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Reduced visibility and audibility prompt antipredator behaviour even in a relatively predator-free environment

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Intermittent antipredator behaviours, such as vigilance or increased foraging group size, are behavioural adaptations that allow prey species to forage while simultaneously reducing predation risk. Such behaviours are most useful when environmental conditions permit prey to detect potential predators, and when environmental conditions accurately signal heightened predation risk. When local environmental conditions reduce a prey's predator detection ability, prey may compensate by increasing their vigilance behaviour or forming larger group sizes regardless of actual predation risk. We tested this hypothesis by pairing acoustic recorders and light meters with trail cameras to record white-tailed deer, *Odocoileus virginianus*, vigilance behaviour and group size along gradients of ambient light, noise and human disturbance, as humans are consistently the only ‘predator’ of deer in our study system. Our findings supported our hypothesis that deer are more likely to express vigilance when low-light conditions preclude them from seeing an approaching predator, but noise and human disturbance had no statistical relationship with vigilance behaviour. Conversely, foraging group size increased in high-noise conditions and decreased during periods of high light and human disturbance. These results suggest that deer compensate for reduced predator detection ability by increasing antipredator behaviours even when predation risk is negligible, supporting the notion that landscapes of fear are reliant on the ability to perceive potential predators rather than the presence of predators themselves. Conservation initiatives can capitalize on this information by maintaining conditions that reduce prey species' ability to perceive potential predators and thus confer the benefits of impending predation even in the absence of predators.

Vigilance and grouping behaviour are common antipredator behaviours that allow an individual to continue foraging while avoiding predation by either periodically pausing to scan the landscape for potential threats, or by surrounding themselves with other vigilant individuals to aid in predator detection (i.e. the many eyes hypothesis; Brown & Kotler, 2004; Creel et al., 2014; Olson et al., 2015; Quenette, 1990). Although these behaviours can reduce the overall calories consumed by an individual via decreased foraging time or intraspecific competition, they can simultaneously increase individual fitness since such actions can mitigate predation risk (Dehn, 1990; Ellsworth et al., 2024; Gaynor et al., 2019; Lind & Cresswell, 2005; Olson et al., 2015). While animals generally benefit from such behaviours in the presence of predation risk, individuals might maximize their caloric intake by foraging alone and reducing vigilance behaviour in situations where predation is unlikely (Quenette, 1990; Sirot et al., 2021). Animals are thus presented with a trade-off: trust environmental cues that predation risk is low and reduce antipredator behaviours to maximize food intake, or continue to exhibit antipredator behaviours and suffer reduced food intake but hedge against the unlikely event that a predator appears (Lind & Cresswell, 2005).

In order for antipredator behaviours to be effectively employed, prey species must be able to perceive the incoming predator or threat (Gaynor et al., 2019; Jordan & Ryan, 2015). The degree to which prey express antipredator behaviours can be further influenced by the efficacy of said behaviours. For instance, if conditions reduce the efficacy of an already ineffectual antipredator behaviour, the further reduction in efficacy will likely prompt the prey species to abandon the behaviour. Conversely, if a behaviour is highly efficient and therefore confers a substantial advantage to the prey, conditions that reduce the efficiency of this behaviour will likely prompt increased expression of the behaviour to

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maintain its advantageous outcomes despite the reduced efficiency (Brown, 1999). Vigilance and group size are two antipredator behaviours that are frequently used by some prey species, but whose efficacy is largely dependent on local conditions. For instance, individuals foraging with high levels of background noise are less capable of hearing an approaching predator, and therefore may favour vigilance behaviour over food consumption (Evans et al., 2018; Giordano et al., 2022; Quinn et al., 2006). Likewise, the intensity of light can also alter vigilance behaviour as visual information is limited in low-light conditions. Increased light may allow prey to gather visual cues but simultaneously exposes prey through increased visibility to predators. As a result, some species increase vigilance behaviours under brightly lit conditions (Fernández-Juricic & Tran, 2007; Zhang et al., 2020), while other species reduce vigilance behaviour under such conditions (Lashley et al., 2014).

In addition to being affected by fluctuating environmental conditions such as light and noise (Gaynor et al., 2019), perceived predation risk can also be influenced by the physical environment surrounding the individual (Laundré et al., 2014). Some species mitigate predation risk by selecting habitat patches with ample refuges in which to hide (Heithaus et al., 2009; Palomo-Munoz et al., 2024). Refuges that offer greater vegetation complexity (e.g. variation in stand height or vegetation density) may offer more opportunities to hide, and thus offer greater protection for prey species that rely on hiding as a defence strategy (Atuo & O'Connell, 2017; Schmidt & Kuijper, 2015). If increased vegetation complexity offers increased safety for prey, prey may perceive these environments as lower risk and relax their antipredator behaviour (Schmidt & Kuijper, 2015). Alternatively, prey in complex stands may not moderate their antipredator behaviour since their own sight lines are obscured and their capacity to flee predators may be compromised (Lagory, 1986). Finally, the effect of vegetation on antipredator behaviours may vary across the diel period by prompting heightened antipredator behaviours when vegetation reduces the efficacy of an otherwise successful strategy (e.g. vigilance behaviour in daylight; Iribarren & Kotler, 2012) and prompting reduced antipredator behaviours when vegetation lowers the efficacy of an already ineffective strategy (e.g. vigilance behaviour in darkness; Embar et al., 2011). Because vegetation both protects prey from predators and conceals predators from prey, the structural environment alone is not a reliable indicator of safety. Thus, wildlife must rely on other, nonstructural environmental cues such as light and noise to accurately assess predation risk.

In addition to the protection provided by aspects of the environment, social prey species are capable of directly influencing their predation risk by altering the size of their foraging group. Ungulates may reduce their individual vigilance behaviour in the presence of other conspecifics, presumably because the collective benefit of increased attentive eyes relieves any one individual's responsibility to remain vigilant (Beauchamp, 2003; Lagory, 1986; Lashley et al., 2014; Olson et al., 2015). If no predators are present, however, larger groups may prove disadvantageous since individuals will experience interference competition but gain no safety benefits (Beauchamp, 2003; Creel et al., 2014; Olson et al., 2015). Thus, in the absence of predators, group size does not mediate predation pressure and may have little impact on vigilance behaviour. Instead, fluctuating environmental conditions that impact an individual's ability to perceive an incoming predator may play a larger role in regulating vigilance behaviour than does group size.

Historically, research on antipredator behaviour and landscapes of fear has occurred within regions where substantial predation risk exists (Ciuti et al., 2012). As a result, our understanding of the roles predation risk and environmental cues play in antipredator behaviour may be confounded since it is impossible to isolate the roles of either factor if both are present (Maurer et al., 2022). Urban ecosystems often exclude apex predators but maintain environmental conditions that prevent prey from being certain of predators' absence, such as intense noise and light pollution (Lowry et al., 2013; Nelson-Olivieri et al., 2023; Ordiz et al., 2021; Schirmer et al., 2019). Thus, cities offer a unique environment to study prey reacting to a landscape of fear that they assume contains non-negligible predation risk, but which actually carries relatively little predation risk compared to undeveloped areas (Fischer et al., 2012).

Although apex predators are generally excluded from urban ecosystems (Fischer et al., 2012; Ordiz et al., 2021; Prugh et al., 2009), humans are hyperabundant and represent the primary source of disturbance for many wildlife species in urban landscapes (Frid & Dill, 2002). Indeed, humans have been recognized as global super-predators due to harvest rates that far exceed natural predation (Darimont et al., 2015) and frequent disturbances that prompt changes in wildlife behaviour and activity patterns (Gaynor et al., 2020; Palmer et al., 2023; Suraci et al., 2019). Similar to apex predators, the formative influence of the human superpredator is not limited to predation events. Nonhunting humans still pose a threat to wildlife directly (e.g. wildlife–vehicle collisions, etc.; McCance et al., 2015) and indirectly (e.g. window strikes, introduction of non-native predators or competitors, etc.; Doherty et al., 2016; Loss et al., 2012), and still contribute to an environment saturated with cues of risk (Frid & Dill, 2002; Smith et al., 2021). As a result, urban prey may be unknowingly safe from predation by nonhuman apex predators, but still reside within a novel landscape of fear crafted by humans (Ciuti et al., 2012; Frid & Dill, 2002; Palmer et al., 2023; Smith et al., 2021).

Within urban areas, white-tailed deer, *Odocoileus virginianus* (hereafter 'deer'), are an ideal organism to study antipredator behaviour. Deer are common in many American cities (Magle et al., 2019) but are too large to be preyed upon by most synurbic mesopredators (~55 kg; Faurby et al., 2018), and they conspicuously communicate their vigilance through obvious changes in posture (e.g. Gallo et al., 2019; Lashley et al., 2014; see Supplementary Material 1). Additionally, the size and abundance of deer in urban settings allows for easy and ample data collection, as opposed to other less abundant or more cryptic prey species such as cottontails, *Sylvilagus floridanus* (e.g. Lima et al., 2021). Although deer are often used to investigate antipredator behaviour in undeveloped landscapes, few studies have examined their vigilance or grouping behaviour in urban systems (e.g. Gallo et al., 2019). While deer are notoriously tolerant of humans in cities, urban deer still exhibit antipredator behaviour despite the lack of apex predators (Ciach & Fröhlich, 2019; Gallo et al., 2019; Maurer et al., 2022), allowing the opportunity to investigate the nonconsumptive mechanisms that influence such behaviour.

A possible explanation for continued antipredator behaviour in urban environments despite the lack of nonhuman predators is that deer are not reacting to a perceived imminent attack, but rather are compensating for features of the urban environment that lower their ability to perceive their surroundings. Urban light and noise may then offer deer a human shield from their natural predators, but not a stress-free environment, since these disturbances limit their ability to detect a predator's presence (A. C. Collins et al., 2020; Le Saout et al., 2015). To test whether vigilance behaviour in urban deer is associated with ambient conditions that inhibit the perception of potential predators, we measured vigilance behaviour and foraging group size, ambient noise and light and the potential for human disturbance at sampling sites across the Washington, D.C. (U.S.A.) region. We hypothesized that antipredator behaviours are as much a reaction to conditions that inhibit the detection of potential threats as they are a reaction to the threats themselves. As such, we predicted that loud and dark conditions would hinder a deer's ability to detect potential threats, and therefore deer would increase vigilance behaviour and foraging group size in darker and/or louder environments. We also predicted that deer would show heightened antipredator behaviours during times of high human disturbance. Because structurally complex habitat can act as refuges from recreating humans, we define human disturbance as a combination of structural habitat complexity and the number of humans present. By exploring the mechanisms behind antipredator responses in a system with reliably low predation pressure, we hope to gain a better understanding of fear responses in wildlife and to provide better insight into the mechanisms that govern landscapes of fear.

METHODS

Study Area

The Washington, D.C. metropolitan region is home to roughly 6.3 million people, with a mean density of 375.4 people/km^2 (United States Census Bureau, 2020). Approximately 155 km^2 (~21% of landcover) of managed nonresidential greenspace is distributed across the region and is primarily either landscaped park space or beech–oak upland forest (Ossi et al., 2015). The region receives roughly 106 cm of precipitation annually and experiences mean temperatures ranging from 3.1 to 27.2°C across four distinct seasons (National Oceanic and Atmospheric Administration, 2024). The Washington, D.C. metropolitan region resides in the ancestral homeland of the Nacotchtank and Piscataway People (Tayac, 2014).

Site Selection

We established an array of motion-activated wildlife cameras across the Washington, D.C. metropolitan region in 2020 for long-term wildlife monitoring (M. K. M. Collins & Gallo, 2024; Magle et al., 2019). To create the sampling array, a 24 × 24 1 km grid was overlaid on the region and was centred on Washington, D.C. We randomly selected 75 grid cells to host cameras and obtained permission (e.g. permits) to deploy a camera within a greenspace in each of the selected grid cells (M. K. M. Collins & Gallo, 2024). We deployed a single Reconyx Hyperfire 2 infrared flash trail camera (Reconyx Inc., Holmen, WI, U.S.A.) at each sample site. Each camera was set to take a single photograph per trigger with a 15 s delay between triggers. All cameras were fixed to a tree at a height of less than 1 m off the ground and were aimed at game trails. Prior to deployment, we updated the firmware of each camera to enable relative light levels to be recorded in the metadata of each photograph. Cameras were deployed for 4 weeks during July and October of 2021, and January and April of 2022.

Although the long-term array contained 75 cameras, we used a subset of 24 sites in this study due to a limited number of acoustic recorders. We selected a stratified random sample from this larger camera array to represent a gradient of development intensity by identifying the percentage of impervious surface within 500 m of each camera and the distance between each camera and the nearest major roadway. Both metrics were then binned to reflect three equally sized categories per metric (i.e. high, moderate, low). Both binned metrics were then combined to create nine unique classifications from all possible combinations of the two metrics (e.g. high impervious near major roadway, moderate impervious far from a major roadway, etc.). Predictably, no sites were categorized as ‘high impervious surface and high distance from roadway’, so this category was removed. Some categories were only sparsely represented in our array ($N \leq 5$ sites), and thus all sites representing those categories were retained. For categories represented by more than five sites, we randomly selected four to five sites within each classification (Fig. 1). The bin widths for each metric and the number of sites representing each category are available in Supplementary Material 2.

Deer Observations and Behavioural Coding

Two trained individuals reviewed each photograph independently to numerate and identify each animal to species. If the two reviewers disagreed on an identification, a third reviewer was used to settle the discrepancy. Photographs of white-tailed deer then underwent additional review to determine whether the deer was vigilant or nonvigilant, as well as to record the number of deer in each photograph. We defined vigilant as a body posture in which the deer's head was held above its body, whereas nonvigilant behaviour consisted of the deer holding its head below its body, laying its head on the ground or engaging in grooming behaviour (Supplementary Material 3). We excluded photographs from analysis if the deer's head was not visible or if the deer's head was even with its body. We counted the number of deer in each photograph regardless of whether their heads were visible. Although photographs provided an instantaneous record of group size, the foraging group size could be larger than that documented in a single photograph. Thus, to account for this, we assigned the maximum number of individuals observed within 15 min of time t at site i as the observation-specific group size ($s_{i,t}$).

Calculating Ambient Light Levels

Ambient light in lux, $l_{i,t}$, was obtained using the unitless relative light values, C0DATA and C1DATA, recorded by the camera with each trigger and stored in the photograph's metadata. We accessed photograph metadata using the ‘exifr’ package in R version. 4.2.0 (Dunnington & Harvey, 2021). We converted these values to lux using the following equations provided by the camera manufacturer, and we retained the larger of the two quotients as the lux value, provided that it was greater than zero:

$$\mathrm{Lux1}_{i,t} = \frac{(\mathrm{C0DATA} - 2 \times \mathrm{C1DATA})}{\mathrm{CPL}} \tag{1}$$

$$\mathrm{Lux2}_{i,t} = \frac{(0.6 \times \mathrm{C0DATA} - \mathrm{C1DATA})}{\mathrm{CPL}} \tag{2}$$

$$l_{i,t} = \max\left(\mathrm{Lux1}_{i,t}, \mathrm{Lux2}_{i,t}, 0\right) \tag{3}$$

We calculated counts/lx (CPL) using the following set of constants specific to this model of trail camera (Reconyx Hyperfire 2, LED-flash): $\mathrm{ATIME_{ms}} = 27.2$, $\mathrm{AGAIN}x = 16$ and $\mathrm{GA} = 21.4$, where ATIME is the integration time (ms), AGAINx is the ambient light sensor gain setting and GA is the glass attenuation factor.

$$\mathrm{CPL} = \frac{(\mathrm{ATIME_{ms}} \times \mathrm{AGAIN}x)}{(\mathrm{GA} \times 53)} \tag{4}$$

Calculating Ambient Noise

In addition to a camera, we also deployed an AudioMoth acoustic recording device (Hill et al., 2019) at each site to record 1 min of audio every 10 min. Due to equipment limitations, we rotated 12 acoustic recorders between our 24 sites such that each acoustic recorder was active for approximately 2 weeks at one site

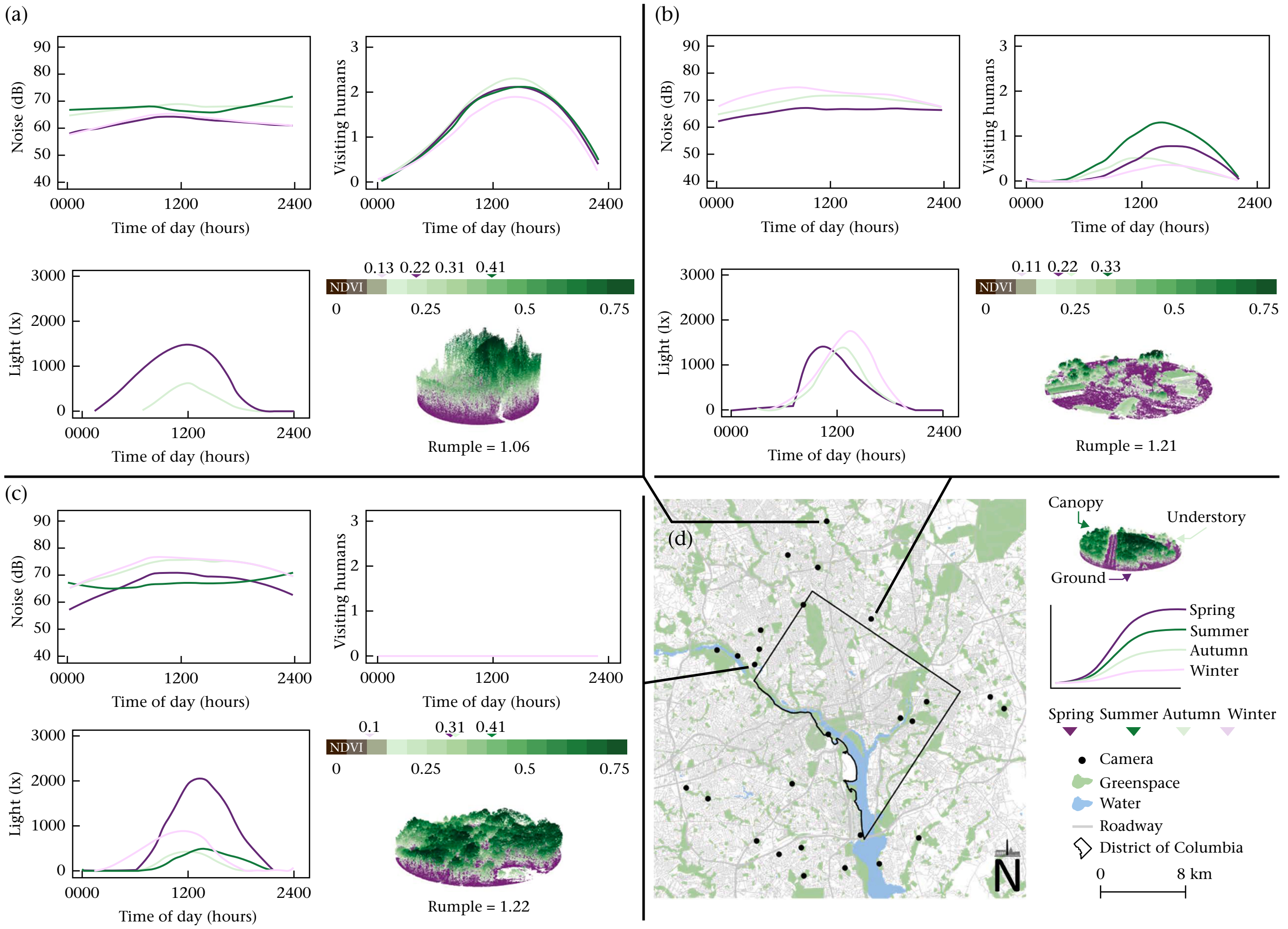

Figure 1. Map of cameras deployed with audio recorders for this analysis across the Washington, D.C. metropolitan area. Three sampling sites (a, b, c) visualizing variation in ambient noise and light conditions per hour of day, the number of human visitors within one deer home range per hour of day and the vegetative intensity (normalized difference vegetation index, NDVI) per season, and (d) the three-dimensional rendering of the habitat structure within one deer home range around each camera.

before moving to another site. While cameras were active for 4-week sampling periods, this analysis only uses photographs taken during the 2-week period in which an acoustic recorder was active at the respective site. Acoustic recorders had a sampling rate of 32 kHz and a medium gain, and were affixed to a tree roughly 1.5 m from the ground within 10 m of the camera.

Ambient noise, $s_{i,t}$, was characterized using median sound pressure level (SPL) calculated using the PAMGuide processing techniques provided in Merchant et al. (2015) in R. When calculating SPL, we used the technical specifications provided by Open Acoustic Devices: transducer sensitivity = -18; gain = 15; zero-to-peak voltage = 3.3, analysis type = broadband. An SPL was calculated for each 0.5 s of each 1 min recording period, resulting in 120 SPLs per recording. We then used the median of those 120 values to represent the ambient noise present at the site for that 10 min period. We then associated each SPL value with any deer observations made in the following 10 min of the respective recording. We chose to associate deer observations with the closest preceding audio recording since we assumed deer would be responding to conditions that had already occurred rather than anticipating future noise levels (i.e. SPL readings that occurred after the deer observation).

Quantifying Relative Risk

To account for the relative risk of encountering humans, $r_{i,t}$, we multiplied a metric of habitat openness by the number of humans visiting the site, $h_{i,t}$.

$$r_{i,t} = o_{i,t} \times h_{i,t} \tag{5}$$

Where $h_{i,t}$ is the cumulative number of humans within one urban deer home range (17.3 ha; Roden-Reynolds et al., 2022) around site i during hour t. Our study design rarely captures photographs of humans since cameras are purposefully located away from human trails. Instead of using photographic observations to quantify human activity at each site, we used human mobility data from ADVAN Research (https://advanresearch.com/) via the Dewey platform (www.deweydata.io). ADVAN Research uses cell phone data to aggregate human foot traffic information at specific points of interest (POIs) in the United States. We used the weekly patterns data set to retrieve the number of raw visits/h at each POI within our study area between 28 June 2021 and 8 May 2022. Because POIs are stored as points, we created a Voronoi polygon around each POI that retained the weekly patterns data from the respective POI point. Around each sampling site, we created a 235 m fixed radius buffer to correspond to an urban deer home range. We then calculated the mean number hourly visits for each Voronoi polygon that intersected the deer home range buffer to obtain our human activity variable, $h_{i,t}$.

We calculated habitat openness, $o_{i,t}$, by subtracting the mean vegetative intensity within the home range buffer, $v_{i,t}$, from one and dividing the resulting value by the structural complexity of the understory within the same buffer, c_i.

$$o_{i,t} = \frac{1 - v_{i,t}}{c_i} \tag{6}$$

Here, $v_{i,t}$ is the normalized difference vegetation index (NDVI) and is calculated using remotely sensed near-infrared (b_{IR}) and red (b_{r}) spectral bands obtained from Landsat 8 (United States Geological Survey, n.d.). Remotely sensed data were processed using the 'sf,' 'raster' and 'terra' packages in R (Hijmans, 2023a, 2023b; Pebesma, 2018).

$$v_{i,t} = \frac{b_{\mathrm{IR}} - b_{\mathrm{r}}}{b_{\mathrm{IR}} + b_{\mathrm{r}}} \tag{7}$$

We used rumple to characterize vegetative complexity, c_i, at each site, which is the ratio of the three-dimensional ($\mathrm{SA_{3D}}$) and two-dimensional ($\mathrm{SA_{2D}}$; i.e. footprint) space that vegetation occupies created using remotely sensed LiDAR points. Due to the multijurisdictional nature of our study area, LiDAR data are housed across multiple repositories, which are listed in Supplementary Material 2.

$$c_i = \frac{\mathrm{SA_{3D}}}{\mathrm{SA_{2D}}} \tag{8}$$

Thus, more complex and heterogenous three-dimensional surfaces yield higher ratios, and simpler three-dimensional surfaces yield smaller ratios since they more closely resemble their two-dimensional footprint. Because our analysis was concerned with the understory, we only used LiDAR points within 2 m of the forest floor. Rumple was calculated using the 'lidR' package in R (Roussel et al., 2020).

Vegetated regions in our study area never experience NDVI values of exactly 1, but are always greater than 0 (equation 7). As a result, the numerator of equation (6) is always positive and less than or equal to 1. Likewise, c_i is a ratio and is always positive (equation 8). As a result $o_{i,t}$ is always positive and less than 1 (equation 6). Since the value of habitat openness, $o_{i,t}$ (equation 6), is always between zero and one, equation (5) allows habitat complexity to govern the effect of humans since complex habitats ($o_{i,t}$ approaching 0) with ample refuges artificially reduce the number of humans observed at the site (effect of humans), while simple habitats ($o_{i,t}$ approaching 1) with few places to hide permit the full effect of humans at the site to be felt.

Model Formulation and Fitting

Finally, we constructed a global logistic regression model for vigilant behaviour at site *i* during time *t* consisting of relative risk ($r_{i,t}$), documented herd size ($g_{i,t}$), ambient light ($l_{i,t}$) and ambient noise ($n_{i,t}$).

$$\text{Vigilance} \sim \text{Bernoulli}\left(p_{i,t}\right) \tag{9}$$

$$\text{Logit}\left(p_{i,t}\right) = \beta_{s[t]} + \beta_1 \times r_{i,t} + \beta_2 \times g_{i,t} + \beta_3 \times l_{i,t} + \beta_4 \times n_{i,t} \tag{10}$$

To model group size, we constructed a similar Poisson regression model, but excluded documented herd size ($g_{i,t}$) as an independent variable since this became the dependent variable:

$$\text{Group size} \sim \text{Poisson}(\lambda_{i,t}) \tag{11}$$

$$\text{Log}(\lambda_{i,t}) = \beta_{s[t]} + \beta_1 \times r_{i,t} + \beta_2 \times l_{i,t} + \beta_3 \times n_{i,t} \tag{12}$$

Prior distributions for all coefficients, except the intercept, were normally distributed with a mean of zero and standard deviation of 100. We accounted for seasonal changes in deer biology in both the vigilance and group size model by including sampling season (i.e. summer, autumn, winter, spring) as a random intercept, $\beta_{s[t]}$:

$$\beta_{s[t]} \sim \text{normal}(\mu, \sigma) \tag{13}$$

Where each season-specific intercept was derived from a single mean, μ and standard deviation, σ with priors of $\mu \sim N(0{,}100)$ and $\sigma \sim \text{InverseGamma}(1{,}5)$. Each independent variable was scaled to have a mean of zero and a standard deviation of one.

To estimate the coefficient values, we ran four 200 000-iteration MCMC chains with a 100 000-iteration burn-in period using NIMBLE version 1.1.0 in R (de Valpine et al., 2017). Each parameter's trace plot was visually inspected to ensure adequate mixing, and Gelman–Rubin statistics were confirmed to equal one for each estimated parameter. We considered a parameter to be significant if its 95% credible interval did not contain zero.

Ethical Note

This study was exempt from institutional ethical review due to the noninvasive sampling method and observational study design. No animals were captured or manipulated for this study.

RESULTS

A total of 3928 observations of white-tailed deer were recorded across 24 sampled sites. Due to malfunctioning equipment, we excluded four sites from our analysis. We only recorded a total of 28 observations of coyotes across six of the sites, suggesting that nonhuman predators are rare in our study system. Approximately 81% of deer observations were not useable either because the photograph did not meet our inclusion criteria (e.g. head was not visible, animal was fleeing, etc.), or because audio data were not available for those observations (e.g. acoustic recorder batteries died). Our final data set consisted of 734 observations of white-tailed deer. Approximately 72% ($N = 532$) of observed deer were nonvigilant, while the remaining 28% ($N = 202$) were classified as vigilant. Deer were documented in groups ranging from one to six individuals (mean ± SD = 1.72 ± 1.07). Ambient light values varied from 0.00 to 9423.87 lx (mean ± SD = 669.20 ± 1380.54 lx), while ambient noise varied from 60.54 to 85.99 dB (mean ± SD = 71.56 ± 5.48 dB). Habitat openness ranged from 0.38 to 0.79 (mean ± SD = 0.62 ± 0.09), and cumulative hourly raw visitors ranged from 0.00 to 25.50 (mean ± SD = 1.98 ± 4.75). As a result, relative risk scores ranged between 0.00 and 13.98 (mean ± SD = 1.18 ± 2.67). In addition to differences across sites, environmental conditions also varied across seasons and times of day, creating a dynamic set of circumstances influencing deer behaviour (Fig. 1).

Our analysis revealed a negative correlation between vigilance and ambient light (Fig. 2; $\beta = -0.34$, 95% CI [−0.58, -0.13]). Deer were 29% less likely to display vigilance behaviour (odds ratio = 0.71, 95% CI [0.56, 0.87]) in conditions where visible light increased

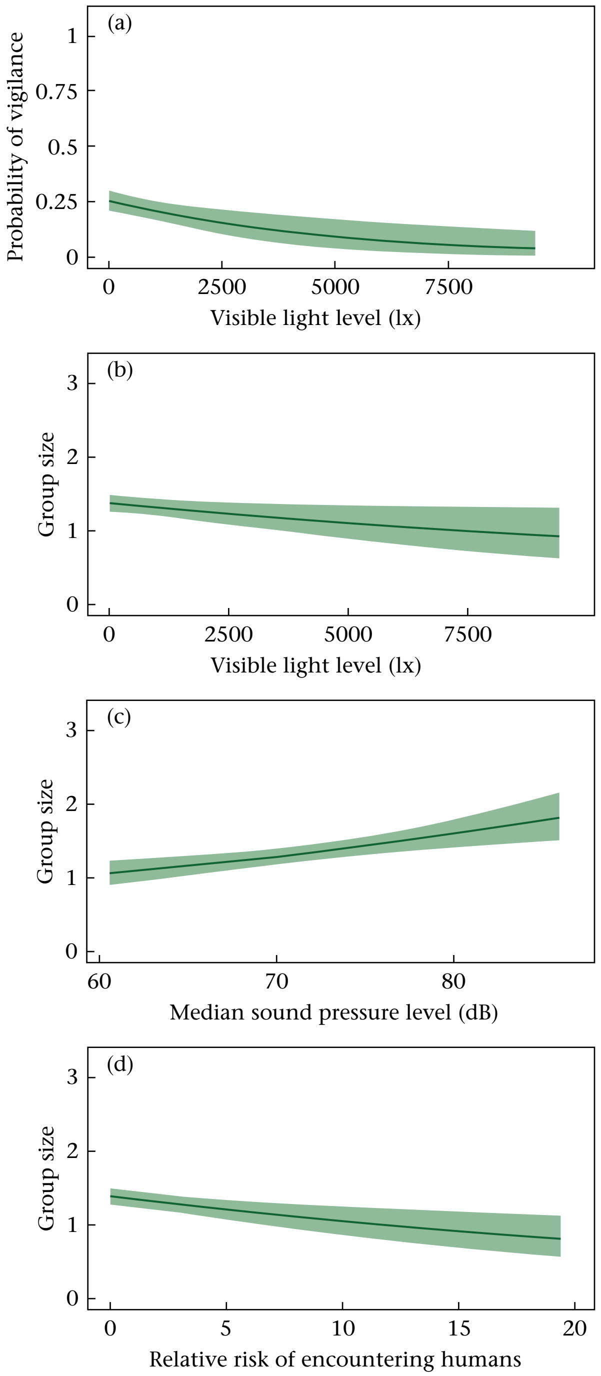

Figure 2. (a) Effects of visible light on the probability of deer being vigilant. (b, c, d) Effects of visible light, median sound pressure and relative risk, respectively, on deer group size. Predicted responses use the mean intercept across seasons and are depicted as a dark line. Shaded polygons depict the 95% credible interval.

by one standard deviation from the mean. Herd size (β = -0.13, 95% CI [−0.32, 0.06]), ambient noise (β = 0.09, 95% CI [−0.10, 0.28]) and relative risk (β = -0.04, 95% CI [−0.25, 0.15]) all contained zero within their 95% credible intervals. Season-specific intercepts were estimated to be -0.35 (95% CI [−0.69, 0.005]) in summer, -2.18 in autumn (95% CI [−2.95, -1.52]), -1.04 in winter (95% CI [−1.29, 0.79]) and -1.36 in spring 95% CI [−1.84, -0.91]). Thus, when all other variables were held constant at their mean, the season-specific probability of being vigilant was 41.33% in summer, 10.16% in autumn, 26.11% in winter and 20.42% in spring.

Similar to vigilance behaviour, our analysis also found a negative correlation between group size and ambient light (Fig. 2; β = -0.06, 95% CI [−0.12, -0.004]) and relative risk (β = -0.10, 95% CI [−0.16, -0.04]). However, group size and ambient noise displayed a positive relationship (Fig. 2; β = 0.12, 95% CI [0.05, 0.18]). Intercepts were estimated to be 0.34 (95% CI [0.20, 0.47]) in summer, -0.04 in autumn (95% CI [−0.28, 0.18]), 0.76 in winter (95% CI [0.69, 0.84]) and 0.09 in spring 95% CI [−0.10, 0.27]). Thus, when all other variables were held constant at their mean, the average season-specific foraging group size was 1.40 in summer, 0.96 in autumn, 2.15 in winter and 1.09 individuals in spring.

DISCUSSION

We hypothesized that antipredator behaviours are a reaction to conditions that inhibit the detection of potential threats as opposed to the threat itself. Our findings suggest that urban white-tailed deer alter their vigilance behaviour based on reduced visibility and adjust their foraging group size based on reduced visibility, increased ambient noise and increased human disturbance. Conversely, group size, ambient noise and habitat-mediated human disturbance did not have measurable effects on vigilance behaviour. Our results support our hypothesis and demonstrate that deer moderate their antipredator based on their ability to perceive changes in predation risk, even when predation risk is reliably low. Together, our results lend further support to the notion that landscapes of fear are manifestations of perception rather than predation (Gaynor et al., 2019; Palmer et al., 2023).

The original landscape of fear definition has always emphasized that perception is the foundation of the phenomenon (Brown, 1999; Laundré et al., 2001). The concept is frequently misunderstood, however, and is instead attributed to the physical presence of predators (Bleicher, 2017). One possible explanation for this misunderstanding is that the most iconic landscape of fear studies (i.e. the ecological ramifications of wolf reintroduction in Yellowstone National Park, U.S.A.; Laundré et al., 2001) focus on ecosystem changes after predator reintroduction, which may falsely imply that the landscape of fear was absent prior to the arrival of predators. Regardless of a community's current predator community, prey species have evolved under intensive predation pressure and generally continue to exercise the evolutionarily stable trait of being attentive to possible threats regardless of whether they are manifested (Beauchamp & Ruxton, 2007; Bleicher, 2017; Le Saout et al., 2015). Because landscapes of fear are perceived, it is not possible to measure or map them directly (Gaynor et al., 2019). Instead, behavioural responses to potential threats, such as antipredator behaviours like vigilance and group size, can be used to gain insight into the factors that contribute to landscapes of fear.

Our analysis found that vigilance behaviour decreased and groups disbanded during the day when the intensity of light increased. Low-light conditions make it difficult for mammals to see individuals farther in the distance without the aid of bold and contrasting coloration, which predators generally lack (Penteriani & Delgado, 2017). Thus, limited visibility reduces the efficacy of an otherwise effective antipredator strategy and requires additional effort to be allocated to the strategy to compensate (Iribarren & Kotler, 2012). Deer in our study demonstrated this phenomenon by expressing greater vigilance behaviour and forming larger groups during low-light conditions but abandoning these precautions once brighter conditions were restored. Alternatively, it is also possible that deer have evolved a heightened sense of fear at night because most predators are nocturnal and night-time has thus always been a particularly dangerous time irrespective of the light level (Gaynor et al., 2020; Gerkema et al., 2013).

Noise also had a negative correlation with foraging group size, but had no statistical relationship with vigilance. Prey species tend to be familiar with sounds associated with predation from a young age (e.g. Magrath et al., 2007). Such immediate recognition suggests that auditory cues are critical to prey survival and explains why cue-masking noises would trigger antipredator responses such as coalescing into larger groups. It is curious that noise did not have a similar effect on vigilance rates in deer in our study, however. One potential explanation for this discrepancy is that ambient noise hinders the ability of deer to effectively communicate with distant individuals. Most white-tailed deer vocalizations are relatively quiet and may thus be easily missed if ambient noise is elevated (Atkeson et al., 1988). Thus, noisy environments may force deer into closer proximity to assist in communication as opposed to the detection of predators.

Although dark and loud conditions both contributed to heightened antipredator behaviour in deer, the threat of human contact, mediated by vegetative structure, had a negative correlation with foraging group size and no relationship with vigilance behaviour. Prey are known to adjust their antipredator behaviour in response to differing predator behaviours, with coursing predators (e.g. canids) prompting larger foraging groups and ambush predators (e.g. felids) eliciting vigilance behaviour (Creel et al., 2014; Palomo-Munoz et al., 2024). Hunting literature suggests that humans act as coursing predators (Montgomery et al., 2022), but no studies have yet investigated whether recreating humans resemble coursing or ambush predators in their behaviour patterns. Human presence had no effect on vigilance in deer and prompted deer to disband into smaller groups rather than form larger groups. Neither response is consistent with expected behaviours towards either coursing or ambush predators, suggesting that human behaviour does not mimic either predation type. However, if deer consider humans threatening and disband into smaller groups to avoid detection, then deer in our study area may hold that the risk of human encounters outweighs the benefits offered by larger group sizes. Alternatively, deer may recognize that humans pose a greater threat to other predators and instead use humans as a shield against predators (i.e. human shield hypothesis; Berger, 2007). Deer may then rely on increased human disturbance to dissuade predation and thus engage in reduced antipredator behaviours when humans are in the vicinity (Granados et al., 2023; Maurer et al., 2022). To better understand how humans contribute to animal behaviour, future research should explore responses of predators and prey to fine-scale behaviour and movement patterns of recreating humans.

While light, noise and human disturbance were our variables of interest, our models also revealed nuanced seasonal differences in antipredator behaviour by including season as a random intercept. Vigilance probability was greatest in the darkest conditions during the summer season, but was similar to that of autumn, winter and spring during brighter conditions. Conversely, deer tended to form larger groups in winter, whereas group sizes during the remaining seasons were relatively similar to one another. These differences can primarily be attributed to the breeding season and resource limitations experienced in winter relative to the abundance of resources in summer. Abundant summer foliage permits increased foraging efficiency, which opens the activity budget to other behaviours, such as increased vigilance. During the resource-limited winter, however, ungulates tend to forgo vigilance in place of food acquisition behaviours because greater search time is required to access food (Clare et al., 2023; Winnie et al., 2006). Additionally, the deer breeding season (autumn) yields pregnant females during the winter months. When reproductive, individual fitness is most benefited by maximizing the development of offspring through consumption of food as opposed to maximizing parental safety (Benoit et al., 2023). The need to favour survivorship in summer might further explain why vigilance peaked in the nonreproductive summer season but was lower during the breeding (autumn), gestational (winter) and lactating (spring) seasons (Hamel & Côté, 2008; Powolny et al., 2014; Schmitz, 1992). Deer tend to form larger groups in winter, a behaviour that has been attributed to gains in foraging efficiency made possible by the collective vigilance of other group members (i.e. the many eyes hypothesis; Clare et al., 2023; Messier & Barrette, 1985; Sorensen & Taylor, 1995). However, our analysis found no significant relationship between group size and vigilance probability.

While our analysis did show significant relationships between antipredator behaviour and light, noise and human disturbance, we recognize that these relationships may be weak relative to those observed in systems with substantial predation pressure (Ellsworth et al., 2024; but see also Creel et al., 2014; Le Saout et al., 2015; Schuttler et al., 2017). Even under the loudest or darkest conditions, we found that deer formed groups of less than three individuals, and the probability of vigilance remained below 50% (Fig. 2). Still, it is compelling that deer in our study area continue to display antipredator behaviours since the region has relatively no predation pressure and such behaviours can be costly to individual fitness in the absence of predators (Beauchamp, 2003; Creel et al., 2014; Olson et al., 2015). That deer expressed any degree of antipredator behaviours in a landscape of negligible predation risk demonstrates that predator presence is not the sole factor that drives landscapes of fear, even if it is a major component of the phenomenon. If predator presence is the sole driver of landscapes of fear, then deer in our study area should not demonstrate antipredator behaviours.

While both predation and abiotic factors contribute to landscapes of fear, neither variable can be consequential if the prey cannot perceive changes in these conditions. While the original landscape of fear definition emphasized the central importance of perception, subsequent work has frequently misunderstood the concept as being driven by predator presence rather than by perception (Bleicher, 2017). However, recent scholarship has recentred the role of individual perception within landscapes of fear, since an individual cannot adjust their behaviour to a threat they cannot perceive (Gaynor et al., 2019; Jordan & Ryan, 2015). Although ecosystem dynamics are complex and multifaceted, ecologists frequently use the top—down/bottom—up conceptual framework to understand ecosystem functions (Hunter & Price, 1992). However, perception is not a decidedly top—down or bottom—up phenomenon, and is thus generally omitted from our fundamental understanding of ecosystems despite its obvious importance (Laundré et al., 2014). Because perception of top—down factors can be dependent on bottom—up factors, we propose that considering perceptual capacity as a ‘middle—out’ factor would contribute to a greater understanding of ecosystem functions even within our most simple theoretical frameworks. While top—down regulation is of obvious importance in the formation of a fear landscape, consideration of bottom—up (i.e. light level and noise) and middle—out (i.e. perception) factors can provide a more holistic understanding of the landscape of fear and assist in conservation management (Laundré et al., 2010, 2014).

The reintroduction of predation risk has been lauded as a successful method of achieving specific management goals (Atkins et al., 2017; Bedoya-Pérez et al., 2019; Beringer, 1994; Laundré et al., 2001). Such reintroductions are often infeasible in densely developed landscapes, however, and in successful cases may still fail to achieve the ecological effects of apex predators in less developed landscapes (Kuijper et al., 2016). Instead, humans might be able to induce sufficient behavioural responses from prey through intentional habitat manipulation (Frey et al., 2018;

Whittingham et al., 2006; Whytock et al., 2020); the introduction of human hunting cues (Potratz et al., 2024; Wevers et al., 2020); or through managed hunts, particularly outside of the hunting season (Cromsigt et al., 2013). Although these actions would likely reintroduce landscapes of fear in urban settings, such actions may be effort-intensive and costly. Conversely, our analysis suggests that managers in urban spaces can use relatively passive approaches while still capitalizing on the landscape of fear phenomenon by manipulating bottom–up factors to impede middle–out factors. For instance, efforts to remove light pollution may result in greater vigilance behaviour while efforts to reduce noise pollution might yield smaller foraging groups. Together, these actions might contribute to reduced browsing pressure and thereby maintain a healthier understory habitat for ground-dwelling species (Gaynor et al., 2021). By capitalizing on middle–out factors, conservation initiatives may benefit from modified top–down regulation even in the absence of predators.

While camera traps effectively measure vigilance and group size in deer, this method is not without limitations. Stationary camera traps have limited fields of view and thus fail to capture individuals that travel within a group but do not walk in front of the camera. This limitation may have resulted in artificially low measures of group size or predation risk (i.e. predator presence/prevalence). Additionally, our cameras took photographs (~1 frame every 15 s) rather than recording videos (~20 frames/s). While photographs can be used to measure vigilance/nonvigilance, more subtle antipredator behaviours, such as apprehension, cannot be measured as effectively. Furthermore, we used camera traps to measure relative light levels throughout our study. However, traditional light meters may offer more sensitive measures of ambient light. Finally, we used cell phone data to approximate pedestrian activity within our study area. While these data offer unique insights into human activity within greenspaces, they do not capture individuals travelling without cell phones (e.g. children). These data also fail to capture vehicular traffic, which undoubtedly has an impact on deer behaviour. Future studies may provide more nuanced insights by using equipment with greater sensitivity and precision.

Conclusion

Antipredator behaviours are advantageous to prey but can only be effective if prey are able to detect predators (Gaynor et al., 2019; Jordan & Ryan, 2015). Animals with the cognitive capacity to perceive predators may be dependent upon environmental conditions that either facilitate or hinder the detection of predators, such as ambient light and noise. Our study found that deer showed heightened antipredator behaviours under noisy and dark conditions despite reliably low predation pressure. These findings suggest that landscapes of fear require bottom–up and middle–out factors in addition to top–down pressures. As the world becomes brighter and louder (Bennie et al., 2015; Buxton et al., 2017), understanding the nonstructural aspects of predator–prey dynamics will become increasingly critical to the conservation and maintenance of ecosystems.

Author Contributions

Daniel J. Herrera: Writing – review & editing, Visualization, Investigation, Data curation, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Lara Abedin:** Writing – review & editing, Data curation. **Gabriela Palomo:** Methodology, Writing – review & editing, Data curation. **Merri Collins:** Writing – review & editing, Data curation, Methodology. **Jishan Chowdhury:** Writing – review & editing, Data curation. **Krista Shires:** Methodology, Writing – review & editing, Data curation. **Travis Gallo:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization, Supervision, Investigation, Formal analysis.

Data Availability

The data and code used in this analysis are available as Supplementary Material and publicly available on GitHub (https://github.com/Dan-Herrera/light-noise-and-deer-behaviour).

Declaration of Interest

The authors report no conflict of interest.

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Supplementary Material

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