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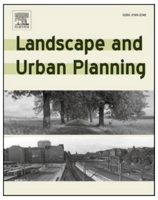

Urbanization affects the behavior of a predator-free ungulate in protected lands

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HIGHLIGHTS

- Cameras reveal deer behavior changes with urbanization despite predator absence.
- Deer use of human paths increased with distance from urbanization.
- Grouping behavior increased closer to urbanization likely from resource subsidies.
- Predator-free deer are crepuscular with slight deviation in urban proximity.

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ABSTRACT

Natural habitats have been converted to urban areas across the globe such that many landscapes now represent matrices of developed and protected lands. As urbanization continues to expand, associated pressures on wildlife will increase, including effects on animals in adjacent protected habitats. For prey species (e.g., ungulates), an understanding of the ecological impacts of urbanization is typically confounded by coincident effects from co-occurring predators. Yet, understanding how urbanization affects prey behaviors in the absence of predators is becoming increasingly relevant as many top predators face extirpation. We placed camera traps at varying distances from urban areas within protected areas in the Florida Keys, USA, to evaluate the influence of urbanization on the behavior of the key deer (*Odocoileus virginianus clavium*), an endangered species that has been without non-human mammalian predators for ~ 4000 years. We predicted that as distance to urban areas decreased, key deer would use sites at the same rate, exhibit bigger group sizes, and shift activity patterns to be more nocturnal. Our results indicate that intensity of site use decreased with proximity to urban areas, potentially reflecting human avoidance. Group size increased closer to urban areas, consistent with other studies relating this behavior to anthropogenic subsidies and vigilance for humans. Activity patterns changed but did not become more nocturnal near urban areas as predicted by global analyses relating human disturbance to wildlife nocturnality. Our results have important implications for ungulate behavioral ecology and, taken together, suggest that influences on protected species from adjacent land uses are an important consideration when planning land use and designing protected areas.

1. Introduction

The ongoing conversion of natural habitats to urban land cover leaves wildlife with altered resource regimes and smaller, more fragmented habitats (Horváth, Ptacnik, Vad, & Chase, 2019). To combat this problem, modern conservation efforts have focused on setting aside protected lands (Brandon & Wells, 1992; Rodrigues et al., 2004; Scott et al., 2001). Although biodiversity in protected areas is presumed safe from future development (Cove, Fergus, Lacher, Akre, & McShea, 2019), urbanization threatens to significantly degrade biodiversity of protected areas globally in the next few decades (McDonald, Kareiva, and Forman 2008). Those projections were primarily based on patterns of urban

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spread and resulting loss of protected habitat. However, the net effects of human land use change on biodiversity are likely more dire because of concurrent and associated species invasions (McKinney, 2006; Reed, Serr, Maurer, & Burford Reiskind, 2020), reduced habitat connectivity (Horváth et al., 2019), and impacts on wildlife behavior (Ditchkoff, Saalfeld, & Gibson, 2006). Thus, understanding how urbanization affects wildlife in protected areas by changing their behavior is necessary to facilitate improvements in urban and landscape planning (Jokimäki et al., 2011).

A growing body of work has documented changes in wildlife behavior due to expanding anthropogenic development (e.g., Lowry, Lill, & Wong, 2013). For example, urbanization is commonly reported to affect habitat use (e.g, Berger, 2007; Elfström, Zedrosser, Støen, & Swenson, 2014; Jones, Cove, Lashley, & Jackson, 2016), activity patterns (Carter, Shrestha, Karki, Pradhan, & Liu, 2012; Gaynor, Hojnowski, Carter, & Brashares, 2018; Maurer, Thawley, Fireman, Giery, & Stroud, 2019; Nix, Howell, Hall, & McMillan, 2018; Ordiz, Sæbø, Kindberg, Swenson, & Støen, 2017), and grouping and foraging patterns (Ditchkoff et al., 2006; Tablado & Jenni, 2017). Whereas many large predators avoid urban areas, other species are often attracted to human development. Activity patterns in most cases shift to favor nocturnal activity with increasing human disturbance, presumably to avoid peaks in human activity during the day (Gaynor, Hojnowski, Carter, & Brashares, 2018). Grouping behavior has been studied less, but in general is expected to increase with proximity to urban areas to improve vigilance for humans and in response to resource subsidies relaxing competition (e.g., Hidalgo-Mihart, Cantú-Salazar, López-González, Fernandez, & González-Romero, 2004; Yirga et al., 2015). However, most studies monitor wildlife behavior in urban settings rather than in protected areas that are being encroached upon (Gallo, Fidino, Lehrer, & Magle, 2019; Parsons et al., 2018). Moreover, inferences into the ultimate mechanism driving wildlife behavioral changes in urban areas or proximal natural lands may be confounded by the presence of multiple factors that act alongside, or interact with, urbanization (Tablado & Jenni, 2017).

One potentially confounding factor that is fundamentally important for prey species is predation risk. Being eaten is the most severe proximate fitness consequence and, thus, prey decisions are often based first on evading predation (Lima & Dill, 1990). Predators confound inferences into the effects of urbanization on prey behavior because they affect prey behaviors such as habitat use (Brown, 1999; Valeix et al., 2009; Werner, Gilliam, Hall, & Mittelbach, 1983), activity patterns (Fancourt, Hawkins, Cameron, Jones, & Nicol, 2015; Foster et al., 2013), and grouping (e.g., Caraco, Martindale, & Pulliam, 1980; Creel, Schuette, & Christianson, 2014). It has been hypothesized that apex predators fear humans more than prey do and, thus, prey habitat use may shift into urban areas to avoid natural predators via human-shielding (Berger, 2007). Studies have revealed this pattern in ungulates, bears, and small mammals (Berger, 2007; Elfström et al., 2014; Jones et al., 2016). In the case of human-shielding, the impacts of urbanization on prey behavior are indirect because they are mediated via effects on predator behavior. Thus, urbanization may affect prey behavior differently in the absence of predators. Given the global decline in top predators (Estes et al., 2011), understanding effects on prey behavior in the absence of predators is important for future land and resource management.

The Florida key deer (*Odocoileus virginianus clavium*) presents a unique case study for understanding the effects of urbanization and predators on prey behavior. Key deer are endemic to the Florida Keys, USA, and have been without mammalian predators for an evolutionarily relevant timespan. Most white-tailed deer (*Odocoileus virginianus*) populations maintain some risk of predation (including hunting). Although apex predators have been extirpated from many systems, prey behaviors that evolved in the presence of predators may persist. Further, co-occurring medium-sized predators, chiefly coyotes (*Canis latrans*), may still influence behaviors, although coyotes may interact with urbanization differently than apex predators and clear consensus is lacking for their effects on deer (Chitwood, Lashley, Moorman, & DePerno, 2014; Gallo, Fidino, Lehrer, & Magle, 2019; Jones et al. 2016). In contrast with other white-tailed deer, key deer have occurred without non-human predators for roughly 4,000 years. The Florida Keys were isolated when sea levels rose with the melting of the Wisconsin glaciation and the islands subsequently lost top predators (Hoffmeister, 1974). Key deer are federally endangered, and the primary causes of historical population decline were habitat loss, hunting, and vehicular strikes (Hardin, Silvy, & Klimstra, 1976; Harveson, Lopez, Collier, & Silvy, 2007; Lopez et al., 2004; Peterson, Lopez, Frank, Porter, & Silvy, 2004; Peterson et al., 2005), hence the protection of habitat on the islands where they occur. While there is a body of work showing that other subspecies of white-tailed deer respond to environmental cues by adjusting group size (Cherry, Conner, & Warren, 2015; Lashley et al., 2014), foraging behavior (e.g., Biggerstaff, Lashley, Chitwood, Moorman, & Deperno, 2017; Cherry, Warren, & Conner, 2017), activity patterns (Biggerstaff et al., 2017; Cherry et al., 2018; Crawford et al., 2019; Lashley et al., 2018), and habitat use (Kie & Bowyer, 1999; Kilgo, Labisky, & Fritzen, 1998; Lashley et al., 2015; Lingle, 2002), the majority of the work on the influence of urbanization on white-tailed deer subspecies has been done with key deer (e.g., Folk & Klimstra, 1991; Hardin et al., 1976; Harveson et al., 2007; Lopez et al., 2004; Peterson et al., 2004, 2005; but see Gallo, Fidino, Lehrer, & Magle, 2019; Jones et al., 2016).

Throughout previous studies of the effects of urbanization on key deer ecology, their “domestication” has arisen as a prominent theme (Peterson et al., 2005). That is, many deer appear to readily take advantage of human resources, and even direct feeding, resulting in a possible preference for urban areas. However, previous inferences were based largely on animals encountered and tracked from access roads within developed areas or from habitat edges fringing protected lands. Although key deer may move and disperse throughout their range in the Keys, past work showed that they generally exhibit relatively small home-ranges (mean 95% core area of 0.3 km^2 for females, 0.88 km^2 for males; Lopez, Silvy, Labisky, & Frank, 2003). Therefore, it is unclear whether previous sampling schemes were representative of the overall population or a limited population segment. Further investigation of the effects of urbanization is merited across the full distribution of key deer, i.e., from urban edges to more remote areas within protected lands.

To advance our understanding of key deer ecology and the broader ecology of prey in the context of urbanization, we used remotely triggered camera traps to survey key deer throughout the extent of protected areas on Big Pine Key and evaluate behavior (detection rates, group size, and activity patterns) at different distances from urban areas. Based on previous work summarized above, we formed three predictions: 1) rates of key deer site use are not affected by proximity to urbanization because they are without predators (i.e., prediction of the human-shielding hypothesis); 2) key deer group sizes increase with proximity to urbanization due to a concentrating effect from anthropogenic resource subsidies; and 3) key deer activity patterns shift to be more nocturnal closer to urbanization to avoid diurnal peaks in human activity.

2. Methods

2.1. Study area

The National Key Deer Refuge is located on Big Pine Key and No Name Key in Monroe County, Florida, USA, and is managed by the United States Fish and Wildlife Service (hereafter: USFWS). It contains approximately 35 km^2 of land distributed among variably sized tracts and interspersed with urban private property and commercial centers (i.e., human development). Our study was restricted to the approximately 24 km^2 of refuge land on Big Pine Key. Herein we use the terms urbanization and development interchangeably to refer to areas within the Big Pine Key land cover matrix where humans live or have built infrastructure. The remaining non-urban areas are predominantly federal or state owned but do include some undeveloped private lands. Habitat in the Keys follows an elevational gradient from coastal lowland (e.g., scrub mangrove *Rhizophora mangle* habitats and buttonwood *Conocarpus erectus* transition areas) and freshwater marsh (e.g., *Cladium* spp.), to upland hardwood hammock (e.g., *Metopium toxiferum; Bursera simaruba*) and pine rockland (*Pinus elliottii*) at the highest elevations.

2.2. *Camera trapping data collection*

From 16 January through 4 April 2013 we conducted a camera trap survey of 15 trap-nights at each of 112 sites in the National Key Deer Refuge on Big Pine Key. We randomly identified 56 locations (28 each in the northern and southern half of the refuge, respectively) from a 300-meter grid overlaid on refuge land, making minor adjustments in the field to optimize animal detection rates (e.g., selecting natural funnels). We actively selected the second set of 56 locations in an adaptive resampling approach based on mesopredator detections from the first survey for a total of 112 camera sites. Further details about sampling design were previously published, but site selection was unbiased for key deer as they were camera trap 'bycatch' (Cove, Gardner, Simons, Kays, & O'Connell, 2018; Cove, Gardner, Simons, & O'Connell, 2018). At each location, we placed two trail cameras (Reconyx PS800 or PC850) opposing each other at an approximate height of 0.25 m, affixed to trees or rocks. To minimize count inflation, we counted groups of deer as a single detection (noting group size) and discarded captures that occurred within an hour of the last recorded detection, except when easily determined to be distinct (via, e.g., pelage patterns, antlers, or unique marks). Thus, patterns in detection rates were not necessarily related to patterns in group size.

2.3. *Intensity of site use models*

Camera trap detection rate (i.e., number of detections in a sampling period) is commonly used to assess intensity of site use and relative abundance of a variety of species and was recently determined to be an effective measure to quantify deer use of sites (Parsons et al., 2017). We used a model comparison approach to determine if distance from urbanization was a supported model term predicting deer detection rates. We also considered three other covariates that likely influence site use (explained below).

We considered 15 generalized linear models based on hypotheses for the factors influencing key deer site use. The response variable was total detections per site, and we used a negative binomial distribution to model overdispersion in the response (mean = 26.1; variance = 561). The negative binomial distribution entails the estimation of a dispersion parameter, θ (theta). We considered all potential model structures for three predictor variables and their possible interactions, plus the null model (no covariates); this yielded 15 models. We only included models with interactions in subsequent model comparison if interactions were significant ($p \leq 0.05$). This resulted in 10 candidate models for comparison (Table 1).

Predictor model terms included a trapping site's linear distance from development, LiDAR-derived elevation, and a binary predictor denoting whether the camera site was on a human-constructed trail. For site elevation, we used the mean digital elevation map (DEM) value within a 25 m buffer around the site coordinates to reduce bias from the specific sampling microsite. Distance and elevation data for detection rate models and subsequent analyses were obtained from USFWS land cover data, associated with sampling locations using GIS, and scaled to z-scores for coefficient comparisons.

We fit all generalized linear models with program R (R Core Team, 2018) using package MASS (Venables and Ripley, 2002). We ranked model performance by AICc score and Akaike weight (Liddle, Mukherjee, & Parkinson, 2009) using the package bbmle (Bolker & R Development Core Team, 2020) and assessed explanatory power for top-performing models by calculating pseudo R^2 values using Nagelkerke's method (Nagelkerke, 1991). We note that although we use p-values to evaluate interaction terms and report p for model coefficient estimates, these values should be interpreted with caution after AIC model selection. To illustrate potential interactions of interest in models of detection rates or group size (below), we used the top-ranking model to predict the response with a mock dataset generated by varying interacting covariates and keeping other covariates constant at their mean or reference level. Given an interaction including distance from development, we first refit the model without z-correcting this term to display the interaction effect on the raw scale and then predicted the response evenly over its range (n = 43). For an interaction with binary trail, we predicted the response at each level (0 or 1), and for elevation we used five different values: the mean elevation and two increments of a half standard deviation in either direction from the mean.

Table 1
Selection statistics for 10 negative binomial generalized linear models predicting key deer detection rates from camera trapping surveys in the National Key Deer Refuge on Big Pine Key, FL, USA (January–April 2013). An asterisk within a model structure denotes an interaction effect and a 1 represents the null model. Distance from human development is denoted by develop. ΔAICc is the difference in AICc score, ω is the Akaike weight, K is the number of parameters estimated, and LL is the log likelihood. All models included an estimate for the negative binomial dispersion parameter, θ.

Model	ΔAICc	ω	K	LL
develop * trail + elevation	0	0.349	6	−466.3
develop + elevation	1.0	0.213	4	−469.0
develop * trail	1.3	0.184	5	−468.1
develop + trail + elevation	2.1	0.123	5	−468.5
develop	3.2	0.069	3	−471.2
develop + trail	4.8	0.031	4	−470.9
trail + elevation	6.7	0.012	4	−471.9
elevation	7.0	0.011	3	−473.1
1	8.6	0.005	2	−475.0
trail	9.0	0.004	3	−474.1

2.4. *Group size models*

Whereas detection rates provide inference into site use and potentially relative abundance (Parsons et al., 2017), group sizes per detection represent a key social behavior. We calculated group size for each detection by recording the number of individual deer in a photo sequence. Two sites were not considered because they had no deer detections. For modeling purposes, we scaled the response variable by subtracting 1 so that the minimum response value was 0, thus representing a response distribution suitable for models of count data. We used a negative binomial distribution to model overdispersion (mean = 0.127; variance = 0.187). We report results based on this scaled response but scaled back (adding 1 to predicted response values) to generate figures illustrating interaction effects.

In a parallel process to detection rate analyses, we fit and ranked generalized linear models using the same three predictor terms with the MASS package in program R, except for these models the response was group size per detection. Because more interactions were significant (than for detection rate models), we arrived at 14 candidate models out of the 15 possible structures (Supplementary Table 1). We again ranked model performance by AICc score and Akaike weight with the R package bbmle (Bolker & R Development Core Team, 2020). As in detection rate models, we scaled continuous covariates (elevation and distance from development) to z-scores and present associated coefficient estimates.

2.5. *Comparing activity patterns*

To evaluate the relationship between key deer activity patterns and distance from developed land cover, we quantified overlap in patterns of activity (i.e., distribution of detection times; Lashley et al., 2018) between deer at urban versus non-urban locations. We designated a subset of sampling sites as either urban or non-urban based on their proximity to the nearest developed land (as designated by USFWS land cover data) plus a 100 m buffer. Camera sites within 200 m of buffered urban land cover were considered urban and locations greater than 500 m away were considered non-urban. We excluded other sites between 200 m and 500 m from development. Although these distance delineations were in effect arbitrarily designated, they integrate considerations from our camera trapping array and key deer home range size (Lopez, Harveson, Peterson, Silvy, & Frank, 2005) to allow us to evaluate an effect of urbanization on diel activity.

We used the R package overlap (Ridout & Linkie, 2009) to compare activity patterns for the urban and non-urban sites. In this approach the camera trap images (i.e., detection times) are considered random samples from continuous distributions and activity patterns are determined by applying kernel density estimates for each group of data. Subsequently a coefficient of overlap (Δ) is calculated that falls between 0 and 1 (i.e., zero to complete overlap).

3. Results

3.1. Factors predicting intensity of site use

The camera trapping survey resulted in 2927 unique key deer detections. The top-ranking model (lowest AICc) included a term for site elevation and an interaction between trail (on/off) and distance from development. This top model received 35% of the AICc model weight (Table 1) and had a pseudo R^2 value of 0.14. The second ranked model, including terms for distance from development and elevation, received 21% of the AICc weight ($R^2 = 0.10$). The third ranked model contained an interaction between distance from development and trail but no elevation term; it received 18% of the weight ($R^2 = 0.12$). The remaining AICc weight was primarily distributed among three models receiving between 12% and 3%, while the final four models had 1% or less. Because we are interested in testing for an effect from variables of interest (not making specific model predictions), we focus on just the most supported model for interpretation and disregard the other nine.

In the top-ranking model fit (Table 2) the most influential term (i.e., largest z-corrected coefficient estimate) was an interaction between distance to development and trail ($p = 0.032$). Detections increased further from urbanization, and this increase was accentuated on trails (Fig. 1). The model term with the second largest effect on detection rates was elevation; it showed a positive association with detection rates, however the confidence interval for the coefficient estimate overlapped zero by a small margin ($p = 0.051$). The main effects for distance from development and trail were less influential, with confidence intervals that overlapped zero more substantially ($p > 0.1$). The estimate for the negative binomial dispersion parameter (θ) within the top model was 1.77 ± SE 0.24.

3.2. Factors predicting group size

Mean group size for the 2927 detections was 1.13 ± 0.43 SD. The top-ranking model of group sizes included a term for trail and an interaction between elevation and distance from development. This model received 99% of the AICc weight and had a pseudo R^2 value of 0.043. The second-ranking model contained a term for distance from development and an interaction between elevation and trail, but only received 1% of the AICc weight ($R^2 = 0.037$). All other models were below 0.1% (Supplementary Table 1). We again focus on just the most supported model by AICc score.

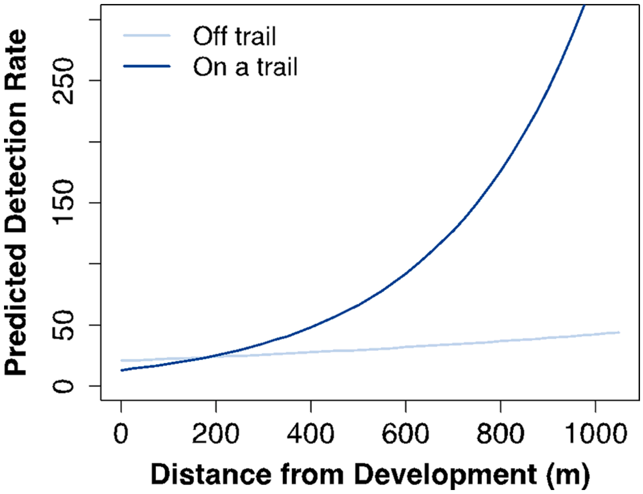

Fig. 1. The association between distance from human development and key deer detection rates was contingent on whether a sampling site was on a trail. The interaction between these factors suggests that detections increased much more on trails, compared to off, with increasing distance from development. We used our top-ranking model fit to predict detections per sampling period both on and off trails, while varying distance and setting elevation to its mean. Data were collected via camera trapping surveys in the National Key Deer Refuge, FL, USA, over January–April 2013.

In the top model fit (Table 3), trail had the strongest effect on group size, showing a positive relationship as group size increased on trails. There was also a significant interaction between elevation and distance from development ($p < 0.001$), suggesting that as distance from development increased at low elevations, group size remained relatively consistent, but at high elevations group size decreased (Fig. 2). The main effects for distance from development and trail were significant ($p < 0.01$), and group size declined as these terms increased. The estimate for θ was 0.403 ± SE 0.072.

3.3. Activity pattern overlap

We quantified urban and non-urban key deer activity patterns based on 940 detections in 63 urban sites and 578 detections in 6 non-urban sites. The coefficient of overlap (Δ) was 0.867. Activity patterns observed at both site types were strongly crepuscular overall (Fig. 3). There were three notable differences between the two patterns that accounted for the 13% difference. First, deer at non-urban sites exhibited a later and less pronounced morning activity peak but a more

Table 2
Model fit results for the top-ranking model of key deer detection rates. Rates were derived by counting detections from camera trapping surveys at each of 112 sites in the National Key Deer Refuge, FL, USA, over January–April 2013. The negative binomial dispersion parameter estimate (θ) was 1.77 ± SE 0.24. Bolded p values are significant ($p \le \alpha = 0.05$).

Coefficient	Estimate	SE	p
intercept	3.19	0.081	**<0.001**
develop	0.123	0.081	0.13
elevation	0.149	0.076	0.051
trail	0.0743	0.20	0.71
develop*trail	0.436	0.20	**0.031**

Table 3
Model fit results for the top-ranking model of key deer group size. A group size was assigned to deer detections from camera trapping surveys at each of 112 sites in the National Key Deer Refuge, FL, USA, over January–April 2013. The negative binomial dispersion parameter estimate (θ) was 0.403 ± SE 0.072. Bolded p values are significant ($p \le \alpha = 0.05$).

Coefficient	Estimate	SE	p
intercept	−2.27	0.075	**<0.001**
develop	−0.309	0.064	**<0.001**
elevation	−0.184	0.066	**0.005**
trail	0.654	0.14	**<0.001**
develop*elevation	−0.416	0.077	**<0.001**

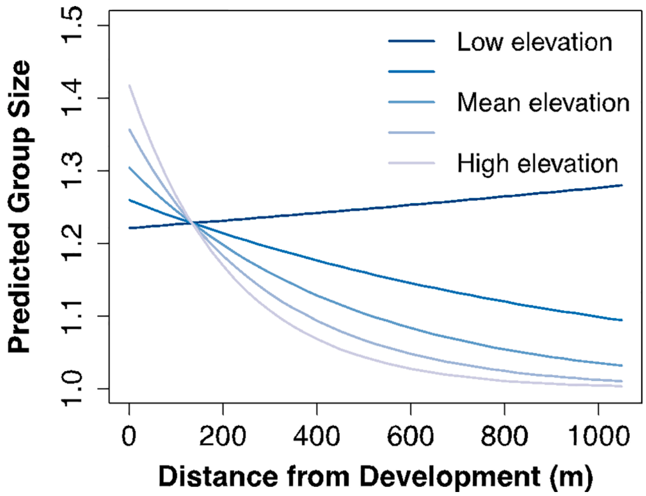

Fig. 2. The relationship between predicted key deer group size and distance from nearest human development was dependent on elevation. An interaction between these terms suggests that group size declined with distance from development, except in low elevation sites. We compared models and used the top-ranking fit to predict group size at five different elevation scenarios evenly spanning two standard deviations, varying distance and setting the model term for trail constant at 1 (on a trail). Data were collected via camera trapping surveys in the National Key Deer Refuge, FL, USA, over January–April 2013.

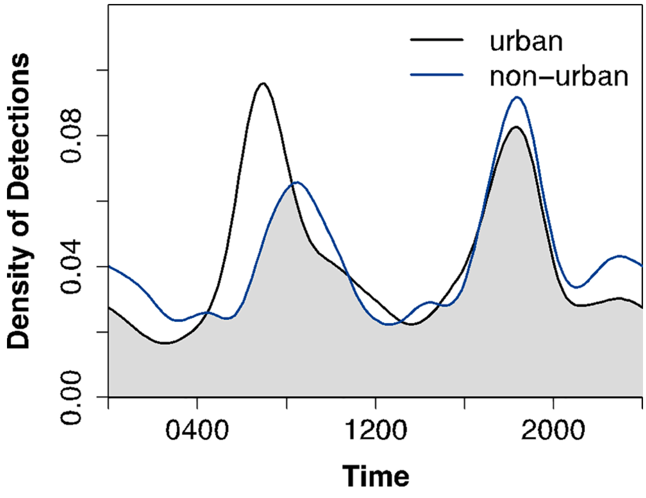

Fig. 3. The overlap in diel activity patterns between urban and non-urban key deer is shown in gray, comparing respective density plots for detection timestamps from camera trapping data. Urban deer were detected at camera trap sites within 200 m of urban land cover, while non-urban deer were detected greater than 500 m away. The coefficient of overlap (Δ) for the crepuscular curves was 0.867. Data were collected via camera trapping surveys in the National Key Deer Refuge, FL, USA, over January–April 2013.

pronounced evening peak within the bimodal crepuscular structure. Second, non-urban deer showed minor increases in activity preceding their major morning and evening crepuscular peaks. Third, non-urban nocturnal activity was higher overall.

4. Discussion

4.1. *Intensity of site use*

We predicted that intensity of key deer site use would not vary with proximity to urbanization. However, we found that site use did vary, and the relationship was contingent on whether a given site was on a human-constructed trail. Illustrating this interaction showed a pattern of intensity of site use increasing further from development (i.e., irrespective of trails; Fig. 1), which runs counter to previous surveys utilizing other methodologies in the Keys (e.g., Harveson et al., 2007; Peterson et al., 2005). These studies concluded that key deer were becoming more "urbanized," but our camera trapping survey does not support that inference. Rather, the patterns in intensity of site use that we observed reflect possible human avoidance. This result also sheds light on the hypothesis that prey use urban areas as human shields against predation. In a system in which non-human predators have been largely absent for ~ 4000 years, we in effect found support for the human-shielding hypothesis—absent predation risk, intensity of site increased away from urban areas, despite the availability of human resource subsidies (Peterson et al., 2005). The logical basis for the human-shielding hypothesis is that the direct threat posed by predators theoretically outweighs the threat posed by humans in and around urban areas (Geffroy, Samia, Bessa, & Blumstein, 2015). Key deer present a model that removes predators from this equation, and our results suggest that the threat of humans may shift site use to more remote areas within protected lands.

As deer detections increased further from development, this increase was much more pronounced on human trails (Fig. 1). Maintained trails are typically clear of visual obstruction, and therefore this result may be influenced by camera detection bias (Kolowski & Forrester, 2017). However, trails represent a path of least resistance and are commonly used across taxa on Big Pine Key (Cove, Gardner, Simons, & O'Connell, 2018). Key deer may also follow this pattern and utilize trails to decrease energy costs in movement. Energetic concerns are especially important for lactating female deer, a seasonal state when conserving energy is critical (Lashley et al., 2015). The result of lower deer detection rates on trails closer to development is parsimoniously explained by avoidance of humans, as trail use by humans is likely highest closest to urban areas. Extending this logic, higher detection rates on trails further from development may be due to deer taking advantage of these cleared corridors given a reduced need to avoid human interactions. Although elevation did not have a statistically significant effect on intensity of site use, the positive relationship between elevation and detection rate may be interpreted as biologically significant and is consistent with previous work suggesting that upland areas (e.g., hardwood hammock and pine rockland) are preferred habitats for adult key deer (Jacobs, Lashley, & Cove, 2021; Lopez et al., 2004).

4.2. *Group size*

Our prediction that group size would increase closer to urbanization was largely supported by the data, but with interesting nuance as we observed an interactive effect between distance from urbanization and elevation. Group sizes were greatest in high elevation areas closest to development. As distance from development increased, group size markedly declined in higher elevations but remained relatively consistent at low elevations (Fig. 2). Group size is likely limited in remote, higher elevation habitats because they are less productive and/or overbrowsed compared to lower elevation sites that feature dense grasses and other vegetative cover. A negative main effect for elevation lends support to this idea, suggesting that overall, group sizes were lower in higher elevation habitats.

The larger group sizes in high elevation areas closer to development are most likely explained by adjacent resource supplementation, both unintentional (e.g., via lawns, ornamental plants, and artificial water sources) and intentional (e.g., illegal feeding and watering). Anthropogenic activity in the Florida Keys is concentrated in high elevation areas away from sea level, and thus associated resource supplementation may concentrate deer that occur near urban areas at these higher elevations. While group size is inversely correlated with vigilance, such that increasing group size allows relaxed vigilance in proximity to predators (Lashley et al., 2014), the continued "domestication" of key deer aligns more with the prediction that certain deer habituate to humans and increasing group sizes are driven by a reliance on subsidies (Peterson et al., 2004), not necessarily vigilance against humans.

The observation that group size did not decrease further from development at low elevations presents an interesting scenario that merits further study. One explanation is that low habitats are consistently undeveloped, contain natural water and food resources, and provide more understory cover that deer use for protection for fawns or young of the year (Jacobs, Lashley, & Cove, 2021). Our top model additionally suggested a positive association between grouping behavior and human-constructed trails. Camera detection bias may explain this relationship to some degree, but human paths are generally easier for a group of deer to travel than natural corridors.

Grouping activity around human development and associated resource provisions may have the potential to facilitate disease spread. Lumpy jaw (see Fagan, Oosterhuis, & Benirschke, 2005) is present in the key deer population and can spread via common feed sources, and infectious diseases and parasites represent sources of key deer mortality (Nettles et al., 2002). Elevated grouping behavior in urban areas may have also contributed to the high key deer mortality associated with the outbreak of Neotropical screwworm (*Cochliomyia hominivorax*) in 2016–2017 (Skoda, Phillips, & Welch, 2018). Resource provisioning that aggregates multiple species, and thus elevates rates of intraspecific interaction, could further complicate disease dynamics between vectors since baiting has been shown to increase mesopredator parasite loads (Brookshire, Dykstra, Loftin, & Lashley, 2020; Cove, Maurer, & O'Connell, 2017).

4.3. Activity patterns

We predicted that key deer activity patterns would shift to be more nocturnal closer to urban areas to avoid diurnal human activity. This prediction was not supported by our results and, rather, we observed relatively similar crepuscular deer activity patterns at both putatively urban and non-urban camera trapping sites (Fig. 3). Yet, key dissimilarities provide insight into the effects of urbanization. Deer observed furthest from human development exhibited a later and reduced morning activity peak but a more pronounced evening peak, showed slight increases in activity preceding crepuscular peaks, and displayed slightly higher overall nocturnal activity—opposite from our predictions. Notably, this pattern is not consistent with predictions that wildlife exhibit more nocturnal activity when in closer proximity to humans due to temporal avoidance (Gaynor et al., 2018), but may reflect the consequences of key deer habituation to humans in developed areas.

It has been suggested that crepuscularity is an antipredator behavior (Caro, 2005; Loe et al., 2007). Given a subtropical daily thermal environment combined with a longstanding lack of predation risk, we may have predicted heightened key deer nocturnality in general, and particularly as compared to white-tailed deer populations subject to predation risk in more temperate regions. However, key deer activity patterns did not strongly differ from other populations co-occurring with predators and hunting (e.g., Biggerstaff et al., 2017; Lashley et al., 2018). In fact, the crepuscular signature for key deer activity patterns may be stronger. Our findings therefore contrast with the idea of crepuscularity as an antipredator strategy and may suggest an alternative mechanism underlying this activity pattern in white-tailed deer. Key deer behavior could highlight the trade-off between thermoregulation (i.e., avoiding peak temperatures) and daily photic conditions to find optimal forages. Further examination of deer activity patterns more broadly is merited for further inferences into underlying mechanisms.

4.4. Caveats and considerations

Our camera trapping study was the first systematic survey of the National Key Deer Refuge on Big Pine Key. However, one limitation of our work is that it provides only a snapshot of key deer behavior, with observations from one season in one year. Thus, it is possible that differences between our results and previous work could be explained by seasonal variation in behavior. Although Jacobs, Lashley, & Cove (2021) present corroborating patterns from camera trap surveys conducted later in the spring season (when fawns are dropped) in a different year, we nonetheless suggest that further work is needed to parse out dynamics and underlying mechanisms in other seasons when behaviors change (e.g., the rut) or when habitat and climate are limiting factors (e.g., during the summer when most lowland sites are flooded and daytime temperatures are high). We additionally note that the original purpose of our surveys was to detect mesopredators and small mammals (Cove, Gardner, Simons, & O'Connell, 2018). Although this makes the data collection largely unbiased for key deer detections, we did have a high incidence of cameras placed along trails to detect free-roaming cats. It is unclear how this affects our key deer inferences, and while we accounted for an effect from trails with model terms, future surveys might benefit from evenly sampling sites on and off trails to revisit this relationship.

Another takeaway from our study is that although our data revealed important relationships between urbanization and key deer behavior, our top-performing models lacked substantial explanatory power overall. Pseudo R^2 values for models of intensity of site use and group size suggest that we were able to explain approximately 14% and 4% of the variance in those response variables, respectively. While this does not necessarily limit inference into effects from urbanization, it does suggest that a multitude of unconsidered factors likely drive behavioral variation in this system. For example, all explanatory covariates that we considered were site-level spatial variables, and future work would benefit from exploring temporally dynamic factors related to weather, climate, or deer biology.

Our results present interesting considerations for the management of white-tailed deer in other areas. Big Pine Key represents a kind of microcosm in which we could study the behavior of key deer throughout a large percentage of their distribution. Such spatial coverage is difficult to achieve in other, non-insular locations, which may be why key deer have become a model for studying the effects of urbanization on white-tailed deer. The applicability of our findings to other systems depends on context. The decline of apex predators (Estes et al., 2011) suggests a scenario in which deer may occur without predation risk more frequently, and thus deer behavior in relation to urbanization may change to resemble that documented in our study. Further research is needed to determine how medium predators like coyotes factor into this scenario, as they may influence behaviors but present less risk and tend to utilize urban areas more readily than apex predators (Bragina et al., 2019; Gallo, Fidino, Lehrer, & Magle, 2019; Jones et al. 2016). Potential future scenarios also include the recolonization of historical habitats by apex predators, such as puma (*Puma concolor*; e.g., Thompson & Jenks, 2010). Our findings provided support for the human shield hypothesis, underscoring the possibility that deer will further encroach upon urban areas when apex predators appear in adjacent lands. Finally, an extreme scenario of future urbanization for some regions will entail land conversion whereby protected habitat "islands" exist within an urban matrix. Our study of the island-dwelling and predator-free key deer may provide insight into ungulate and prey behavior in such contexts.

5. Conclusions

Our examination of site use, group size, and activity patterns for the key deer revealed valuable information with relevance for planning and managing land use. We summarize this information below in four points.

(1) Human-constructed trails in protected areas (and likely in undeveloped areas generally) can be important animal movement corridors and may increase wildlife use of areas containing such pathways. Landscape planners should consider this dynamic, e.g., when configuring greenway and back country trail designs.

(2) In the absence of top predators, patterns in key deer intensity of site use seem to reflect human avoidance. As urbanization increases in the future, the human shield hypothesis will likely garner more attention in urban planning. Our observations in predator-free Big Pine Key contrasted with patterns expected via the human-shielding hypothesis (i.e., that prey utilize urban environments to avoid predators), thereby lending support to this theory. Future research can build on inferences into site use made here, e.g., by quantifying the relationship between true abundance and proximity to urbanization.

(3) Crepuscular activity rhythms in deer may be broadly consistent, irrespective of predation and urbanization. Further research is merited in this area, but our data revealed only minor deviations in activity close to urbanization, including unexpected lower nocturnality relative to remote areas, and an overall crepuscular signature comparable to or exceeding that of populations with predators (e.g., Lashley et al., 2018). This information is relevant to temporal aspects of landscape and urban planning, such as transportation planning in the context of deer-vehicle collisions.

(4) Our results suggest that human-derived resource subsidies (i.e., forage and water) are strongly at play in shaping the grouping behavior of wildlife in protected areas adjacent to urban landscapes. Increased group sizes around urban areas may bias perceptions that deer are more common around anthropogenic land use. Managers may consider strategies to mitigate subsidy availability and proximity to reduce wildlife interactions and curb possible disease spread. Potential strategies include broader policy and local ordinances, but also education and outreach campaigns geared toward eliminating intentional resource subsidies and reducing unintentional resources for prey populations.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2022.104391.

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