

1 **Vigilance response of a key prey species to anthropogenic and natural threats in Detroit**

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24 **Abstract**

25 Rapid urbanization coupled with increased human activity induces pressures that affect predator-  
26 prey relations through a suite of behavioral mechanisms, including alteration of avoidance and  
27 coexistence dynamics. Synergisms of natural and anthropogenic threats existing within urban  
28 environments exacerbate the necessity for species to differentially modify behavior to each risk.  
29 Here, we explore the behavioral response of a key prey species, cottontail rabbits (*Sylvilagus*  
30 *floridanus*), to pressures from humans, domestic dogs, and a natural predator, coyotes (*Canis*  
31 *latrans*) in a human-dominated landscape. We conducted the first camera survey in urban parks  
32 throughout Detroit, Michigan in 2017-2020 to assess vigilance response corresponding to a  
33 heterogeneous landscape created from variation in the occupancy of threats. We predicted a  
34 scaled response where cottontail rabbits would be most vigilant in areas with high coyote  
35 activity, moderately vigilant in areas with high domestic dog activity, and the least vigilant in  
36 areas of high human activity. From 8,165 independent cottontail rabbit detections in Detroit  
37 across 11,616 trap nights, one-third were classified as vigilant. We found vigilance behavior  
38 increased with coyote occupancy and in locations with significantly high domestic dog activity,  
39 but found no significant impact of human occupancy or their spatial hotspots. We also found  
40 little spatial overlap between rabbits and threats, suggesting rabbits invest more in spatial  
41 avoidance; thus, less effort is required for vigilance. Our results elucidate strategies of a prey  
42 species coping with various risks to advance our understanding of the adaptability of wildlife in  
43 urban environments. In order to promote coexistence between people and wildlife in urban  
44 greenspaces, we must understand and anticipate the ecological implications of human-induced  
45 behavioral modifications.

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56 **Introduction**

57           The 20th and 21st centuries have seen unprecedented population growth and expansion of  
58 cities, with 60% of the global population expected to live in urban centers by the year 2030  
59 (United Nations, 2018). Urbanization coupled with other increased anthropogenic pressures has  
60 fundamentally changed ecosystems worldwide (Foley et al 2005, Grimm et al 2008, Pickard et al  
61 2017, Chen et al 2020). Cities result in fragmenting natural habitats that restrict gene flow,  
62 change species assemblages, and alter the behavior of animals and people alike (Romano 2002,  
63 Tigas et al 2002, Crooks et al 2004, Lowry et al 2013, Johnson and Munshi-South 2017). These  
64 environmental perturbations have implications for wildlife and a myriad of ecological  
65 interactions including predator-prey relationships.

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

79 1995, Gliwicz et al 2008, Reilly et al 2017). Modification of behavior has therefore become  
80 necessary for the survival of both predators and prey in urban environments, as risks govern  
81 behavior (Lima 1998). However, despite the recent burgeoning of urban ecology studies, how  
82 humans and domestic animals alter mammalian vigilance behavior remains understudied.

83       Highly adaptable species and those with relatively smaller body sizes are more successful  
84 at coexisting with humans in urban areas (Bateman and Flemming 2012). Carnivores,  
85 particularly large bodied carnivores, have historically faced intense persecution from humans  
86 (Munoz-Fuentes et al. 2010). Large predators depredate livestock and compete with humans for  
87 resources including space and prey, often resulting in humans employing lethal interventions  
88 (Mech 1995, Witmer and Whittaker 2001, Treves 2003, Muhly and Musiani 2009). However,  
89 many mid to small-sized predators are able to thrive in areas of high anthropogenic influence  
90 (Wilkinson and Smith 2001, Ikeda et al 2004). In particular, coyotes (*Canis latrans*) have  
91 adapted to living with humans in part, by exploiting anthropogenic food subsidies and shifting  
92 diurnal movement in response to human disturbance (Kitchen et al 2001, Gese and Bekoff 2004).  
93 This, in conjunction with wide extirpations of the grey wolf (*Canis lupus*), has allowed coyotes  
94 to expand their range to the entirety of the United States beyond previous restrictions to the  
95 central and western portions of the country (Crooks 1999, Hody and Kays 2018). Domestic dogs  
96 (*Canis familiaris*) have similarly become abundant within urban areas and thus, can exert top-  
97 down pressures as a member of the carnivore community (Ordeñana et al. 2010). These  
98 ecological and behavioral changes in carnivores can have cascading effects on their prey species,  
99 subsequently altering their behavior.

100       Concurrent with predators employing strategies for coexistence, their prey must also  
101 mitigate risks in human dominated landscapes. Threats for prey species in urban environments

102 are often exacerbated by multiple sources including direct mortality from natural and  
103 anthropogenic sources. Prey may employ similar strategies to mitigate risks from humans as they  
104 do to mitigate risks from natural predators (Parsons et al. 2016). As such, fear effects in urban  
105 environments can result in prey modifying temporal activity or habitat selection to reduce  
106 predation risks (Chambers and Dickman 2002, Dowding et al. 2010). Discernment between  
107 immediate and distal threats requires delegating time to vigilance in order to assess and respond  
108 to risks across the landscape. However, there are tradeoffs because more time spent being  
109 vigilant means less time foraging, mating, and performing other behaviors like grooming  
110 (Quenette 1990). Environmental conditions including vegetation height, tree cover, and the  
111 distribution of water sources can interact to produce varying levels of predation risk and thus  
112 influence the amount of time prey spend being vigilant (Scheel 1993, Tchabovsky et al 2001).

113 Cottontail rabbits (*Sylvilagus floridanus*) are a key prey source for many mammalian  
114 carnivores as well as avian predators and occasionally snakes in urban environments throughout  
115 the United States (Beasom and Moore 1977, Litvaitis and Shaw 1980, Wittenberg 2012).  
116 Because rabbits are an important part of coyotes' diet, along with small rodents, coyotes exert  
117 top-down pressures to control their populations (Poessel, Mock, and Breck 2017). Cottontail  
118 rabbits have high reproductive rates that result in rapidly growing populations that interact,  
119 directly or indirectly, with humans in gardens, yards, parks and other green spaces throughout  
120 city limits (Hunt et al 2014, Baker et al 2015). We conducted a non-invasive camera survey to  
121 investigate the vigilance behavior of rabbits in response to anthropogenic and natural threats. Our  
122 work occurred throughout Detroit, the largest city in Michigan, located in the Great Lakes region  
123 of the USA from 2017-2020. Here, we delineated human, coyote, and domestic dog risk zones to

124 detect differences in cottontail vigilance response and investigated the potential factors  
125 influencing vigilance.

126       Species exploiting urban environments may exhibit higher plasticity to cope and  
127 acclimate with anthropogenic threats (Samia *et al.* 2015). The gray squirrel (*Sciurus*  
128 *carolinensis*), another common urban prey species, is less wary of humans in areas more densely  
129 populated by humans (Parker and Nilon 2008). This suggests a level of acclimation to human  
130 presence, which we reasonably anticipate occurring in cottontail rabbits who are exposed to  
131 similar pressures of human activity in an urban environment. Therefore, we expect a similar level  
132 of acclimation in cottontail rabbits where they are less vigilant in areas heavily populated by  
133 humans. Because of the similarities in body size and behavior between domestic dogs and  
134 coyotes, we anticipate rabbits will show more vigilance in areas with high domestic dog presence  
135 than areas with high human presence. However, domestic dog populations are generally larger in  
136 urban areas because of association with humans. In Detroit, we anticipate some level of  
137 acclimation to their presence from cottontail rabbits and therefore, we expect the response to  
138 dogs to be less dramatic than the response to coyotes. However, unaccompanied dogs could  
139 illicit pronounced fear responses. Overall, we expect a scaled response where rabbits will be  
140 least vigilant in areas with high human activity, with vigilance response increasing slightly in the  
141 areas with high domestic dog activity, and the most vigilance being displayed in areas of high  
142 coyote activity, as coyotes are an actual formidable predator of rabbits (Figure 1). Results will  
143 further our understanding of how a key prey species behaves in dynamic urban landscapes,  
144 information necessary to foster safe and positive interactions between people and wildlife  
145 coexisting in the city.

146

147 **Materials and Methods**

148 **Study Site**

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

159

160 **Data Collection/Camera Survey**

161 We deployed unbaited, remotely triggered cameras (Reconyx© PC 850, 850C, 900,  
162 900C) throughout city parks to monitor the wildlife community from October – March in 2017-  
163 2020. Placement within the parks was determined based on evidence of wildlife presence such  
164 as scat, and vegetation type. Park size determined the number of cameras deployed, ranging from  
165 1-7 cameras. For parks with multiple cameras, we deployed cameras with a minimum distance of  
166 500m between individual cameras. Cameras were affixed to medium sized trees approximately  
167 0.5-1m off the ground. We programmed cameras to take three images when triggered at high  
168 sensitivity with one second between each image and a 15-second quiet period. Every image was  
169 independently sorted and confirmed by at least two members of the Applied Wildlife Ecology

170 Lab at the University of Michigan. We only used images confirmed as rabbit as well as their  
171 associated threat species of interests: humans, domestic dogs, and coyotes. Both gray (*Urocyon*  
172 *cinereoargenteus*) and red foxes (*Vulpes vulpes*) are also potential predators of cottontails, but  
173 sample sizes were too low to include in our analysis. Team members were excluded from human  
174 images.

175

### 176 **Hotspot Analysis and Occupancy Modeling**

177 To determine the level of risk from each of our three potential predator focal species, we  
178 used two method to capture their spatial variation in parks across Detroit. First, we used kernel  
179 density analysis to construct utilization distributions from rabbit, human, coyote, and domestic  
180 dog camera triggers in ArcMap (v. 10.6.1). To test for significant spatial clustering (i.e.,  
181 hotspots), we applied the Getis-Ord-GI\* statistic to species triggers, which summarizes spatial  
182 autocorrelation with resultant high positive z-scores indicating clustering and low negative z-  
183 scores indicating dispersion (Getis and Ord 1992). Specifically, significant trigger hotspots and  
184 coldspots are derived from z-scores greater than 1.96 and less than -1.96 ( $\alpha < 0.05$ ), respectively.  
185 Finally, we overlaid significant trigger hotspots for rabbits with associated threats to determine if  
186 rabbits avoided hotspots for humans, dogs, or coyotes across the city. In other words, we  
187 assessed whether trigger hotspots for rabbits were congruent with any of the threats. Evidence of  
188 spatial avoidance may represent a sufficient evasion strategy that necessitates less vigilance  
189 behavior.

190 Second, we constructed single-species, single-season occupancy models for humans,  
191 domestic dog, and coyotes, which corrects for imperfect detections from repeated surveys  
192 (MacKenzie *et al.* 2003; Mackenzie & Royle 2005). In our case, we used one-week sampling



193 interval to generate detection histories. By holding occupancy constant, we first built detection  
194 models with camera model (CAM), understory vegetation at camera (UAC), number of trap  
195 nights (TN), and park size (AREA) as covariates. We then used the top detection model to build  
196 occupancy models with housing density within 500 meters (HOUSE), prey trap success  
197 (PREYTS), UAC, and AREA. PREYTS was calculated at the camera level as the ratio of  
198 cottontail rabbit, squirrel, chipmunk (*Tamias striatus*) and small mammal total triggers by  
199 number of trap nights. We identified top models using Akaike's Information Criterion corrected  
200 for small sample sizes (AICc) based on the lowest  $\Delta$ AIC and greatest weight ( $w$ ). We also  
201 assessed goodness-of-fit for each model using the chi-squared discrepancy method in the  
202 'ResourceSelection' package. We constructed detection histories using 'camtrapR', and  
203 completed occupancy modeling in 'unmarked' packages. All analysis was completed in Program  
204 R.

205

## 206 **Vigilance Scoring**

207 We extracted behavioral information from images in order to quantify vigilance response  
208 in cottontail rabbits. For each image containing a rabbit, we scored vigilance based upon the  
209 position of the body and head (Figure 3). For images with two individuals, each individual was  
210 given its own classification and counted as independent from other individuals in the image.  
211 Rabbits were considered "vigilant" if their head was in an upright position; while "non-vigilant"  
212 was assigned when their head was down in a foraging position. For images where the rabbit did  
213 not display an obvious head up or head down stance, we used six other classifications: moving,  
214 active, eating, sniffing, out of frame, and unknown. "Moving" included any rabbit in motion,  
215 which was often indicated by motion blur in the images. We considered moving to be a potential

216 indicator of vigilance as it could denote rabbits leaving an area due potentially to a detected  
217 threat. “Sniffing” included rabbit attention turned to monitoring an aspect of its environment  
218 with its head up such as sniffing twigs. Because we are investigating the impact of canid species  
219 on rabbit behavior and canids often mark their territory (Bowen and Cowan 1980), we  
220 considered sniffing to potentially indicate vigilance as it is a show of risk assessment. Both  
221 sniffing and moving were left out of our initial vigilant vs non-vigilant analysis but were  
222 included in the vigilant category in our extended analysis. “Active” was used for activity where  
223 the animal’s attention was pointed inward at themselves. This included any rabbits scratching,  
224 licking, or otherwise attending to their fur, this also included stretching. “Eating” was used in the  
225 event that a rabbit had its head up, but clearly had vegetation in its mouth or the image series  
226 showed it chewing. Although both active and eating involve attention being pointed inward at  
227 the rabbit, we did not include them as non-vigilant in our analysis as we could not confirm non-  
228 vigilance. “Out of frame” included any images where the rabbit exited the frame of the picture  
229 and nothing was in the image. Images that were sorted as out of frame were removed from the  
230 data set and not counted in the final total. Finally, “unknown” was used for rabbits where only  
231 parts of the whole body were in the picture, the head was too blurry to determine, or if the body  
232 position could not be determined for any other reason. Unknown photos were also removed from  
233 the final total. Each individual was only designated one category per each image in which it  
234 appeared. All images with rabbits present were used to best estimate the amount of time actually  
235 spent in front of the camera at the particular station. We only used photos where rabbits were in  
236 the frame, meaning our photos are estimates of time spent in frame. Each image was scored  
237 independently for vigilance by at least two members of the Applied Wildlife Ecology Lab at the

238 University of Michigan. Any discrepancies that were not resolved resulted in classifying the  
239 image as unknown.

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

248

## 249 **Statistical Analysis**

250 We used negative binomial generalized linear models (GLM.nb) to determine which  
251 factors best-explained cottontail rabbit vigilance across cameras. We used results from the  
252 hotspot analysis to identify locations of significant high use based on kernel density estimates  
253 from detection data to categorize threat levels for humans, domestic dogs, and coyotes. This  
254 resulted in a binary explanatory variable indicating whether a hotspot was presence (1) or  
255 absence (0) for each threat. We also used occupancy estimates from top models for coyotes  
256 (COYO), humans (HUMO), and domestic dogs (DOGO) as threat covariates. We also included  
257 environmental and abiotic factors in our analysis. We calculated distance from each camera  
258 station to water sources (WATER), to roads (ROADS), and the area of each park (AREA, in  
259 acres) using ArcMap. We quantified understory cover (VEG) as a binary variable of whether  
260 trees, tall shrubs, bushes, or grasses were present or not in the field of view at the camera level.

261 Support for models was evaluated using Akaike's Information Criterion (AICc) to select  
262 top-performing model ( $\Delta AIC < 2$ ) with highest weight ( $w$ ). We also assessed goodness-of-fit for  
263 each model using the chi-squared discrepancy method the 'ResourceSelection' package. We  
264 completed modeling in the 'lme4' package and model selection in the 'MuMIn' package. All  
265 analysis was completed in Program R.

266

## 267 **Results**

268 We obtained 8,165 cottontail rabbit detections from 58 camera locations in Detroit across  
269 11,616 trap nights from our 2017-2020 surveys (Table 1). The average trap night per camera for  
270 the survey period was 99.8 (Range: 18-121) including two cameras which malfunctioned after 18  
271 days, excluding the outliers the average was 101.2 (Range: 74-121). For parks with > 1 camera  
272 station, cameras were spaced on average 1.4 km apart within parks spaced an average distance of  
273 3.2 km apart. We recorded 1,345 human detections at 27 camera stations, 484 domestic dog  
274 detections at 33 stations, and 271 coyote detections at 29 stations. Three stations (one in 2017  
275 and two in 2019) had no coyote, domestic dog, or human detections. No cameras had significant  
276 trigger densities for all three threat species at the same station for the entire duration of study  
277 based on Getis-Ord  $G_i^*$  statistics (Figure 4). Instead, coyotes had significantly high trigger  
278 densities to form a hotspot at only one station in 2019. Domestic dogs had hotspots at the same  
279 station across two different years. Humans had hotspots at three stations across the three years of  
280 study, with two of those stations recurring across years. Rabbits had significant trigger densities  
281 at the same two stations across two years. We found spatial aggregation of rabbits with dog at  
282 one hotspot location in two years. However, we saw no significant overlap in hotspots between  
283 rabbits and humans or coyotes (Figure 4).

284 Top occupancy models for all threats included HOUSE with PREYTS being important  
285 for both canid species (Table S1). Detection models highlighted SIZE for all threats as important  
286 as well as TN, UAC, and CAM for humans and domestic dogs. Although comparable, estimates  
287 from top models indicated occupancy was highest for humans and lowest for coyotes throughout  
288 Detroit city parks ( $\bar{\psi}_{\text{HUMAN}}=0.684$  SE=0.057;  $\bar{\psi}_{\text{DOG}}=0.662$  SE=0.058;  $\bar{\psi}_{\text{COYOTE}}=0.598$  SE=0.061).

289 Of the rabbit detections, with vigilance being determined by head position, we  
290 categorized 2,774 images as vigilant (i.e., head-up, 34%) and 1,327 images as non-vigilant (i.e.  
291 head down, 16.3%). We classified the remaining 4,064 photos into the following categories:  
292 17.4% moving, 1% active, 1.8% sniffing, and 1% eating. Over a quarter of the total images were  
293 either unknown or out of frame, with these categories both being removed from analysis.

294 Models further support differential effects of threats on rabbit vigilance (Table 2). The  
295 top model (highest  $w$  with  $\Delta$  AIC<2) indicated that the presence of domestic dog hotspots ( $\beta =$   
296 2.63,  $p=0.002$ ), coyote occupancy ( $\beta = 0.869$ ,  $p=0.013$ ), vegetation cover ( $\beta = 0.735$ ,  $p = 0.031$ )  
297 and distance to water ( $\beta=0.0001$ ,  $p = 0.078$ ) all positively influenced vigilance, when response  
298 represented the number of images with rabbits exhibited vigilance behavior. Though park size,  
299 roads, and human occupancy are in other top models, none of these variables had significant beta  
300 coefficients in explaining rabbit vigilance. Results of top models were consistent when using the  
301 extended categories of vigilance to include counts of moving and sniffing. The intercept-only  
302 model was included in top models when using ratio of vigilance photos. Therefore, we did not  
303 have sufficient power to investigate whether other variables explained the variation in the  
304 proportion of vigilant photos.

305

306 **Discussion**

307           Urban wildlife must employ various behavioral strategies to cope with risks in their  
308 environment from naturogenic and anthropogenic sources (Blecha et al 2018, Stillfried et al  
309 2017). Like other urban prey species, cottontail rabbits are facing predation threats that are  
310 dynamic in an increasingly urbanized world (Santiago-Alarcon 2017, Duarte and Young 2011,  
311 Mccleery 2009). We anticipated a scaled response where rabbits showed the lowest vigilance in  
312 areas of high human density, then progressively increased with in areas of high domestic dog  
313 density and even more in areas of high coyote density. Our analysis showed that occupancy of  
314 coyote positively influenced vigilance, consistent with expectations. We did find that rabbit  
315 vigilance behavior was heightened in hotspots of domestic dogs across the city. Further,  
316 consistent with our expectation, rabbit vigilance was not significantly affected by human  
317 occupancy suggesting more acclimation in a human-dominated landscape. Similarly, Gámez and  
318 Harris (in press) found no response of human occupancy on carnivore occupancy throughout  
319 Detroit in the same parks we surveyed here to access rabbit vigilance behavior. We also found  
320 that rabbit vigilance was significantly higher with more vegetation cover, which could be a  
321 response to lower visibility to detect predators.

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

330 deer (*Odocoileus virginianus*) in the mid-Atlantic region of the United States (Schuttler et al.  
331 2017). Parsons *et al.* (2016) found that white-tailed deer and gray squirrel avoided humans with  
332 and without dogs more strongly than coyotes throughout the southeastern United States. Their  
333 findings were notably in contrast with other studies such as Parker and Nilon (2008) that  
334 suggested squirrels habituated to human activity in urban areas.

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

347 Our hotspot analysis indicated very little spatial overlap between species, with domestic  
348 dogs and rabbits being the only two species to have significant densities at the same camera  
349 location in the same year. As a result, we conclude that generally, rabbits are investing more in  
350 spatial avoidance, requiring less effort for vigilance. By mostly avoiding their predators, rabbits  
351 may be better able to maintain constant levels of vigilance across the landscape rather than  
352 heightening vigilance in areas their predators occupy at significant densities. These hotspots of

353 activity might also be confounded by other factors affecting vigilance that were not incorporated  
354 in our models. For example, rabbits might be selecting environments based on proximity to  
355 housing, overall vegetation density, or grass cover that might be less desirable for their predators,  
356 allowing the rabbits to spend less time being vigilant.

357 Notably, our analysis was limited in scope by only examining behavior in areas where  
358 these species co-occur. It is entirely possible that spatial or temporal partitioning plays a larger  
359 role in mediating predator-prey interactions than vigilance solely in prey. We examined  
360 interactions within patches in the city, but neglected to examine the amount of interaction  
361 occurring between these spaces. Quantifying the level of risks between patches in the city could  
362 be the next step in examining threat impacts on prey behavior. Furthermore, seasonality may  
363 influence vigilance behavior and interact with food availability (Favreau et al 2018, Périquet et al  
364 2017). Our survey did not sample during warmer months. However, one could argue risk  
365 assessment in cottontail rabbits may be more extreme in the winter months when predators are  
366 more food-limited.

367 A growing number of studies on prey behavior have shown increasing evidence for  
368 multiple factors affecting predator prey dynamics including human influence and urbanization  
369 (Gallo et al 2019, Magle et al 2014). Our work contributes to the growing number of studies on  
370 urban wildlife and particularly predator-prey dynamics within urban systems. Further, we  
371 underscore that studying behavioral ecology across city topologies including cities where human  
372 populations are declining such as Detroit is necessary for understanding how humans, not just  
373 their built environment, affect wildlife to better promote coexistence between humans and  
374 wildlife (Guerrieri et al. 2012, Herrmann et al. 2016). Understanding the dynamics of predators  
375 and their prey in urban systems will be key to the continued coexistence of wildlife and humans



376 in urban spaces. Our results elucidate how a common prey species changes, or fails to change,  
377 their vigilance behavior across anthropogenic and naturogenic risk factors in an urban  
378 ecosystem. Ultimately, these findings advance our understanding of the adaptability of wildlife  
379 in human-dominated environments.

380

381

### 382 **Author contributions**

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

386

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397

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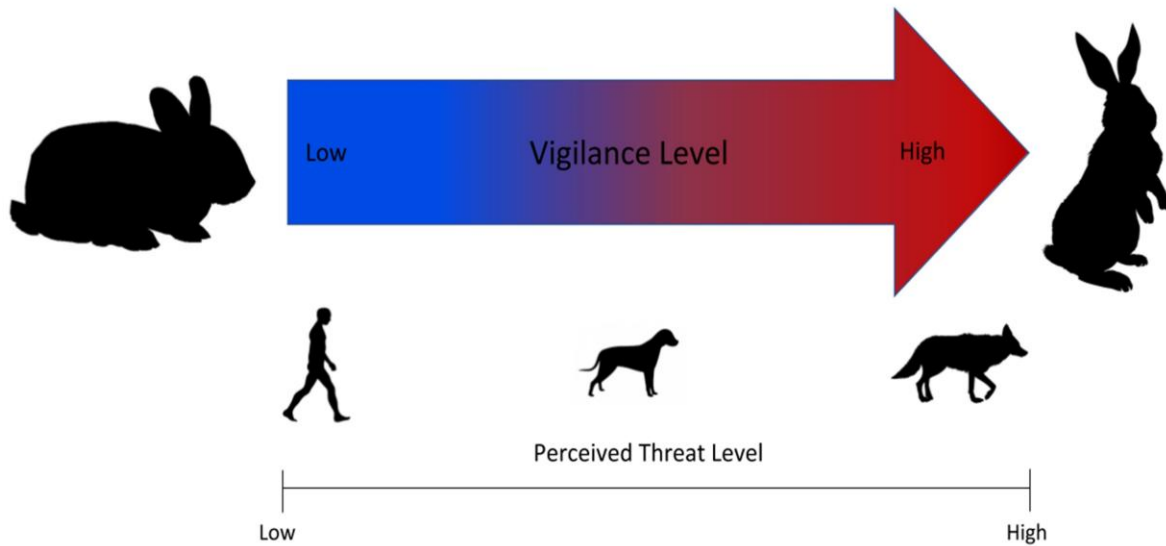
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564 **Figure legends**

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566 **Figure 1** Expected vigilance response of cottontail rabbits with scaled response across natural

567 and anthropogenic threats.



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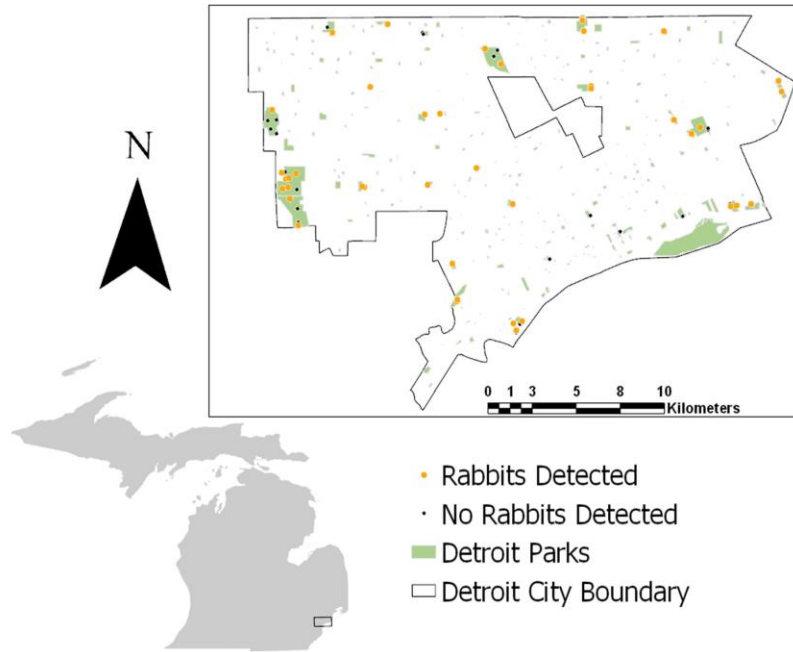
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577 **Figure 2** Study site in Detroit with dots indicating camera placement from 2017-2020. Orange  
578 dots indicate camera stations where rabbits were detected in at least one of the years of study.  
579 Black dots indicate camera stations where no rabbits were detected in any years.



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591 **Figure 3** Vigilance classifications based on body position of cottontail rabbits: A) vigilant, head-  
592 up; B) non-vigilant, head down; C) active; D) eating; E) moving; and F) sniffing.



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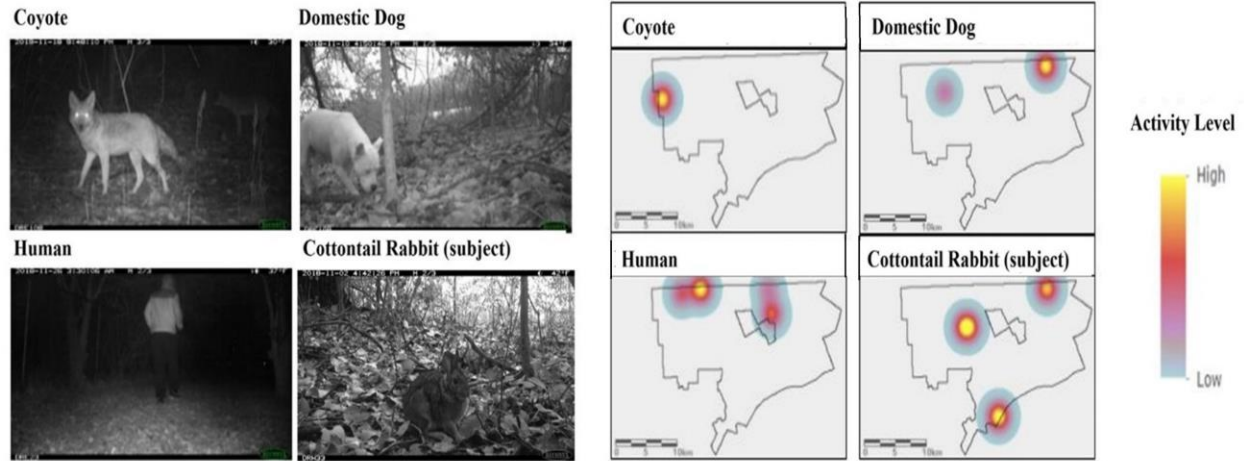
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604 **Figure 4** Spatial use within Detroit for rabbits and their three threat species as shown by  
605 significant hotspots based on kernel density activity patterns from camera images in the city of  
606 Detroit parks from 2017-2020.



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619 **Table 1**

620 Number of detections for cottontail rabbits and associated threats tested that may influence their vigilance  
621 behavior in urban parks, Detroit Michigan 2017-2020.

<b>Park</b>	<b>Rabbit</b>	<b>Human</b>	<b>Domestic Dog</b>	<b>Coyote</b>
Balduck	495	22	44	0
Bishop	204	4	9	0
Butzel	2111	1	5	3
Chandler	18	3	7	7
Comstock	48	144	26	1
Conner	288	4	4	21
Eliza Howell	42	0	1	20
Farwell	325	47	31	1
Fields	28	25	36	0
Ford	259	8	32	6
Fort Wayne	1552	3	9	16
Hammerberg	120	0	2	1
Lasky	12	79	0	0
Maheras	102	7	4	29
Marruso	1005	21	77	0
McCabe	3	0	0	0
O’Hair	30	0	8	0
Palmer	42	7	8	8
Patton Memorial	557	28	3	26
Romanowski	75	7	0	0
Rouge	636	4	22	32
Stoepel #2	213	13	29	3

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630 **Table 2**

631 Top models ( $< 2 \Delta \text{AICc}$ ) explained rabbit vigilance behavior using detection data from camera  
632 survey in Detroit city parks, 2017-2020. Response variable is number of photos with rabbit head-  
633 up. Explanatory variables were: COYO (coyote occupancy), DS (presence of domestic dog  
634 hotspot), HS (presence of human hotspot), VEG (vegetation cover), WATER (distance to water),  
635 and SIZE (size of the park in acres). Model output for top models includes  $R^2$ , AICc,  $\Delta \text{AICc}$ ,  
636 and model weight ( $w$ ).

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<b>Model</b>	<b><math>R^2</math></b>	<b>AICc</b>	<b><math>\Delta \text{AICc}</math></b>	<b><math>w</math></b>
COYO + DS + WATER + VEG	0.2535	553.7	0	0.210
COYO + DS + VEG	0.2109	554.5	0.73	0.146
COYO + DS + VEG + SIZE	0.2436	554.5	0.77	0.143
COYO + DS	0.1715	554.9	1.16	0.118
COYO + DS + VEG + ROAD	0.2364	555.1	1.32	0.109
COYO + DS + WATER	0.2011	555.2	1.44	0.102
COYO + DS + WATER + VEG + SIZE	0.2645	555.5	1.73	0.088
COYO + DS + WATER + VEG + HS	0.2629	555.6	1.86	0.083

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645 Table S1

Candidate Model	K	AICc	dAICc	w	GOF p-value
<b>COYOTE</b>					
$\rho$ (SIZE) $\psi$ (HOUSE + PREYTS)	5	1005.33	0	0.53	0.0799
$\rho$ (.) $\psi$ (HOUSE)	3	1005.82	0.48	0.41	0.0759
<b>DOG</b>					
$\rho$ (TN +CAM + SIZE +UAC) $\psi$ (HOUSE + UAC + SIZE + PREYTS)	10	1480.97	0	0.43	0.576
$\rho$ (TN) $\psi$ (.)	3	1481.04	0.08	0.42	0.298
$\rho$ (TN) $\psi$ (HOUSE)	4	1483.36	2.4	0.13	0.375
<b>HUMAN</b>					
$\rho$ (TN +CAM + SIZE +UAC) $\psi$ (HOUSE)	7	1510.98	0	0.39	0.756
$\rho$ (TN+CAM + SIZE +UAC)	6	1512.13	1.15	0.22	0.451
$\rho$ (TN +CAM + SIZE +UAC) $\psi$ (SIZE)	7	1512.22	1.24	0.21	0.215
$\rho$ (TN +CAM + SIZE +UAC) $\psi$ (SIZE + HOUSE)	8	1512.62	1.64	0.17	0.474

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