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Urban Ecology Section – Behavioral adaptations to life in the city

Vigilance response of a key prey species to anthropogenic and naturogenic threats in Detroit

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Abstract

Rapid urbanization coupled with increased human influence induces pressures that affect predator-prey relations through a suite of behavioral mechanisms, including alteration of avoidance and coexistence dynamics. Synergisms of natural and anthropogenic threats existing within urban environments exacerbate the necessity for species to differentially modify behavior to each risk. Here, we explore the behavioral response of a key prey species, cottontail rabbits (*Sylvilagus floridanus)*, to anthropogenic and naturogenic pressures in a human-dominated landscape by examining their vigilance levels in green spaces within the city of Detroit, Michigan. We conducted the first camera survey in urban parks throughout Detroit in 2017-2020 to assess vigilance behavior corresponding to a heterogeneous landscape of risks stimulated by humans, domestic dogs, and a natural predator, coyotes (*Canis latrans*). We predicted a scaled response where cottontail rabbits would be most vigilant in areas with high coyote activity, moderately vigilant in areas with high domestic dog activity, and the least vigilant in areas of high human activity. From 8,165 independent cottontail rabbit detections in Detroit across 11,616 trap nights, one-third were classified as vigilant. We found no significant impact of humans or coyotes spatial hotspots, but vigilance behavior in rabbits significantly increased in hotspots of high activity from domestic dogs. We found little spatial overlap between rabbits and threats, suggesting rabbits invest more in spatial avoidance; thus, less effort is required for vigilance. Our results elucidate strategies of a prey species coping with various risks to advance our understanding of the adaptability of wildlife in urban environments. In order to foster safe and positive interactions between people and wildlife in urban greenspaces, we must understand and anticipate the ecological implications of human-induced behavioral modifications.

Introduction

The 20th and 21st centuries have seen unprecedented population growth and expansion of cities, with 60% of the global population expected to live in urban centers by the year 2030 (United Nations, 2018). Urbanization coupled with other increased anthropogenic pressures has fundamentally changed ecosystems worldwide (Foley et al 2005, Grimm et al 2008, Pickard et al 2017). Cities fragment natural habitats to restrict gene flow, change species assemblages, and alter the behavior of animals and people alike (Romano 2002, Tigas et al 2002, Crooks et al 2004, Lowry et al 2013, Johnson and Munshi-South 2017). These changes in the environment further have implications for the wildlife that co-occur with humans and a myriad of ecological interactions including predator-prey relationships.

Non-consumptive fear effects induced by humans are pervasive in urban environments and drive behavioral changes in wildlife (Ciuti et al 2012, Gaynor et al 2018). For example, eastern grey squirrels (*Sciurus carolinensis*) in New York City have become sensitive to human movements and show behavioral plasticity in their ability to adjust flight initiation distance based on human activity (Bateman and Fleming 2014). Exposure to human audio cues reduced foraging time and increased the amount of time spent being vigilant in badgers (*Meles meles*) in Great Britain as compared to exposure to non-human predator audio cues (Clinchy et al 2016). Behavioral plasticity in predator and prey species alike directly influence their ability to avoid and coexist with intense human pressures in urban centers (Muhly et al 2011, Lowry et al 2013). While prey modify their behavior to avoid attempted predation, predators modify their behavior to account for prey behavior and to increase the likelihood of success of their predation attempts. Specifically, prey are forced to modify their behavior spatially or temporally to avoid threats from humans as well as associated domestic animals or natural predators (Fenn and Macdonald

1995, Gliwicz et al 2008, Reilly et al 2017). Modification of behavior has therefore become necessary for the survival of both predators and prey in urban environments, as risks govern behavior (Lima 1998). However, despite the recent burgeoning of urban ecology studies, how humans and domestic animals alter mammalian vigilance behavior remains understudied.

Highly adaptable species and those with relatively smaller body sizes are more successful at coexisting with humans in urban areas (Bateman and Flemming 2012). Carnivores, particularly large bodied carnivores, have historically faced intense persecution from humans (Munoz-Fuentes et al. 2010). Large predators depredate livestock and compete with humans for resources including space and prey, often resulting in humans employing lethal interventions (Mech 1995, Witmer and Whittaker 2001, Treves 2003, Muhly and Musiani 2009). However, many mid to small-sized predators are able to exist successfully in areas of high anthropogenic influence (Wilkinson and Smith 2001, Ikeda et al 2004). In particular, coyotes (*Canis latrans*) have adapted to living with humans in part, by exploiting anthropogenic food subsidies and shifting diurnal movement in response to human disturbance (Kitchen et al 2001, Gese and Bekoff 2004). This, in conjunction with wide extirpations of the grey wolf (*Canis lupus*), has allowed coyotes to expand their range to the entirety of the United States beyond previous restrictions to the central and western portions of the country (Crooks 1999, Hody and Kays 2018). These ecological and behavioral changes in carnivores can have cascading effects on their prey species, subsequently altering their behavior.

Concurrent with predators employing strategies for coexistence, their prey must also mitigate risks in human dominated landscapes. Threats for prey species in urban environments are often exacerbated by multiple sources including direct mortality from natural and anthropogenic sources. Prey may employ similar strategies to mitigate risks from humans as they do to mitigate risks from natural predators (Frid and Dill 2002). As such, fear effects in urban environments can result in prey modifying temporal activity or habitat selection to reduce predation risks (Chambers and Dickman 2002, Dowding et al. 2010). In a dynamic landscape full of risks, prey species must differentiate risk-levels and respond in accordance with the most immediate and fatal considerations inducing the strongest anti-predator strategies. Such discernment requires delegating time to vigilance in order to assess and respond to risks across the landscape while also fulfilling reproductive needs. However, there are tradeoffs because more time spent being vigilant means less time foraging, mating, and performing other behaviors like grooming (Quenette 1990). Environmental conditions including vegetation height, tree cover, and the distribution of water sources can interact to produce varying levels of predation risk and thus influence the amount of time prey spend being vigilant (Scheel 1993, Tchabovsky et al 2001).

Cottontail rabbits (*Sylvilagus floridanus*) are a key prey source for many mammalian carnivores as well as avian predators and occasionally snakes in urban environments throughout the United States (Beasom and Moore 1977, Litvaitis and Shaw 1980, Wittenberg 2012). Cottontail rabbits have high reproductive rates that result in rapidly growing populations that interact, directly or indirectly, with humans in gardens, yards, parks and other green spaces throughout city limits (Hunt et al 2014, Baker et al 2015). We conducted a non-invasive camera survey to investigate the vigilance behavior of rabbits in response to anthropogenic and natural threats. Our work occurred throughout Detroit, the largest city in Michigan, located in the Great Lakes region of the USA from 2017-2020. Here, we delineated human, coyote, and domestic dog risk zones to detect differences in cottontail vigilance response and investigated the potential factors influencing vigilance.

The gray squirrel (*Sciurus carolinensis*), another common urban prey species, is less wary of humans in areas more densely populated by humans as opposed to areas less densely populated by humans (Parker and Nillon 2008). Therefore, we expect a similar level of acclimation in cottontail rabbits where they are less vigilant in areas heavily populated by humans. Because of the similarities in body size and behavior between domestic dogs and coyotes, we anticipate rabbits will show more vigilance in areas with high domestic dog presence than areas with high human presence. However, as domestic dogs are generally associated with humans, we expect the response to dogs to be less dramatic than the response to coyotes. Therefore, we expect a scaled response where rabbits will be least vigilant in areas with high human activity, with vigilance response increasing slightly in the areas with high domestic dog activity, and the most vigilance being displayed in areas of high coyote activity, as coyotes are an actual formidable predator of rabbits (Figure 1).

Materials and Methods

Study Site

We implemented a systematic camera survey throughout metro parks in Detroit, the largest city in Michigan covering 359.2 km^2 of land (Figure 2). The declining city holds a human population of 672,000 people with an average density of ~5,144 people per square mile (U.S. Census Bureau, 2016). The Detroit metro park system contributes to the green space and available habitat for wildlife within the city. All 28 total parks sampled within the city are intrinsically impacted (whether directly or indirectly) by humans and are embedded within an urban matrix including roads, neighborhoods, and buildings. The parks range in size from ~0.016 - 4.79 km^2 with varying levels of vegetation and human influence. In Detroit, the largest native carnivore present is the coyote. However, domestic dogs are also present and may exert pressures on the coyote's natural prey species such as rabbits.

Data Collection/Camera Survey

We deployed unbaited, remotely triggered cameras (Reconyx© PC 850, 850C, 900, 900C) throughout city parks to monitor the wildlife community from October – March in 2017-2020. Placement within the parks was determined based on evidence of wildlife presence and vegetation type. Park size determined the number of cameras deployed, ranging from 1-7 cameras. For parks with multiple cameras, we deployed cameras with a minimum distance of 500m between individual cameras. Cameras were affixed to medium sized trees approximately 0.5-1m off of the ground. Cameras were programmed to take three images when triggered at high sensitivity with one second between each image and a 15 second quiet period. Every image was independently sorted and confirmed by at least two members of the Applied Wildlife Ecology Lab at the University of Michigan. We only used images confirmed as rabbit as well as their associated threat species of interests: humans, domestic dogs, and coyotes. Team members were excluded from human images.

Hotspot Analysis

To determine the level of risk from each of our three potential predator focal species, we calculated kernel density to identify significant hotspots of activity using ArcMap (v. 10.6.1). The resultant heat map indicated areas of high occurrence for coyotes, domestic dogs, and humans. We then overlaid kernel density values for each threat with hotspots for rabbits to calculate the relative overlap. Finally, using the Getis-Ord-GI* statistic, we tested for significant overlap of kernel densities at a camera level to signal spatial avoidance. Evidence of spatial avoidance may represent a sufficient evasion strategy that necessitates less vigilance behavior.

Vigilance Scoring

We extracted behavioral information from images in order to quantify vigilance response in cottontail rabbits. For each image containing a rabbit, we scored vigilance based upon the position of the body and head (Figure 3). For images with two individuals, each individual was given its own classification and counted as independent from other individuals in the image. Rabbits were considered "vigilant" if their head was in an upright position; while "non-vigilant" was assigned when their head was down in a foraging position. For images where the rabbit did not display an obvious head up or head down stance, we used six other classifications: moving, active, eating, sniffing, out of frame, and unknown. "Moving" included any rabbit in motion, which was often indicated by motion blur in the images. We considered moving to be a potential indicator of vigilance as it could denote rabbits leaving an area due potentially to a detected threat. "Sniffing" included rabbit attention turned to monitoring an aspect of its environment with its head up such as sniffing twigs. Because we are investigating the impact of canid species on rabbit behavior and canids often mark their territory (Bowen and Cowan 1980), we considered sniffing to potentially indicate vigilance as it is a show of risk assessment. "Active" was used for activity where the animal's attention was pointed inward at themselves. This included any rabbits scratching, licking, or otherwise attending to their fur, this also included stretching. "Eating" was used in the event that a rabbit had its head up, but clearly had vegetation in its mouth or the image series showed it chewing. Although both active and eating involve attention being pointed inward at the rabbit, we did not include them as non-vigilant in our analysis as we could not confirm non-vigilance. “Out of frame” included any images where the rabbit exited the frame of the picture and nothing was in the image. Images that were sorted as out of frame were removed from the data set and not counted in the final total. Finally, “unknown” was used for rabbits where only parts of the whole body were in the picture, the head was too blurry to determine, or if the body position could not be determined for any other reason. Unknown photos were not removed from the final total. Each individual was only designated one category per each image in which it appeared. All images with rabbits present were used to best estimate the amount of time actually spent in front of the camera at the particular station. We only used photos where rabbits were in the frame, meaning our photos are estimates of time spent in frame. Each image was scored independently for vigilance by at least two members of the Applied Wildlife Ecology Lab at the University of Michigan. Any discrepancies that were not resolved resulted in classifying the image as unknown.

We calculated multiple metrics of vigilance as a response variable to each risk factor. Initially, we used the raw number of images classified as vigilant per camera. Our second measure of vigilance was the ratio of vigilant photos to the total number of photos. This was used as a proxy for the relative amount of time spent being vigilant at each camera. For both these metrics, we expanded the classification of vigilant beyond head up versus head down and included moving and sniffing as vigilant. We used the total raw counts for these combined categories as well as the ratio of those categories out of the total number of detections as our “vigilant” response variable.

Statistical Analysis

We used negative binomial generalized linear models (GLM.nb) to determine which factors best explained cottontail rabbit vigilance. We used results from the hotspot analysis to identify locations of significant high use based on kernel density estimates from detection data to categorize threat levels for humans, domestic dogs, and coyotes. This resulted in a binary explanatory variable indicating whether a hotspot was presence or absence for each threat. We also included environmental and abiotic factors in our analysis. Distance from each camera station to water sources (WATER), to roads (ROADS), and the area of each park (AREA, in acres) was calculated using ArcMap. Understory cover (VEG) was quantified as a binary variable of whether trees, tall shrubs or bushes, but not grass were present or not in the field of view at the camera level.

Support for models was evaluated using Akaike's Information Criterion (AICc) to select top-performing model (Δ AIC<2) with highest weight (*w*). We completed modeling and model selections using the 'lme4' and 'MuMIn' packages in R.

Results

We obtained 8,165 independent cottontail rabbit detections in Detroit across 11,616 trap nights from our 2017-2020 camera trap surveys. Additionally, we recorded 1,345 humans, 484 domestic dogs, and 271 coyotes. Three stations (one in 2017 and two in 2019) had no coyote, domestic dog, or human detections. No cameras had significant densities for all three threat species at the same station for the entire duration of study based on Getis-Ord Gi* statistics (Figure 4). Instead, coyotes had significant densities at only one station in 2019. Domestic dogs had significant densities at the same station across two different years. Humans had significant densities at three stations across the three years of study, with two of those stations recurring across years. Rabbits had significant densities at the same two stations across two years. These hotspots overlapped with significant dog densities in two years at the same station. However, we saw no significant overlap between rabbits and humans or coyotes (Figure 4).

Of the rabbit detections, with vigilance being determined by head position, we categorized 2,774 images as vigilant (i.e, head-up, 34%) and 1,327 images as non-vigilant (i.e. head down, 16.3%). The remaining 4,064 photos were classified into the following categories: 17.4% moving, 1% active, 1.8% sniffing, and 1% eating. Over a quarter of the total images were either unknown or out of frame, with out of frame photos removed from analysis. We found that vigilance did significant vary by threat level ($\chi^2 = 37.74$, $p < 0.0001$) with a greater response induced by domestic dogs (Figure 5).

Models further support differential effects of threats on rabbit vigilance. The top model (highest w with Δ AIC<2) indicated that the presence of domestic dog hotspots ($\beta = 2.12$, $p=0.016$), distance to water ($\beta=0.0002$, $p = 0.046$), and vegetation cover ($\beta = 0.837$, $p = 0.0171$) all positively influenced vigilance (Table 1). Though park size and the presence of human hotspots are in other top models, neither of these variables had significant beta coefficients in explaining rabbit vigilance. Results were consistent when using the extended categories of vigilance to include moving and sniffing. The intercept only model was included in top models when using ratio of vigilance photos with the extended categories of vigilance as response variables. Therefore, we did not have enough explanatory power to investigate other factors influencing the proportion of vigilance behavior.

Discussion

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Urban wildlife must employ various behavioral strategies to cope with risks in their environment from naturogenic and anthropogenic sources (Blecha et al 2018, Stillfried et al 2017). Like other urban prey species, cottontail rabbits are facing ever changing dynamics of predation threats in an increasingly urbanized world (Santiago-Alarcon 2017, Duarte and Young 2011, Mccleery 2009). We anticipated a scaled response where rabbits showed the lowest vigilance in areas of high human density, then progressively increased with in areas of high domestic dog density and even more in areas of high coyote density. Although we did not see the scaled response in the direction we expected, our analysis showed that in the presence of domestic dogs, rabbit vigilance behavior is heightened and rabbits exhibited the least amount of vigilance in response to humans. Furthermore, distance to water and vegetation cover also increased vigilance level significantly.

While it is possible rabbits have acclimated to human presence (Dunagun et al. 2019, Samia et al. 2015), their response to domestic dogs indicates that they continue to perceive them as a threat. Domestic dogs are morphologically similar to coyotes, but occupy much higher densities in urban areas and may represent a novel threat similar enough to a natural predator to induce a stronger vigilance response. Coyotes may not occur above the density threshold required to induce behavioral modifications in rabbits in Detroit. Dogs may have functionally replaced coyotes in this capacity posing greater predation risk to cottontail rabbits. Similarly, vigilance behavior increased in association with domestic dogs, but not coyotes in white-tailed deer (*Odocoileus virginianus*) in the mid-Altantic region of the United States (Schuttler et al. 2017).

Ziege et al. (2016) found European rabbits were less vigilant in urban areas as compared to their counterparts in rural areas. This suggests that perhaps the important difference in vigilance lies in the urban-rural gradient, rather than entirely within the urban matrix. Similar to rural areas where there is more vegetation cover than urban areas, we found vigilance increased within areas with more vegetation cover. Rabbits occurring in areas with more vegetative cover increased their vigilance, which could indicate fear that the covered environment may obscure predators. In Missouri, Jones et al. (2014) reported that forest cover did not influence rabbit or squirrel occupancy across an urban-rural gradient study. We also found that as rabbits moved further away from water their vigilance level increased, which could reflect increased exposure to more disturbed areas in the urban matrix. Urban systems represent a novel landscape for rabbits that requires dynamic changes in vigilance based on the environment and threats of specific locations within the landscape.

Our hotspot analysis indicated very little spatial overlap between species, with domestic dogs and rabbits being the only two species to have significant densities at the same camera location in the same year. As a result, we conclude that generally, rabbits are investing more in spatial avoidance, requiring less effort for vigilance. By mostly avoiding their predators, rabbits may be better able to maintain constant levels of vigilance across the landscape rather than heightening vigilance in areas their predators occupy at significant densities. These hotspots of activity might also be confounded by other factors impacting vigilance that were not incorporated in our models. For example, rabbits might be selecting environments based on proximity to housing, overall vegetation density, or grass cover that might be less desirable for their predators, allowing the rabbits to spend less time being vigilant.

Notably, our analysis was limited in scope by only examining behavior in areas where these species co-occur. It is entirely possible that spatial or temporal partitioning plays a larger role in mediating predator-prey interactions than vigilance solely in prey. We examined interactions within patches in the city, but neglected to examine the amount of interaction occurring between these spaces. Quantifying the level of risks between patches in the city could be the next step in examining threat impacts on prey behavior. Furthermore, seasonality may influence vigilance behavior and interact with food availability. Our survey did not sample during warmer months. One could argue risk assessment in cottontail rabbits may be more extreme than the winter months when predators are likely more active.

A growing number of studies on prey behavior have shown increasing evidence for multiple factors, including human influence and urbanization, affecting predator prey dynamics (Gallo et al 2019, Magle et al 2014). Our work contributes to this growing number of studies on urban wildlife and particularly predator-prey dynamics within urban systems. Understanding the dynamics of predators and their prey in urban systems will be key to the continued coexistence of wildlife and humans in urban spaces. Our results elucidate how a common prey species change, or fail to change, their vigilance behavior across anthropogenic and naturogenic risk factors in an urban ecosystem. Ultimately, these findings advance our understanding of the adaptability of wildlife in human-dominated environments.

Author contributions

S.L and N.C.H. conceived the study. S.L. wrote the manuscript and conducted analysis with support from S.G. and N.C.H. S.L. and N.A. designed graphics. All authors contributed to field efforts, data curation, and editing the manuscript. N.C.H. secured funding and supervised work.

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Figure legends

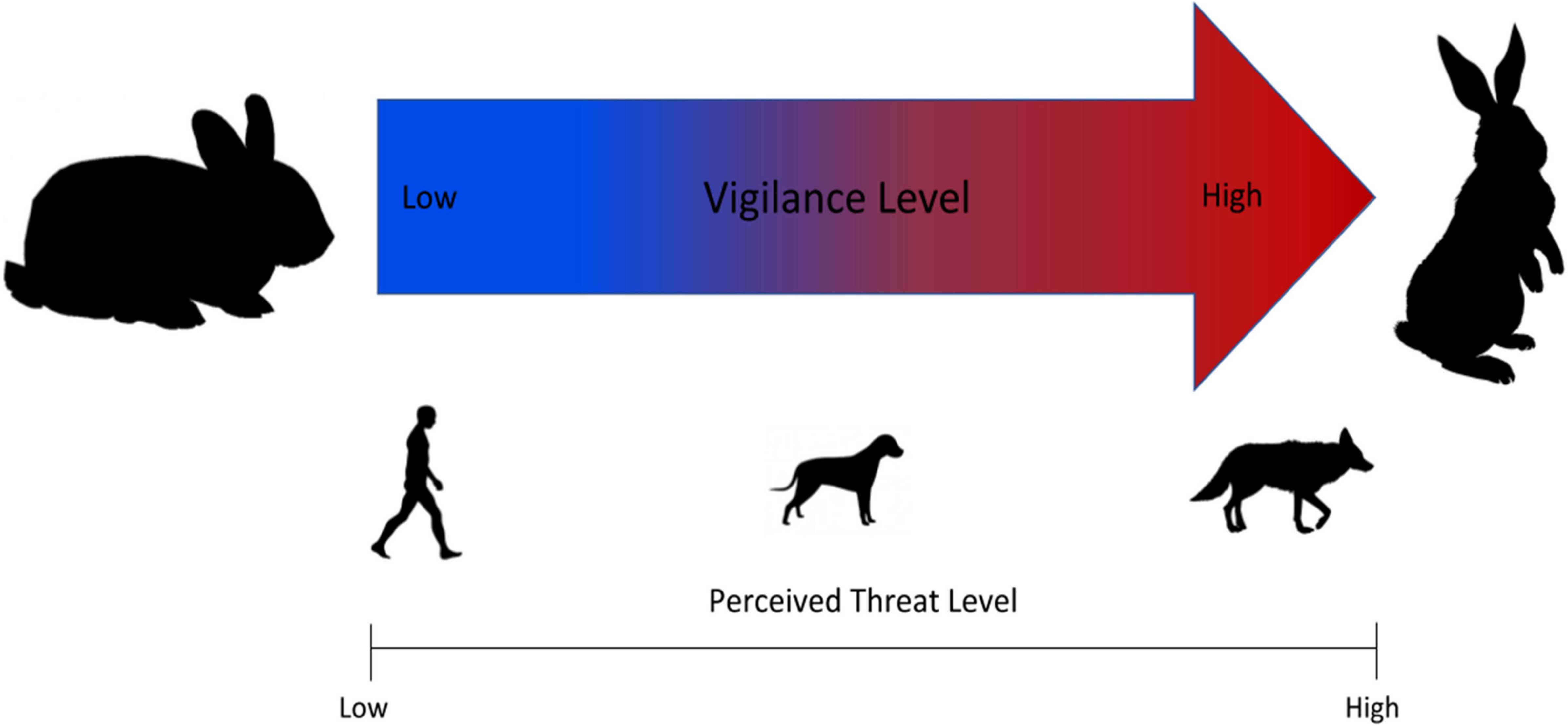
Figure 1 Expected vigilance response of cottontail rabbits. Rabbit vigilance was anticipated to be highest around coyotes as they present a high predation risk, somewhat high around dogs because of their similarities to coyotes, and lowest around humans due to the likelihood that rabbits have come to see human presence as less of a threat. Vigilance was measured as the amount of time spent assessing the environment for predators by examining rabbit posture.

Figure 2 Study site in Detroit with dots indicating camera placement including camera station locations from 2017-2020. Orange dots indicate camera stations where rabbits were detected in at least one of the years of study. Black dots indicate camera stations where no rabbits were detected in any years. All cameras were placed on trees with as much space as the park size would allow between them, with no cameras being closer than 500m.

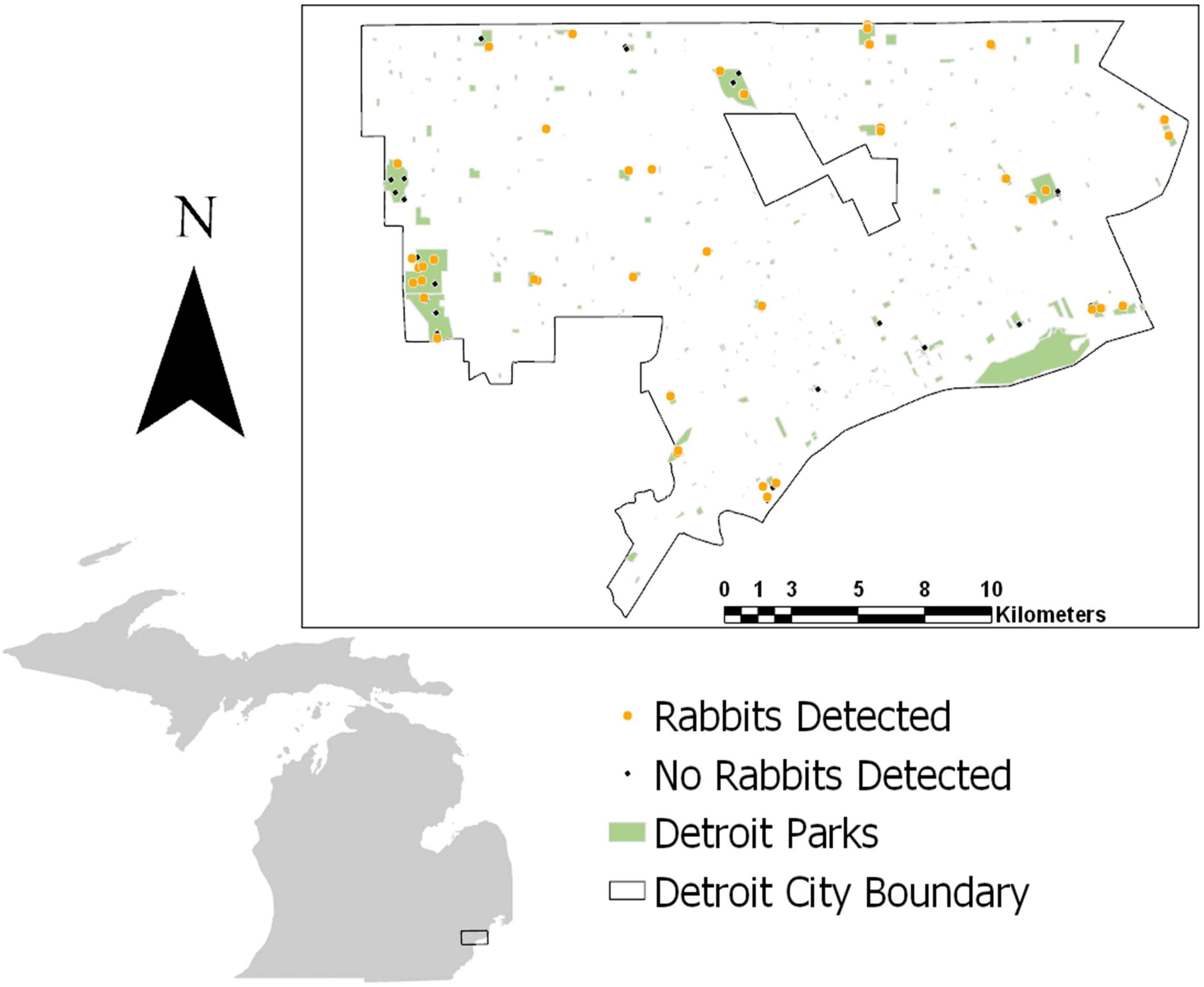
Figure 3 Vigilance classifications based on body positions: A) vigilant, head-up; B) non-vigilant, head down; C) active; D) eating; E) moving; and F) sniffing.

Figure 4 Spatial use within Detroit for rabbits and their three threat species as shown by kernel density activity patterns from camera images in the city of Detroit parks from 2017-2020. Coyotes had significant densities at one station, humans had significant densities at three stations (two of these stations had significant densities for two years), dogs had significant densities at the same station across two years, and rabbits had significant densities at two stations for two years. Example data are shown for each species.

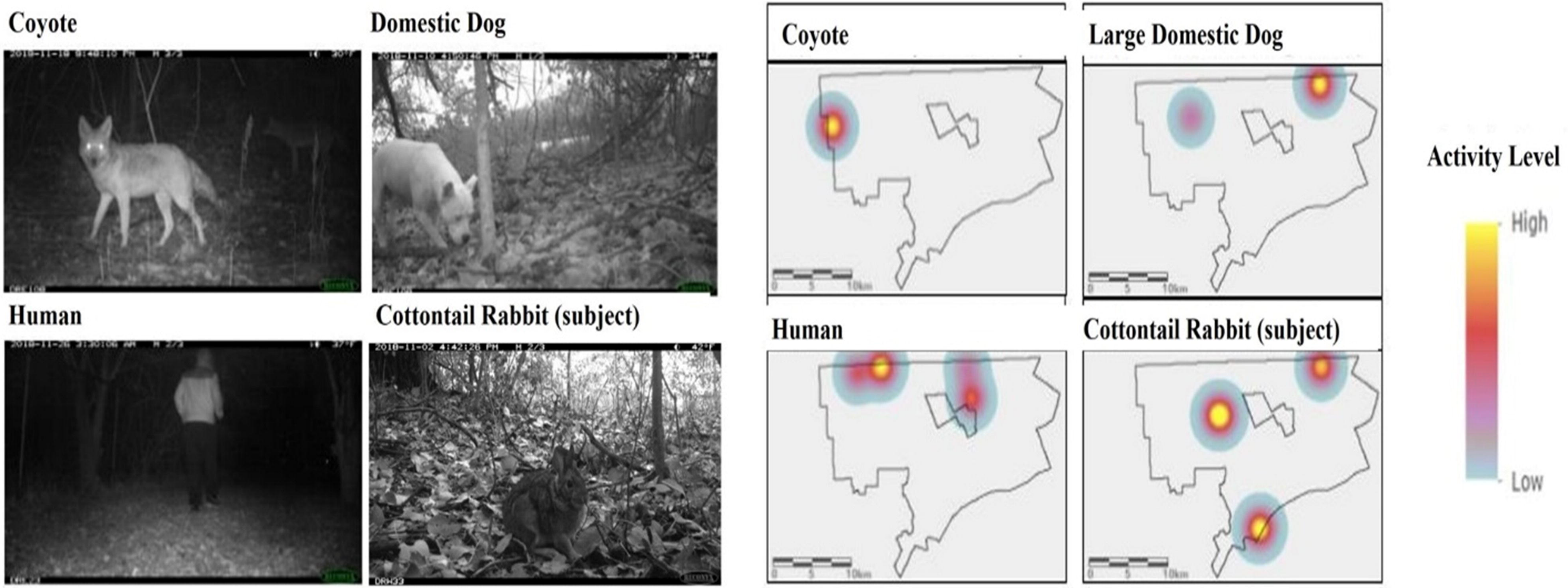
Figure 5 Proportion of vigilant to non-vigilant rabbit photos in the presence of each threat species. Rabbits showed the highest proportion of vigilance in the presence of domestic dogs.

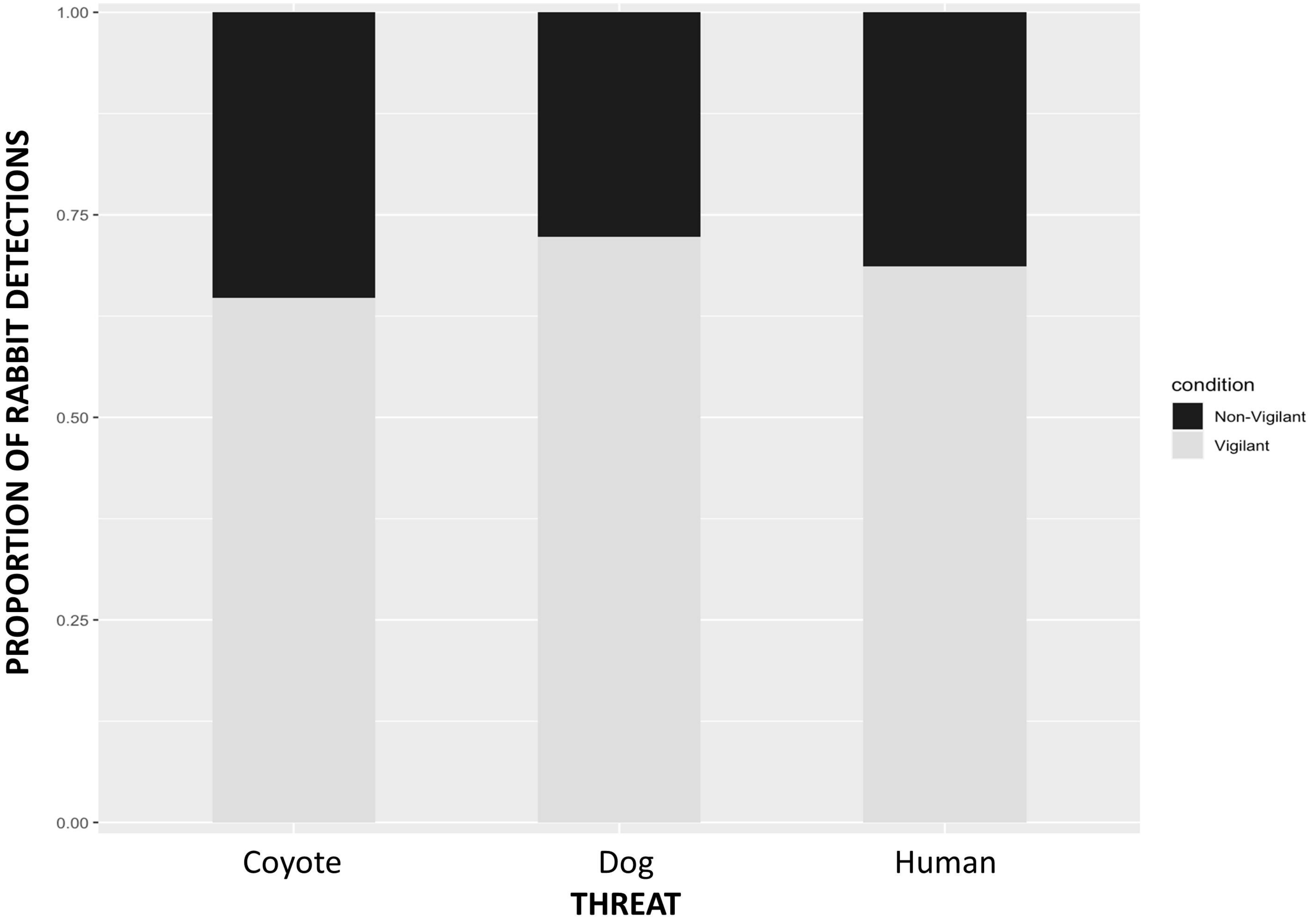


Low
Vigilance Level
High
Perceived Threat Level
Low
High


N
0 1 3 5 8 10
Kilometers
Rabbits Detected
No Rabbits Detected
Detroit Parks
Detroit City Boundary


A
B
C
D
E
F


Coyote
Domestic Dog
Human
Cottontail Rabbit (subject)
Coyote
Large Domestic Dog
Human
Cottontail Rabbit (subject)
Activity Level
High
Low



PROPORTION OF RABBIT DETECTIONS
1.00
0.75
0.50
0.25
0.00
Coyote
Dog
Human
THREAT
condition
Non-Vigilant
Vigilant