), and any wildlife currently present in the park are likely to frequently encounter tourists. The human voice playbacks in this experiment were placed away from roads and not near any vehicles, and likely more closely resemble historical interactions wildlife have had with poachers or park staff that may cull and anesthetize animals on foot (Carruthers 1995). Therefore, human playbacks may symbolize a more a direct threat than tourists in vehicles.

Though we do not have definitive evidence that wildlife in Kruger National Park have historically been afraid of tourists, other studies have found that vehicle-bound tourists in Africa have induced physiological fear (e.g., increase glucocorticoids) and fear-related behaviors (e.g., vigilance, displacement) in wildlife (Tablado and D’Amico 2017; Green and Higginbottom 2000; Szott et al. 2019a,b). In this study, all focal species appear to have habituated to tourist presence (see Bateman and Fleming 2017). Importantly, habituation of hyenas to tourist presence facilitated more co-occurrence between hyenas and their prey compared to sites with the novel human playback stimulus, which hyenas (but not their prey) avoided, thereby limiting predator-prey co-occurrence. This suggests that, as hyenas became habituated to benign human presence (tourists), they may have ‘broken’ the human shield often found with a novel human presence (such as the human voice treatment in this experiment). This habituation may therefore provide hyenas more frequent access to their prey and likely increases their probability of survival in the system (Elton and Nicholson 1942; Pyke et al. 1977).

Though spatial predator-prey co-occurrence was the same in areas with and without tourists, the times at which predators and prey co-occurred was different. Hyenas usually hunt during night and crepuscular hours under the cover of darkness in non-disturbed systems (Ford and Goheen 2015; Kolowski et al. 2007). However, we found that hyenas were more likely to display diurnal behavior in areas with tourists, suggesting that hunting behavior may be more likely to occur during the day as well. However, daytime hyena hunting may allow prey to more easily detect - and consequently avoid - hyena hunts, and hyenas may be more likely to overheat, which may negatively impact hyena persistence in human-dominated systems.

Almost no terrestrial landscape is untouched by human presence (Clinchy et al. 2016). Here, we provide strong evidence that, while novel human presence restricts predator-prey co-occurrence, long-established, non-lethal human presence may have fewer lasting impacts on co-occurrence between predators and their prey. A variety of avenues for future research into human impacts on wildlife interactions are exposed by this project, and we suggest the following research directions:

1. How long does it take for a species to habituate to human presence, if habituation ever occurs? What species-specific traits or contexts affect a species’ (in particular, a predator’s) capacity to habituate?
2. Does changing temporal patterns of predator activity in response to human activity impact a predator’s hunting success, with cascading impacts on fitness?
3. How do other species respond to human presence, and does this knowledge change perceptions of human-wildlife interactions described here? For example, can we predict how the presence of competitors and alternative predators should affect the ability of predators to respond to humans? Does competition from other predators impact a carnivore’s response to human presence, such as the amount of nocturnality?

Interactions between species can shape natural communities through the top-down effects of predators (Ford and Goheen 2015; Schmitz et al. 2010; Suraci et al. 2019), making predator-prey interactions vital to a healthy ecosystem (Clinchy et al. 2016; Trussell et al. 2006). Although predator-prey co-occurrence is not synonymous with increased prey mortality, this study uses experimental evidence to enhance the body of knowledge documenting how human disturbance reshapes predator-prey activity patterns within a complex and biodiverse mammal assemblage. Our work suggests that predator-prey interactions may stabilize when non-lethal human disturbance is established in a protected area.

**ETHICS COMPLIANCE**

All research with wildlife was approved and conducted in accordance with the ethical guidelines specified by Colorado State University IACUC Protocol #1427.

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**COMPETING INTERESTS**

The authors have no competing interests to declare.

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**FIGURES**

**A picture containing grass

Description automatically generatedFigure 1.** Playback experiment. We used a ‘BoomBox’ playback device (Palmer et al. 2022) with (**a**) speakers to broadcast sound recordings of humans, native predators, and non-threatening birds when the (**b**) playback device was triggered by wildlife passing in front of the (**c**) camera trap. Wildlife responses to these audio cues were video recorded using camera traps. Photo of identical setup taken by M.S. Palmer in Grumeti Game Reserve, Tanzania.

**Map

Description automatically generatedFigure 2**. Location of experimental units for this study. The top map (**a**) indicates a site’s treatment type (bird, human, or predator playbacks), while the bottom graph (**b**) indicates which sites were in tourist or non-tourist areas.

**Diagram, schematic

Description automatically generatedFigure 3**. Variables affecting impala, zebra, and hyena spatial occurrences in this study. None of these variables of interest [(**a**) tourism (**b**) land cover, or (**c**) treatment] greatly impacted any species’ (hyena, impala, or zebra) spatial occurrences.

|  |  |  |  |
| --- | --- | --- | --- |
| **Species Pair** | **Bird**  (mean± SD) | **Predator**  (mean± SD) | **Human**  (mean± SD) |
| **Impala and Hyena** | **A picture containing histogram  Description automatically generateda.** 0.35 ± 0.23 | **A picture containing histogram  Description automatically generatedb.** 0.33 ± 0.18 | **A picture containing chart  Description automatically generatedc.** 0.14 ± 0.14 |
| **Zebra and Hyena** | **A picture containing application  Description automatically generatedd.** 0.40 ± 0.23 | **A picture containing chart  Description automatically generatede.** 0.38 ± 0.20 | **A picture containing graphical user interface  Description automatically generatedf.** 0.14 ± 0.16 |

**Figure 4**. Hourly activity estimates (fitted KDE) for predator-prey pairs across time of day (0:00 - 24:00 h). Activity of predator-prey pairs was graphed for observations in bird (column 1), predator (column 2), and human (column 3) treatments. Times when both species were active is shaded in gray. Averages and standard deviations for the percentage (%) of temporal co-occurrence across the day between prey and predators across treatments are provided.

|  |  |  |
| --- | --- | --- |
| **Species Pair** | **Tourist**  (mean± SD) | **Non-Tourist**  (mean± SD) |
| **Impala and Hyena** | **A picture containing application  Description automatically generateda.** 0.32 ± 0.17 | **A picture containing chart  Description automatically generatedb.** 0.28 ± 0.20 |
| **Zebra and Hyena** | **A picture containing timeline  Description automatically generatedc.** 0.31 ± 0.18 | **A picture containing chart  Description automatically generatedd**. 0.37 ± 0.17 |

**Figure 5**. Hourly activity estimates (fitted KDE) for predator-prey pairs across time of day (0:00 to 24:00 h). Activity of predator-prey pairs was graphed for observations at tourist (column 1) and non-tourist (column 2) sites. Co-occurrence in activity between the predator and prey is shaded in gray. Averages and standard deviations for the percentage (%) of temporal co-occurrence across the day between prey and predators across tourist pressure are provided as well.

|  |  |
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**Figure 6. (a)** Predators (blue dashed line) and prey (solid black line) can overlap in time and correlate in space. **(b)** Predators and prey fear the human ‘super predator’ (solid orange line), avoiding humans across time and space and leading to a greater overlap between predator and prey activity. **(c)** Prey can habituate to humans and use humans as a ‘shield’ to avoid predators in space and time, which can have consequences for predator fitness. **(d)** If predators habituate to humans along with their prey, the human shield effect may disappear.