# Temporal refuges differ between human and natural top-down pressures in a subordinate carnivore

Rumaan Malhotra<sup>1</sup>, Samantha Lima<sup>2</sup>, and Nyeema Harris<sup>3</sup>

<sup>1</sup>University of Michigan <sup>2</sup>Purdue University <sup>3</sup>Yale University

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#### Abstract

Animals exhibit variation in their space and time use across an urban-rural gradient. As the top-down influences of apex predators wane due to human-driven declines, landscape level anthropogenic pressures are rising. Human impacts can be analogous to apex predators in that humans can drive increased mortality in both prey species and carnivores, and impact communities through indirect fear effects and food subsidies. Here, we evaluate the time use of a common mesocarnivore across an urban rural gradient, and test whether it is influenced by the intensity of use of a larger carnivore. Using multiple cameratrap surveys, we compared the temporal response of a small carnivore, the raccoon (Procyon lotor), to the larger coyote (Canis latrans) at four sites across Michigan that represented a gradient of pressure from humans. We found that raccoon time use varied by site and was most unique at the rural extreme. Raccoons consistently did not shift their activity pattern in response to coyotes at the site with the highest anthropogenic pressures despite considerable interannual variation, and instead showed the stronger responses to coyotes at more rural sites. Temporal shifts were characterized by raccoons being more diurnal in areas of high coyote activity. We conclude that raccoons do partition time to avoid coyotes. Our results highlight that the variation in raccoon time use across the entirety of the urban-rural gradient needed to be considered, as anthropogenic pressures may dominate and obscure the dynamics of this interaction. In an increasingly anthropocentric world, to understand species interactions, it is imperative that we consider the entire spectrum of human pressures that it may occur within.

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Rumaan Malhotra<sup>1\*</sup>, Samantha Lima<sup>2</sup> and Nyeema C. Harris<sup>3</sup>

 $^1\mathrm{Ecology}$  and Evolutionary Biology, University of Michigan 1101 N. University Ave, Ann Arbor, Michigan 48106

<sup>2</sup>Forestry and Natural Resources, Purdue University 715 W State St, West Lafayette, Indiana 47907

 $^{3}\mathrm{Applied}$  Wildlife Ecology Lab, School of the Environment, Yale University 195 Prospect St. New Haven, Connecticut 06511

\*Correspondent: rumaanm@umich.edu

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#### ABSTRACT

Animals exhibit variation in their space and time use across an urban-rural gradient. As the top-down influences of apex predators wane due to human-driven declines, landscape level anthropogenic pressures are

rising. Human impacts can be analogous to apex predators in that humans can drive increased mortality in both prey species and carnivores, and impact communities through indirect fear effects and food subsidies. Here, we evaluate the time use of a common mesocarnivore across an urban rural gradient, and test whether it is influenced by the intensity of use of a larger carnivore. Using multiple camera-trap surveys, we compared the temporal response of a small carnivore, the raccoon (*Procyon lotor*), to the larger coyote (*Canis latrans*) at four sites across Michigan that represented a gradient of pressure from humans. We found that raccoon time use varied by site and was most unique at the rural extreme. Raccoons consistently did not shift their activity pattern in response to coyotes at the site with the highest anthropogenic pressures despite considerable interannual variation, and instead showed the stronger responses to coyotes at more rural sites. Temporal shifts were characterized by raccoons being more diurnal in areas of high coyote activity. We conclude that raccoons do partition time to avoid coyotes. Our results highlight that the variation in raccoon time use across the entirety of the urban-rural gradient needed to be considered, as anthropogenic pressures may dominate and obscure the dynamics of this interaction. In an increasingly anthropocentric world, to understand species interactions, it is imperative that we consider the entire spectrum of human pressures that it may occur within.

Keywords: coyote, niche, partitioning, landscape of fear, Michigan, urban

# 1 | INTRODUCTION

Cities are a rapidly growing, emergent habitat type with projected increases to 120 million ha globally by 2030 (McDonald et al. 2018). These human pressures increasingly drive the decline of apex predators at a global scale (Ripple et al. 2014; Young et al. 2016). Similar to apex predators, humans can induce non-consumptive consequences on subordinate species through changes in space and time use (Ciuti et al. 2012; Clinchy et al. 2016). However, humans are unique in their top-down pressures in that they can exert fear effects across trophic levels, superseding hierarchies in natural systems (Smith et al. 2017; Suraci et al. 2019). The resultant heterogeneity of apex predator distribution from human pressures can induce differences in community structure as well as coexistence mechanisms within the carnivore guild (Berger 2007; Muhly et al. 2011; Moll et al. 2018). In urban areas, where spatial overlap among species are inevitable due to the limited amount of habitat available, temporal partitioning may be particularly important for species' persistence (Adams and Thibault 2006; Santos et al. 2019; Stark et al. 2020).

Urban-rural gradients provide natural experiments for comparisons of ecosystem function between natural and anthropogenic forces (McDonnell and Pickett 1990; Ellington and Gehrt 2019). Thus far, urban-rural gradients have predominantly highlighted changes in physical characteristics (e.g., body size) that can affect ecological interactions, or changes in biodiversity and species composition across taxa (Marzluff 2001; Urban et al. 2006). Although not specifically casted in an urban-rural framework, there are further evidence that humans and built structures can alter animal behavior (Van Donselaar et al. 2018; Avilés-Rodríguez and Kolbe 2019). For example, a global meta-analysis found that intensity of human pressure can drive increased nocturnality and reduce movement (Gaynor et al. 2018; Tucker et al. 2018). Altered time use due to humans can further translate into altered interspecific interactions (Lewis et al. 2015; Gallo et al. 2019). Recasting the implications of urban expansion from the primary focus of degradation to evolutionary potential occurs by considering them as novel ecosystems that have conservation value (Kowarik 2011; Seto et al. 2011; Alberti 2015). We leverage and expand upon the urban-rural gradient formed by human pressure to examine spatiotemporal dynamics between a widely distributed carnivore and a smaller sympatric competitor.

As a highly adaptive mesocarnivore, coyotes exploit a wide range of habitats and exhibit tolerance to disturbance with their diets and microbial community relating such variation across populations (Flores-Morales et al. 2019; Bekoff and Gese 2003; Colborn et al. 2020). Coyotes exemplify mesopredator release through range expansion that aligns with human caused extirpation of wolves. Though coyotes are subordinate to gray wolves where they are sympatric, they are an aggressor species for several smaller carnivores and account for high rates of mortality for some species (e.g., *Vulpes velox*, *Vulpes macrotis*) (Berger 2007; Bekoff and Gese 2003). As a result, coyotes are commonly cited as a species that can act as both a mesopredator or an apex predator in their community, depending on the presence of the gray wolf (Prugh et al. 2009; Roemer

et al. 2009; Colborn et al. 2020). Similarly, raccoons (Procyon lotor) exhibit tolerance to human pressures and spatially overlap through much of the coyotes North American range (Timm et al. 2017; Kays 2018). Coyote-raccoon interactions are interesting because of how widespread both species are, the size difference that should typify intraguild aggression or predation, and yet lack evidence for any sort of spatial or temporal partitioning (Gehrt and Clark 2003; Donadio and Buskirk 2006; Shedden et al. 2020). There has yet to be a study that examines the temporal dynamics of these two species across the urban-rural gradient.

Raccoons exhibit spatiotemporal variation in behavioral attributes, leading us to expect that the response of raccoons to coyotes may vary by differences in habitat and other characteristics across sites (Beasley et al. 2011). Gehrt and Prange (2007) put forth a convincing argument that raccoons and coyotes do not fit into the mesopredator release hypothesis, and there little evidence that coyotes act as a control on the abundance or spatial use of raccoons (Lesmeister et al. 2015). Telemetry studies of raccoons have found some evidence of mortality due to coyotes, but only as a rare occurrence (Gehrt and Clark 2003; Prange et al. 2003). In North Carolina, the temporal use of coyotes and raccoons largely overlapped and that raccoons overall exhibited low levels of vigilance, indicating low levels of fear from coyotes (Chitwood et al. 2020).

Given that coyotes pose some risk to raccoons based on size and sympatry, but that overall risk is low, we tested whether raccoons showed any finer scale shifts in time based on heterogeneity in coyote risk within a site. Employing a camera survey across an urban-rural gradient, we tested whether raccoon time differed between intensities of coyote spatial use. For context, we tested the variation in raccoon time use across two scales: between sites (across the urban-rural gradient) and within site, between years (interannual variation) (Figure 1), with hypotheses that: a) there raccoon time use at the most urban site would be significantly different than at the other three sites, and b) interannual variation would be more least pronounced at the urban site. Based on the strong fear effects that humans can exert on wildlife, we hypothesized that raccoon time use would not shift on the urban end of the gradient, due to activity patterns of both species avoiding peak hours of human activity. Conversely, we hypothesized that raccoons would shift in areas of intense coyote use on the rural end of the spectrum. As anthropogenic pressures increase, our knowledge of contemporary baseline ecological interactions becomes dated. Thus, it becomes essential to understand how these competitive interactions compare across landscapes with varying human pressures.

# 2 | METHODS

#### 2.1 | Study area

We investigated raccoon temporal dynamics across differing levels of coyote activity at four sites across the state of Michigan, USA (Figure 2) which represent an urban-rural gradient.

1) The Huron Mountain Club (HMC) is a privately-owned property along the southern shore of Lake Superior, encompassing around 6,900 hectares in Marquette County, Michigan, USA. This site has a wide variety of habitats including beech-sugar maple hardwood forests, aspen dominated stands, and coniferous boreal forests. Sympatric large predators include: gray wolves, black bears (*Ursus americanus*), and coyotes. An-thropogenic pressures are limited to a small, seasonally occupied area of human habitation near the north central part of the property. Hunting and fishing occur on the property, and the intensity is presumably low due to restrictive public access.

2) The University of Michigan Biological Station (UMBS), a ~4,000 hectare research station and forest in Pellston County, Michigan, USA served as one of our intermediate disturbance sites. With repeated logging and fire disturbance until 1923, the secondary forest is a mix of transitional hardwood and boreal forests. Douglas and Burt lakes along the north and south, and the town of Pellston and a major highway along west and east, respectively border this study area. Large co-occurring predators include: black bears, coyotes, and coyote-wolf hybrids. We were able to distinguish the few known coyote-wolf hybrids in the area due to them having collars from a different study, which were visible in the camera trap images (Wheeldon et al. 2012). Human pressures resulted from regulated research infrastructures for climate monitoring and housing facilities with low levels concentrated seasonally during the summer.

3) The Shiawassee National Wildlife Refuge (SNWR) is a 9,870 hectare wildlife refuge managed by the US Fish and Wildlife Service. The refuge is comprised of forested hardwood wetlands and lakeplain prairie. The city of Saginaw abuts the northern edge of the refuge and is surrounded by agricultural land for crop farming. The only large native predator present is the coyote. Anthropogenic pressures, in addition to the urban and ex-urban nature of the boundaries, are in the form of recreational visitors. Public hunting for deer and waterfowl, and furbearer trapping are permissible on the refuge in accordance with lawful seasons.

4) The Detroit Metro Parks (DMP) is a collection of greenspaces interspersed throughout southeast Michigan that is managed by the Detroit Parks and Recreation Department. We chose twenty-five of these parks that varied in size from  $\tilde{1.6}$ -480 hectares, tree cover, human visitation, and degree of disturbance. Roads, buildings, or a riverine edge bound all parks. The only large native predator present is the coyote. Strong anthropogenic pressures are present in the form of the surrounding urban matrix, as well as the associated presence of humans and domestic pets across parks

#### 2.2 | Camera trap survey

We deployed remotely-triggered camera traps (Reconyx $\bigcirc$  PC 850, 850C, 900, 900C) throughout each site with camera placement and sampling design proportional to study area size (Table 1). Our study uses data from four surveys at DMP (2017, 2018, 2019, 2020), two surveys at SNWR (2016, 2018), two surveys at UMBS (2015, 2016), and four surveys at HMC (2016, 2017, 2018, and 2019). We captured the heterogeneity of habitat and other environmental features to ensure ecological representation in the micro-site selection of camera traps. Camera traps were affixed to trees > 0.5m diameter and placed 0.5-1.0 m off the ground. Site-specific placement of camera traps was determined by signs of animal activity such as game trails and scat. Camera trap settings included: high sensitivity, one-second lapse between three pictures in a trigger, and a 15-second quiet period between triggers. Camera traps were not baited.

Image identifications were initially crowd-sourced and filtered for carnivores using a public-science program called *Michigan ZoomIN* in combination with a consensus algorithm and expert validation (Gadsden et al. 2021). Carnivore species identifications were later sorted and confirmed by at least two independent researchers in the Applied Wildlife Ecology Lab.

**2.3** | **Temporal activity**Time stamps associated with the camera trap images were used to conduct temporal analyses. Prior to all analyses, a 30-minute quiet period was introduced for every species to account for pseudoreplication, given the tendency of some animals to remain in front of the camera trap and trigger it multiple times. Since surveys were conducted across different times of the year, we scaled times to sunrise and sunset times using the *sunTimes* function in the 'circular' package in R (Ridout and Linkie 2009). 2.31 | Variation between sites

We first compiled all raccoon triggers from each survey within a site to have an aggregate across years of overall raccoon temporal activity at each site. We then compared raccoon temporal activity between sites using the Mardia-Watson-Wheeler (MWW) test, which is a nonparametric test of differences in the angular means between samples of circular data using the 'circular' package in R (version 4.1.0). When the W value is high it results in a significant p value (p < 0.05), which we conclude to mean that the compared temporal activities are unique.

#### 2.3.2 | Seasonal and yearly variation

Our multi-site camera study allowed us to compare differences in raccoon temporal activity based on landscape level differences along an urban-rural gradient. Comparing between seasons can confound inferences from the analyses, due to different seasons potentially resulting in different detection rates (Marcus Rowcliffe et al. 2011). While we did not have identical seasonal coverage for every site, the multiple surveys at every site resulted in coverage for the entire year at every site with the exception of UMBS (Figure S1). To determine if there was consistency at sites regardless of season and year, we compared raccoon activity between each survey within each site, and then looked for broader patterns across sites.

2.3.3 Coyotes on raccoon temporal activity

For each survey, we used a kernel density estimation for the independent covote triggers and designated the cameras that fell within the top quantile of as 'HIGH' coyote intensity of use zones in ArcGIS Pro (version 2.3.1). We used this rather than a fixed cutoff value of expected detection rate because our sites spanned the entirety of the urban-rural gradient and expected detection rates for coyote vary depending on the composition of a site (Magle et al. 2014). Coyote triggers were checked for spatial independence using Moran's I prior to kernel density estimation. We compared raccoon temporal activity between the high covote cameras and the rest of the site using the MWW test. For additional evidence that temporal shifts by raccoons were due to avoidance of covotes, we then compared the overlap between covote and raccoon time use in the two raccoon test groups from the MWW test. To do this, we calculated an overlap ( $\Delta$ ) coefficient of temporal activity for coyotes and raccoons within each group ('HIGH' and 'LOW' coyote intensity of use) along with 95% confidence intervals generated from 10,000 parametric bootstraps of the temporal distribution models.  $\Delta$  values range from 0 to 1, with 0 indicating completely distinct and non-overlapping temporal activity between comparison groups, and 1 indicating complete overlap.  $\Delta_1$  was used for comparisons when one of the sample groups had less than 50 triggers; otherwise  $\Delta_4$  was used to estimate temporal overlap (Ridout and Linkie 2009). Finally, the activity distributions were visually assessed to determine qualitative characteristics of shifts (e.g. raccoons shifting towards increased nocturnality in high coyote zones).

# 3 | RESULTS

We obtained 1,378 coyote and 11,136 raccoon triggers with a 30-minute quiet period across 12 surveys in 82,595 trap nights (HMC- 36,868; UMBS- 12,953; SNWR- 12,477; DMP- 20,297) from 2015-2020. Raccoons and coyotes were the most common carnivores in almost every survey, comprising 57-98% of all the carnivore triggers. In Detroit, where domestic dogs and cats comprised 35% of the triggers, coyotes were the fourth most common carnivore species after raccoons, cats, and dogs.

#### 3.1 | Coyote relative activity

Kernel density estimates indicated coyotes were distributed non-randomly in space (Figure 2). At DMP with heavy anthropogenic pressure (average 77 coyote triggers per camera in "HIGH" coyote zones), coyote activity was concentrated in two heavily forested parks and had few human triggers compared to the rest of the surveyed parks in Detroit. In contrast, at HMC with heavy natural apex pressure, the highest coyote activity occurred in a recreation area that contained several buildings and homes but had few overall triggers (average 3 coyote triggers per camera in "HIGH" coyote zones). Coyote activity formed distinct zones in SNWR and UMBS as well, and the location of hotspots varied by survey. Hotspots at these two sites were not associated with any discernible landscape level measures of anthropogenic pressures. Raccoon triggers were recorded within both the low and high zones of coyote activity across all sites, establishing spatial overlap between the two species

#### 3.2 | Variation in racoon activity between sites (Figure 1a)

Raccoon activity at each site was unique, showing significant differences in every pairwise comparison of sites from MWW tests (Table 1). We expected raccoon activity to be the most distinct at DMP, our most urban site. Instead, we found that raccoon activity was most unique at HMC, showing considerably more use of the diurnal period (Figure 5) and significantly less overlap with the other three sites (combined confidence intervals showing 76-87% overlap) than comparisons between UMBS, SNWR, and DMP (combined confidence intervals showing 87-96% overlap) (Figure 4).

# 3.3 | Seasonal/annual variation in raccoon activity (Figure 1c)

Raccoon activity varied significantly by survey and year for every site with the exception of UMBS (Table 2). At the most urban end of the urban-rural gradient, , raccoon activity was significantly different between every year surveyed at DMP and SNWR. At UMBS, the comparison between the two years approached significance (W = 5.53, p = 0.063). While at HMC the results varied, depending on the years compared. For example, 2016/2017 and 2017/2018 comparisons showed that raccoon time use varied significantly between these years, while raccoon time use between 2018 and 2019 was similar (W = 3.03, p = 0.220). These results

refuted our hypothesis that interannual variation would be weakest at DMP, instead showing that there is considerable variation across years at all sites.

#### 3.4 | Coyote use on raccoon temporal activity (Figure 1b,c)

Overall, our hypothesis for raccoon-coyote temporal interactions was largely correct, with raccoons at DMP consistently exhibiting no shift in time use relative to coyote intensity of use zones. However, there was reduced overlap between coyotes and raccoons within the high coyote zone. Results for the other sites varied by survey year (Figure 3). Below, we first present for each site the results for the comparison of raccoon activity between the high and low coyote zone. Then we provide the comparison of raccoon and coyote temporal activity within the high coyote zone (relative to the same comparison in the low coyote zone), to determine if there is evidence that a shift in raccoon activity between zones is due to temporal avoidance of coyotes.

**HMC:** At the most rural site, we found results for the effects of coyotes varied by survey. The 2016 and 2017 surveys exhibited no shifts, while surveys in 2018 and 2019 showed significant shifts in raccoon activity between coyote low and high zones (W = 15.12, 10.02, p < 0.00 respectively) (Table 1). Results were consistent even when the 2017 survey was broken up into summer and winter survey seasons since it covered an entire year, indicating no shifts in raccoon activity between coyote zones. When comparing coyote and raccoon temporal activity within each zone the 2018 survey showed some evidence of decreased temporal overlap between coyote and raccoons in the high coyote zone, while for 2019 the confidence intervals were too wide to be meaningful (Figure 3).**UMBS:** For both surveys, we found there were significant shifts in raccoon activity between coyote zones (W = 9.63, p < 0.00 for 2016, and W = 7.39, p = 0.025 for 2015). Both surveys showed evidence of reduced temporal overlap between coyote and raccoons in the high coyote zone.

**SNWR:** We found that again, results varied by survey, with two out of three surveys showing significant shifts in raccoon activity between coyote zones; 2016 (W = 6.08, p = 0.047) and 2018 (W = 10.46, p < 0.00) showed shifts, while in 2017 (W = 3.65, p = 0.162) raccoons did not shift activity. Only the 2018 survey showed evidence of reduced temporal overlap between coyotes and raccoons in the high coyote zone.

**DMP:** We found that raccoons exhibited no shifts in activity between coyote zones consistently across for all four years surveyed in our study. Curiously, three out of the four surveys (2018, 2019, and 2020) showed evidence of reduced overlap between raccoons and coyotes in the high coyote zone, with the difference reaching significance in the 2020 survey ( $\Delta_4$  CI in the high coyote zone: 0.46-0.58 vs. low coyote zone: 0.61-0.80).

#### 4 | DISCUSSION

Behavioral adjustments in diet, spatial, and temporal use can reduce competition for resources to promote coexistence (Inouye 1978). We tested for spatial and interannual variation in the time use of raccoons across an urban-rural gradient and measured the use of temporal refuges by raccoons in the presence of coyotes across that same gradient. As expected, we found that raccoon time use varied both across the gradient and between years. More importantly, we highlight that there were consistent patterns across the urban-rural gradient in raccoon temporal response to coyotes. We found that at the most urban site (DMP), raccoons consistently did not shift their temporal activity in response to coyotes, despite significant interannual variation in raccoon activity. In contrast, all other sites showed some evidence of behavioral plasticity in raccoon time use with the intensity of coyote spatial use. These results complement other findings that: a) non-consumptive effects impact the spatial use within the carnivore guild (Newsome and Ripple 2015); and b) that non-consumptive effects (fear effects) are present within the hierarchy of the carnivore guild (Gordon et al. 2015).

Urban systems represent an extreme of human pressures, and the continuing increase in urban habitat makes understanding the unique behaviors and ecologies of wildlife in urban spaces such as Detroit, Michigan particularly important. Breck et al. (2019) found that coyotes at urban sites are bolder in comparison to their rural counterparts, which would support their role as a fear source in cities. In absence of shifts in raccoon activity at our DMP site, it seems that this fear effect does not extend to raccoons. Given that we did find some evidence of temporal avoidance at our other sites, a more plausible explanation is that fear of coyotes is not strong enough to elicit a shift in raccoon time use in the face of a stronger force; the most obvious in an urban system being humans and domestic dogs, as reflected by raccoons at DMP having the least diurnal activity (Figure 5) (Gaynor et al. 2018; Nix et al. 2018; Sévêque et al. 2021). Despite raccoon activity consistently being similar between zones of coyote intensity of use, raccoon activity did seem to show somewhat reduced overlap with coyote activity in the high coyote intensity of use areas. This implies that coyotes were potentially using time differently depending on how heavily used an area was by conspecifics. A plausible explanation would be intraspecific competition (Cunningham et al. 2019), or this result could more generally suggest coyotes are more plastic in their time use than raccoons in urban systems (McClennen et al. 2001). The latter would make sense; although both species are cosmopolitan, raccoons are more human tolerant than coyotes (Crooks 2002; Randa and Yunger 2006).

Surprisingly, it was not the human-dominated urban system that was the most unique in raccoon temporal use amongst the sites, but instead the more pristine HMC in northern Michigan. The overall raccoon activity pattern showed considerable use of the diurnal period during which humans tend to be most active (Figure 6), resulting in low overlap with other sites. HMC also showed the greatest interannual variation in raccoon response to coyotes out of the four sites, once again perhaps reflecting a lack of human impact in the form of food subsidies (Manlick and Pauli 2020). The availability of resources can modulate the strength of competition, and so annual variation in food resources could drive the avoidance response of raccoons to coyotes (Newsome et al. 2015). At the other three sites, human food waste and other human-derived subsidies likely offset years that may otherwise be relatively resource-poor for raccoons (Oro et al. 2013). Unlike UMBS and SNWR, which have nearby towns, HMC is isolated, surrounded by forest and with the few cabins on the property only seasonally occupied.

Our results highlight broad patterns in raccoon temporal use between zones of high and low coyote activity. The mechanisms that underlie these patterns require further study and a temporal shift could very likely have more nuance than simple avoidance by a subordinate carnivore. A shift in temporal use by a subordinate (as shown in our SNWR and DMP sites) might instead reflect indirect avoidance of competition with a larger competitor rather than direct avoidance of antagonistic interactions (Newsome et al. 2015). While our results indicate the response of the raccoon to be driven by a larger predator, it does not preclude an interaction between top-down and bottom-up forces, which may be important to understanding what raccoons are directly responding to across sites and survey seasons (Elmhagen and Rushton 2007). For example, resource availability, such as the abundance of small mammal prey, fluctuates with season and could be a driver of varying levels of competition between coyotes and raccoons (Batzli 1992; Fedriani et al. 2000; Neale and Sacks 2001). At an urban site (e.g., DMP), food subsidies in the form of trash could reduce seasonal variation in resource competition (Oro et al. 2013; Newsome et al. 2015). Thus, we would expect patterns of temporal use, particularly in the presence of a competitor, to vary seasonally (Sovie et al. 2019). Seasonal variation in temporal response may explain the divergent result for the 2017 SNWR survey, which occurred during the summer months. The other two surveys at the site occurred during the fall and the spring, periods which are associated with heightened resource gathering for the imminent winter, and heightened coyote aggression because of the coyote breeding season (Way 2001). Pairing dietary studies that explore the seasonal variation in covote and raccoon diets across all sites with spatiotemporal analyses would elucidate if seasonal variation in resource availability drives resource partitioning between these species.

Though the two sites at the opposite ends of the gradient (i.e., HMC and DMP) best highlight the variation in raccoon temporal activity and temporal response to coyotes, there were site specific patterns for the entire gradient. We intended for our sampling sites to represent opposing gradients of humans and native apex predator presence, which were reflected in the amount of built structures and which carnivores were captured on camera at each site. However, given that we did not test for the effect of the relative activity of apex predators and humans, we cannot discount the possibility that factors other than top-down forces drove the urban-rural gradient we observed in our results. Sites varied in vegetative cover, topography, latitude, and distribution of resources. Though, differences in the sources of top-down forces are the most obvious and likely ecological factor that differs between the sites for generalist species such as raccoons and coyotes. Similar outcomes have been reported for other coyote-subordinate predator systems when compared across sites that vary in the presence of an apex predator (Shores et al. 2019).

# 5 | CONCLUSION

We conclude that there is evidence of temporal partitioning being used by raccoons in the presence of covotes. On the surface, our results seemingly contradict recent works that suggest that covotes are not an important intraguild predator for raccoons, and that raccoons thus do not partition time to avoid covotes (Gehrt and Clark 2003; Chitwood et al. 2020). Instead, we suggest that time use shifts may be at a fine scale, and whether they are present depends on a suite of factors. Therefore for a behaviorally plastic species such as the raccoon, it is difficult to make broad conclusions about time use without considering the considerable variation across the urban-rural gradient they inhabit. Similarly for the coyote, their role as an intraguild aggressor for raccoons is not static across the urban-rural gradient. Instead, the competitive dominance of coyotes is likely dependent on the amount of human pressure and the presence of other larger competitors. Ultimately, as the human footprint on the planet continues to deepen, we need to continue reevaluating interactions across the gradient that it creates. The paradigm in conservation is also shifting to include in situconservation of species in urban habitats, rather than considering these areas solely as suboptimal sink habitats (Magle et al. 2012; Athreva et al. 2013; Mormile and Hill 2017). Studies comparing the ecological roles of species within a community between urban and natural systems are timely. Such work will prove invaluable in understanding how wildlife communities in these novel habitats differ not just in composition, but also in their function.

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# AUTHOR CONTRIBUTIONS

NCH designed the sampling protocol, NCH and RM formulated the idea, NCH, RM, and SL carried out fieldwork and data processing, RM carried out analyses and wrote the manuscript, NH and SL provided heavy editorial duties.

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#### FIGURE LEGENDS

Fig. 1 The three comparisons considered within our study: a) Raccoon temporal activity was compared between sites; b) raccoon activity was compared between years, and across zones of coyote intensity of use within each site; c) the results from the within site comparisons of raccoon time use in response to coyotes were compared across sites.

Fig. 2 Kernel density (KD) heatmaps of coyote spatial use at the four study sites based on the number of independent coyote detections at each camera. From north to south, the Huron Mountain Club (HMC), the University of Michigan Biological Station (UMBS), the Shiawassee National Wildlife Refuge (SNWR), and the Detroit Metroparks (DMP). These represent a single year at each of the sites; hotspots in coyote detections varied by year, and KD maps were generated for each survey.

Fig. 3 Mean temporal overlap ( $\Delta_{\text{temporal}}$ ) between raccoons and coyotes in high and low spatial zones of coyote activity with 95% confidence intervals.

Fig. 4 Mean temporal overlap ( $\Delta$  Overlap) in raccoon activity conducted pairwise between sites with 95% confidence intervals. The letters correspond with each site (H=HMC, U=UMBS, S=SNWR, D=DMP), with the site it was compared to on the axis below. The differences between sites in each pairwise comparison were significant (using the MWW test).

Fig. 5 Raccoon activity across all four sites. Time use of raccoons was summed for all surveys within a site.

# TABLE LEGENDS

Table 1 . Temporal overlap ( $\Delta$ ) coefficients and 95% confidence intervals for raccoon and coyote activity in low and high coyote zones within each camera survey in Michigan. Trap nights equals the total number of cameras multiplied by the number of nights each camera was active. Mardia-Watson-Wheeler test results comparing raccoon activity between the top quantile and the bottom three quantiles of raccoon activity for each survey are contained in the last two columns, where W is the test statistic (approximately Chi-sq distributed), and *p*value are included.

Table 2 . Mardia-Watson-Wheeler test results comparing raccoon activity at each site between each survey year. W is the test statistic (approximately Chi-sq distributed), and associated degrees of freedom and p value are included.

TABLES

Table 1.

Survey period	Site/Year	Trapnights (n)	# Cameras	$\Delta$ ("Ι) Ηιγη	Δ (°Ι) Λοω	W
May-Aug	HMC'19	3445	96	0.32-0.72	0.28 - 0.85	10
Jun-Aug	HMC'18	8338	43	0.49 - 0.76	0.68 - 0.91	15
Jul-Jun JJunJunJUNJunJunJun'18	HMC'17	10874	43	0.65 - 0.83	0.56 - 0.80	3.8
Jun-Oct	HMC'16	14211	101	0.59 - 0.85	0.45 - 0.83	0.9
Jul-Nov	UMBS'16	8586	61	0.65 - 0.85	0.71 - 0.87	9.6
Oct-Dec	UMBS'15	4367	59	0.42 - 0.73	0.66 - 0.86	7.3
Sep-Dec	SNWR'18	3862	41	0.59 - 0.78	0.66 - 0.89	10
May-Aug	SNWR'17	3076	49	0.60 - 0.84	0.54 - 0.88	3.6
Feb-May	SNWR'16	5539	56	0.63 - 0.79	0.61 - 0.81	6.0
Jan-Sep	DMP'20	11713	39	0.46 - 0.58	0.61 - 0.80	3.3
Oct-Feb	DMP'18	4487	41	0.52 - 0.75	0.61 - 0.85	0.3
Nov-Mar	DMP'17	4097	39	0.59-0.83	0.57-0.84	0.6

# Table 2.

Years	Site	W	df	pvalue
19 vs 18	HMC	3.030	2	0.220
18 vs 17	HMC	22.99	2	0.000
17  vs  16	HMC	6.77	2	0.034
16  vs  15	UMBS	5.533	2	0.063
18 vs 17	SNWR	35.319	2	0.000
17  vs  16	SNWR	26.202	2	0.000
20 vs 18	DMP	7.948	2	0.018
$18~\mathrm{vs}~17$	DMP	9.884	2	0.007

Fig. 1





Fig. 2











Fig. S1 Concurrent surveys between sites used in analysis. At least two surveys were conducted at each site between 2015 and 2020. Surveys run chronologically from right to left; those surveys that have two survey periods within a year are surveys that were run through December, into the following year (e.g. HMC 2017 ran from July 2017 through May 2018).



# Fig.S1

**Table S1.** Raccoon activity between sites using Mardia-Watson-Wheeler test. W is the test statistic (approximately Chi-sq distributed), and associated degrees of freedom and *p*value are included. Temporal overlap ( $\Delta$ ) coefficients and 95% confidence intervals are also included to assess the overlap in activity patterns between sites. Raccoon activity at each site was based off the aggregated raccoon triggers for all

surveys with that site.

Site Comparison	W	df	pvalue	$\Delta_{ ext{oerlar}}$	Δ (°I)
HMC vs UMBS	50.001	2	0.00	0.79	0.75 - 0.83
HMC vs SNWR	40.358	2	0.00	0.84	0.79 - 0.87
HMC vs DMP	80.085	2	0.00	0.76	0.72 - 0.80
UMBS vs SNWR	9.654	2	0.01	0.90	0.88-0.93
UMBS vs DMP	9.54	2	0.01	0.94	0.91 - 0.96
SNWR vs DMP	63.218	2	0.00	0.88	0.87-0.90