

URBAN MAMMAL BEHAVIOR ADAPTATION

by

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DEDICATION

For mother earth.

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This research was conducted on lands historically occupied by indigenous people whose histories have been tragically compromised by colonialism and the systematic eradication of their culture and identity. I am both thankful and regretful that I was able to conduct my research on this beautiful land. My heart is filled with thanks for the love and support of Scott, Payton, Troy, and Luke Ritzel throughout this process...and always. Dr. Travis Gallo guided these efforts with unparalleled patience and wisdom. Dr. Cindy Smith and Megan Draheim generously supported this research with sage counsel and endless enthusiasm. Dr. Lauren Stanton provided invaluable, generous support in ethogram development. Dr. John Hadidian and Dr. Suzanne Prange graciously shared a wealth of knowledge on raccoon behavior. Conducting this research required the support and permission of George Mason University, University of Virginia, U.S. National Park Service, U.S. Department of Agriculture, Virginia Department of Conservation and Recreation, Virginia Department of Wildlife Resources, NOVA Parks, Montgomery County Parks, and Fairfax County Parks.

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LIST OF ABBREVIATIONS

Geographic information systems	GIS
kilometer	km
meter	m
millimeter	mm
mile	mi
secure digital	sd

ABSTRACT

URBAN MAMMAL BEHAVIOR ADAPTATION

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As humans continue to engineer and expand urban ecosystems, extant wildlife is increasingly exposed to novel pressures that drive changes in their spatial and temporal patterns, foraging tactics, anti-predator strategies, and other behaviors. Such behavior shifts can increase the potential for conflict with humans and present other challenges to the survival of urban species. Though behavior change in some urban taxa are widely studied, research on changing behavior in urban mammals is limited. Through systematic literature review, chapter one reveals how wild urban mammals are adjusting their behavior and explores the implications of urban-induced behavior adaptation. Chapter two seeks to address the knowledge gap on behavior change in the northern raccoon (*Procyon lotor*) through a comparative behavior analysis of populations in urban Washington D.C. and rural northern Virginia. Results highlight the need for long-term wildlife behavior studies across a variety of urban settings to promote successful urban wildlife management and conservation.

CHAPTER ONE

Introduction

By 2050, 68% of the world's 9.7 billion people will be residing in urban areas (UN, 2019a; UN 2019b). As cities expand to accommodate more people, their impacts to ecosystem processes and biota increase. Urban areas present unique and dynamic challenges for resident wildlife (Alberti, 2015; Birnie-Gauvin et al., 2016; Lowry et al., 2013; Miranda et al., 2013). In response to anthropogenic stressors, urban wildlife may exhibit behaviors differently than their non-urban counterparts (Chapman et al., 2012; DeCandia et al., 2019; Ditchkoff et al., 2006). As learning and behavioral adjustments are the primary ways animals cope with changing environments, the highly modified urban landscape provides a veritable proving ground for the ability of wildlife to adapt (Brown, 2012; Greggor et al., 2016). Decreasing natural habitat – alongside increasing anthropogenic resources – can lead to behavioral shifts in urban wildlife populations that present unique management and conservation challenges (Bateman & Fleming, 2012; Magle et al., 2019; Riley et al., 2010). Efforts to promote urban biodiversity while minimizing human-wildlife conflict will require a comprehensive understanding of what behavior changes are occurring in urban wildlife and how these species are potentially adapting over time.

Although behavior change can occur in wildlife without adaptation, it is helpful to consider behavioral responses, in terms of timescale and permanence, as either regulatory, acclimatory, or developmental (Lopez-Sepulcre & Kokko, 2012; McDonnell & Hahs, 2015). Where behavior changes fall among these three categories of adaptive response can offer insight into the mechanisms of change and whether behaviors may revert to population norms or progress toward permanent adaptation (Dingemanse et al., 2010; McDonnell & Hahs, 2015). Regulatory responses such as changes in alert behavior like harm avoidance or decreased flight initiation distance (FID) often develop within seconds to hours, whereas acclimation (e.g., adjustments in social structures and territoriality) may develop gradually over days and weeks (Bateman & Fleming, 2012; McDonnell & Hahs, 2015). Physiological changes and behavioral syndromes such as neophilia and boldness may indicate more permanent developmental response potentially leading to evolutionary change (Dingemanse et al., 2010; Lopez-Sepulcre & Kokko, 2012; McDonnell & Hahs, 2015). These adaptive responses may complement species survivability in some cases while being detrimental in others (Ellington & Gehrt, 2019; Robertson, 2018; Lopez-Sepulcre & Kokko, 2012; Lowry et al., 2013). As humans continue to alter the habitat and resources available to urban wildlife, knowing how these animals are adapting their behavior is key to understanding how certain species will persist in urban environments (Ryan & Partan, 2014; Soulsbury & White, 2015).

Despite urbanization's significant impact on wildlife, urban wildlife research remains a young and poorly understood field (Birnie-Gauvin et al., 2016; Magle et al., 2019). In their review of urban wildlife research, Magle et al. (2012) found that urban

wildlife studies comprised 2% of total publication volume. Although animal behavior is a common research topic and behavioral changes between urban and non-urban conspecifics are somewhat widely studied, mammals have been underrepresented (Magle et al., 2012; Miranda et al., 2013; McDonnell & Hahs, 2015; Schell, 2018). This is somewhat surprising as changes in mammalian behavior can often be precursors to conflict with humans and understanding how mammals use urban areas is an important component of wildlife management (Gehrt & McGraw, 2007; Karelus et al., 2017). Although selective urban pressures can have contrasting effects among mammalian species, it appears that behavioral flexibility among mammals allows them to better adapt to the urban environment (Santini et al., 2019). Generally, mammals are easily disturbed by human activity which drive changes in their behavior that can impact diet, reproduction, stress levels, diel activity, and disease prevalence (Ditchkoff et al., 2006; Birnie-Gauvin et al., 2016). These changes can lead to adaptations that may have important eco-evolutionary consequences. Despite the importance of understanding behavior changes in urban mammals, there has been no comprehensive review of the current primary literature specific to urban mammal behavior.

Following PRISMA guidelines, I conducted a systematic literature review of research pertaining to urban mammal behavior conducted over the past five decades. The aim of this review was to synthesize all research generating significant findings of behavior change in urban mammal populations (*population*) that were conducted in an urban setting, including those using conspecific and predator decoys, human-interaction, camera trap, trap and release, and/or remote tracking protocols (*interventions*) to assess

behavior change comparative to a non-urban population as defined by each individual study (*comparator*). Further, I sought to coalesce all research identifying specific behavior change (*outcomes*) in urban mammal populations, whether these changes were assessed via direct observation or inferred from remotely sensed/spatial data (*study designs*). Specifically, I was interested in the extent of urban mammal behavior change research and what, taken together, this research reveals in terms of adaptation to the urban environment. In answering this research question, I unveil the predominate types of behavioral adjustments observed in urban mammals, which taxa were most studied, the journals that publish these studies, geographically where these studies were conducted, and how these trends might inform future research. My findings underscore the importance of long-term behavioral studies to fully understand how behavior changes develop into permanent adaptations and to better inform urban wildlife management decisions ranging from conservation to human-wildlife co-existence.

Methods

To quantify the body of research specific to behavioral change in urban mammals, I conducted a systematic literature review following Pullin et al. (2018) using Web of Science and Google Scholar. I searched Web of Science for papers in the primary literature using the following search terms and Boolean operators: ‘urban*’, ‘city’, ‘town’ OR ‘metro’; ‘animal’, ‘wild*’, OR ‘mammal’; ‘beh*’; and ‘chang*’, ‘mod*’, ‘adapt*’, ‘alter*’ OR ‘evol*’. For Google Scholar, I used multiple combinations of primary search terms (urban, animal, behavior, change, mammal, and wildlife) in various sub-sections

(e.g., “in the title”, “anywhere”, “in subject”). I also reviewed citations within each retained paper for additional relevant studies.

I first compared titles to eliminate redundancy from my two searches. I included or excluded papers using pre-defined inclusion/exclusion criteria (Table 1) based on the title and/or abstract. For each study retained, I recorded how data was collected, study region, and the season each study took place. I also recorded species information, behavior studied, whether there was a change in behavior, the direction of effect where appropriate, and the type of adaptation demonstrated by the behavior change. I used the non-evolutionary adaptive responses identified by Ricklefs (1990) to group observed behavior changes into one of three adaptive response categories: regulatory, acclimatory, or developmental (McDonnell & Hahs, 2015).

Table 1 Criteria used to determine inclusion/exclusion of articles for literature review.

Inclusion	
<i>Behavior study</i>	article must be a behavior study; note, spatial studies may be appropriate if there is a stated behavior associated with observed change (e.g., home range)
<i>Urban population</i>	article must study behavior of a species/population in an urban setting
<i>Comparative behavior</i>	articles must study behavior of urban population with comparative reference (either results from same study on a different population or from literature) to indicate behavior change (e.g., urban versus rural)
<i>Relevant species</i>	article must include behavior study on at least one species in the class Mammalia
<i>Publication</i>	must be from a peer-reviewed publication; graduate theses may be included if quality of study is appropriate
<i>Language</i>	article must be either published in English or reliably translated
<i>Grey literature</i>	must provide relevant information specific to urban mammal behavior change
Exclusion	
<i>Irrelevant species</i>	articles on urban animal behavior change in solely non-mammalian and non-wild species (e.g., domestic or feral animals)
<i>Presence/ absence/ abundance studies</i>	articles solely on species abundance, presence or absence of species in urban areas
<i>Nonurban</i>	articles that do not include behavior demonstrated specifically in the urban environment (i.e., studies conducted along an urban-rural gradient may be included but will be excluded if at least one study area is not expressly urban)
<i>Literature review</i>	reviews of literature or publications that do not include novel results
<i>Laboratory study</i>	articles on urban mammalian behavior observed in a laboratory setting
<i>Author duplication</i>	multiple articles written by the same author(s) with the same observed behavior change if it is clear that observations were from the same study
<i>Unavailability</i>	articles not available through university resources, general internet access, etc.

Results

My *Web of Science* search resulted in 640 records, and *Google Scholar* yielded 136 for a total of 776 records. After removing duplicates, I was left with 744 unique records. After applying inclusion/exclusion criteria, I was left with 65 papers from database searches. I then reviewed the citations within each retained paper and found an additional 18 papers that met inclusion criteria for a final total of 83 studies. These 83 studies spanned from 1987 to 2020 and represent 8 general publication categories (Fig. 1). The studies were predominately published in journals specific to zoology and mammalogy.

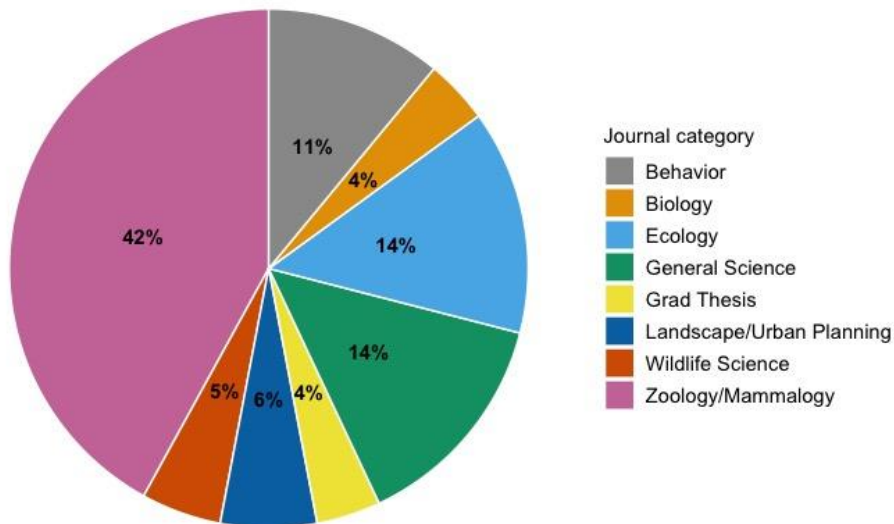


Figure 1. Publication categories of journals that published urban mammal behavior studies and the percentage of papers in each category.

The region with the greatest number of studies was North America (n=43, 52%), followed by Europe (n=17, 20.5%), Australia (n=9, 11%), Asia (n=7, 8.5%), Africa (n=5, 6%), and South America (n=2, 2%). With respect to diet guilds, 44% of the studies were on omnivores (n=37), 40% were on carnivores (n=33), and 16% were on herbivores (n=13). Every region with the exception of South America had studies from each of these three guilds (Fig. 2).

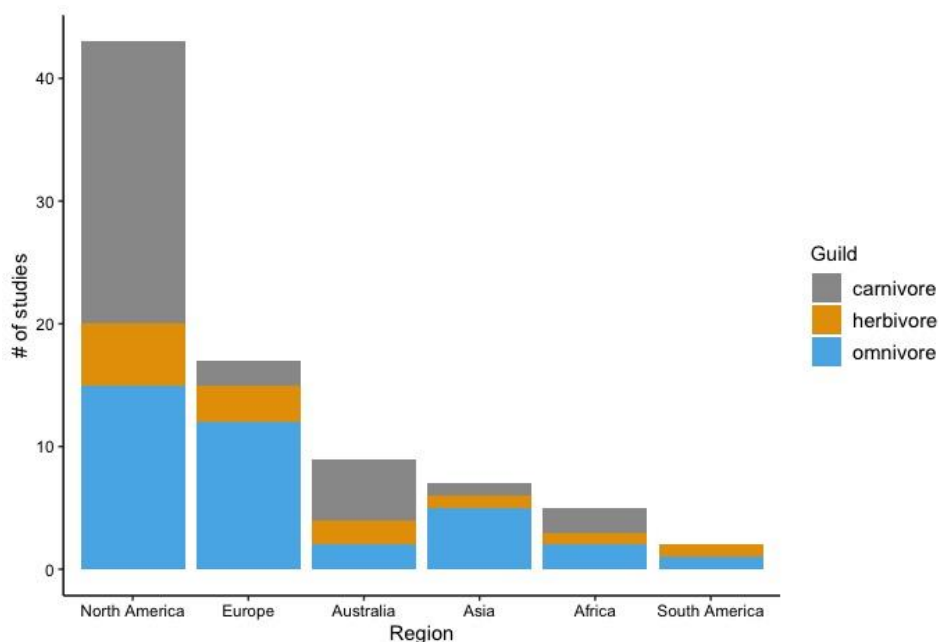


Figure 2. The number of studies that assessed behavioral changes of urban mammals across 6 world continents between 1987-2020. Results are categorized by diet guild.

Although most of the 83 studies focused on one species, 3 included observations on 2 or more species. Overall, 45 mammalian species were studied across 10 orders:

Carnivora (n=37 studies, 43%), Rodentia (n=23 studies, 26%), Primate (n=7 studies, 8%), Artiodactyla (n=5 studies, 6%), Chiroptera (n=4 studies, 5%), Diprotodontia (n=4 studies, 5%), Lagomorpha (n=3 studies, 3%), Didelphimorphia (n=2 studies, 2%), Eulipotyphla (n=1 study, 1%), and Peramelemorphia (n=1 study, 1%). The four most studied species were coyote (*Canis latrans*; n=12; 27%); eastern grey squirrels (*Sciurus carolinensis*; n=5, 11%); Eurasian red squirrels (*Sciurus vulgaris*, n=5, 11%); and black bears (*Ursus americanus*, n=5, 11%).

Behaviors studied

Some studies assessed multiple behaviors, which resulted in 166 observations of 44 different behaviors. Studied behaviors fell into 8 general types: alert behavior (n=45; 27.1%), spatial (n=40, 24.1%), diet preference/foraging/resource use (n=27, 16.3%), activity budget (n=22, 13.3%), diel activity (n=14, 8.4%), behavioral syndrome (n=9, 5.4%), mating/reproduction (n=7, 4.2%), and social (n=2, 1.2%) (Fig. 3). With respect to taxa, all orders included at least one spatial behavior study, with the exception of primates. Of the two most studied orders, researchers primarily looked at alert behavior in Rodentia (n=25/45) and spatial behavior in Carnivora (n=22/40).

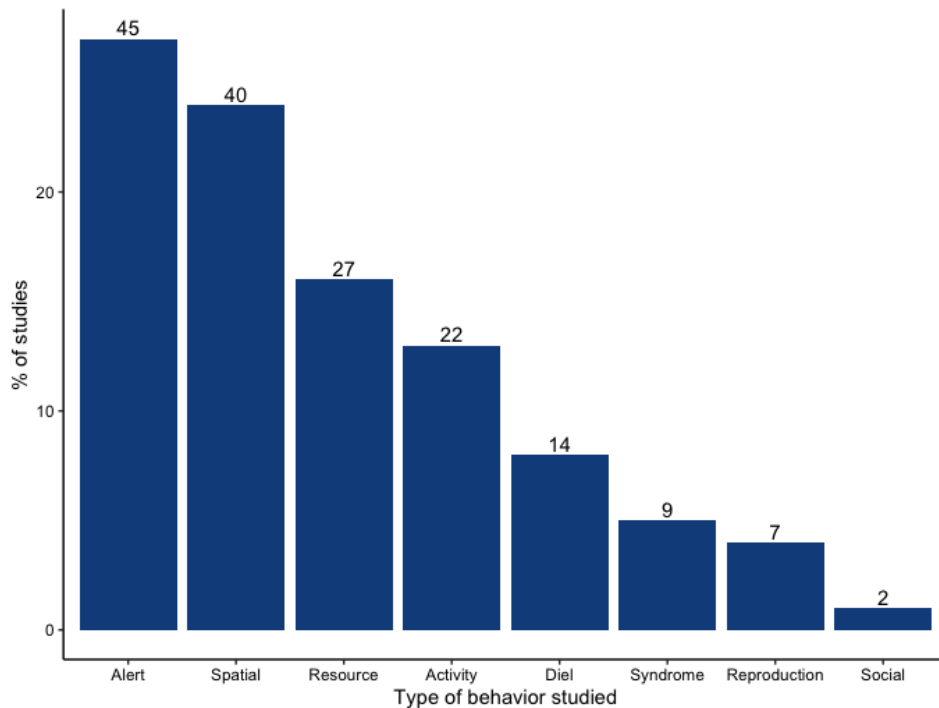


Figure 3. Types of behaviors studied in urban mammals between 1987-2020. Values placed above the bars indicate the total number of observations studied within each behavior type.

Behavior changes

Of the 166 studied behaviors, 93% ($n = 155$) were different from those observed in conspecifics outside the urban setting. In the remaining observations ($n = 11$; 7%), researchers found no change in behavior when comparing urban and non-urban mammal populations. Behavior changes were observed across 10 orders (Table 2) and in all species studied ($n = 41$; 91%) with the exception of Merriam's kangaroo rat (*Dipodomys merriami*) and 3 bats (*Lasionycteris noctivagans*, *Myotis spp.*, and *Eptesicus fuscus*). Among the studies that observed changes in behavior, the direction of change was not always consistent, even among species. In addition, some researchers observed multi-directional shifts in behavior in response to varying environmental stimuli ($n=7$, 4%).

Table 2. Behavior changes found in urban mammals grouped by order and guild. Values in parentheses indicate the number of behaviors studied.

Order	Guild	Behavior Change
Artiodactyla (11)	carnivore (2) herbivore (3) omnivore (6)	anti-predator, avoidance, FID (flight initiation distance), vocalization, home range, nocturnality, resource selection, spatial patterns, travel distance
Carnivora (62)	carnivore (53) omnivore (9)	AD (alert distance), anti-predator, avoidance, FID (flight initiation distance), escape activity, vigilance/caution, activity budget, den selection, denning time, diet preference, dispersal, fecundity, foraging/hunting, home range, movement speed, nocturnality, resource selection, spatial patterns, territoriality, time encamped, time/distance traveling, time foraging, boldness, exploratory
Chiroptera (2)	carnivore (2)	home range, time foraging
Didelphimorphia (3)	omnivore (3)	home range, travel distance
Diprotodontia (5)	carnivore (3) herbivore (2)	vigilance/caution, diet preference, home range
Eulipotyphla (3)	omnivore (3)	avoidance, spatial patterns, diel activity
Lagomorpha (7)	herbivore (7)	anti-predator, vigilance/caution, activity budget, latrine use, spatial patterns, time resting
Peramelemorphia (1)	omnivore (1)	home range
Primate (18)	herbivore (8) omnivore (10)	anti-predator, vigilance/caution, activity budget, conspecific tolerance, diet preference, foraging/hunting, grooming, play, problem-solving, time feeding, time resting, time traveling, exploratory
Rodentia (43)	herbivore (4) omnivore (39)	AD (alert distance), alarm behavior, alert response, anti-predator, concealment distance, FID (flight initiation distance), vigilance/caution, VED (vertical escape distance), activity budget, den selection, denning time, diet preference, dispersal, diurnality, foraging/hunting, GUD (giving-up density), home range, latency, resource selection, spatial patterns, time foraging, aggression

Adaptive response

Acclimation was the most common type of adaptive response (n=105; 68% of total behavior changes) observed among all taxa in the reviewed studies (Supplementary Material, Table S3). Six of the 8 types of behavior change (activity, diel, diet/resource use, mating/reproduction, social, and spatial) reflect acclimatory response to the urban environment (Fig. 4). Of these, decreased home range (n=19; 18% of total acclimatory responses) was the most frequently observed, followed by increased nocturnality (n=9; 9%), diet preference changes (n=9; 9%), and shift in resource selection (n=9; 9%). All observed changes in alert behavior were categorized as regulatory responses (n=43; 28% of total behavior changes). The most common regulatory responses were changes in vigilance/caution behavior (n=11, 4 decreasing, 5 increasing, 2 shifting with no direction noted; 26% of total regulatory behavior changes) and decreased FID (n=9; 21%). Observations of syndrome behavior in urban mammals indicate developmental response to the urban environment (n=7; 5% of total behavior changes). The two most prevalent changes in syndrome behavior were increased boldness (n=3; 43% of total developmental behaviors) and increased exploratory behavior (n=3; 43%). Together, omnivores, carnivores, and herbivores demonstrate more acclimatory response to the urban environment than regulatory and developmental responses, combined (Fig. 5).

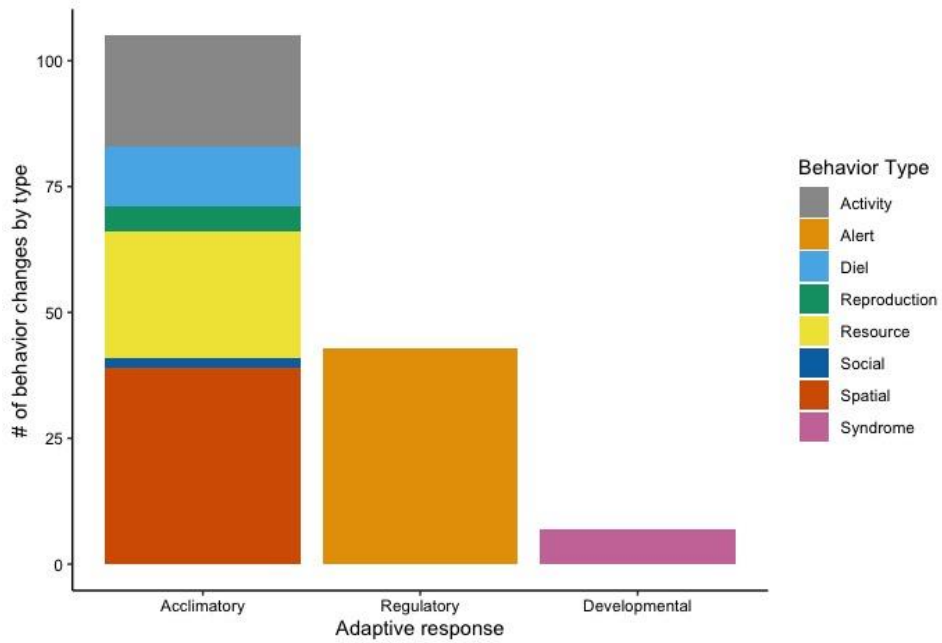


Figure 4. The 8 types of behavior changes observed in urban mammals from 1987-2020 categorized by adaptive response.

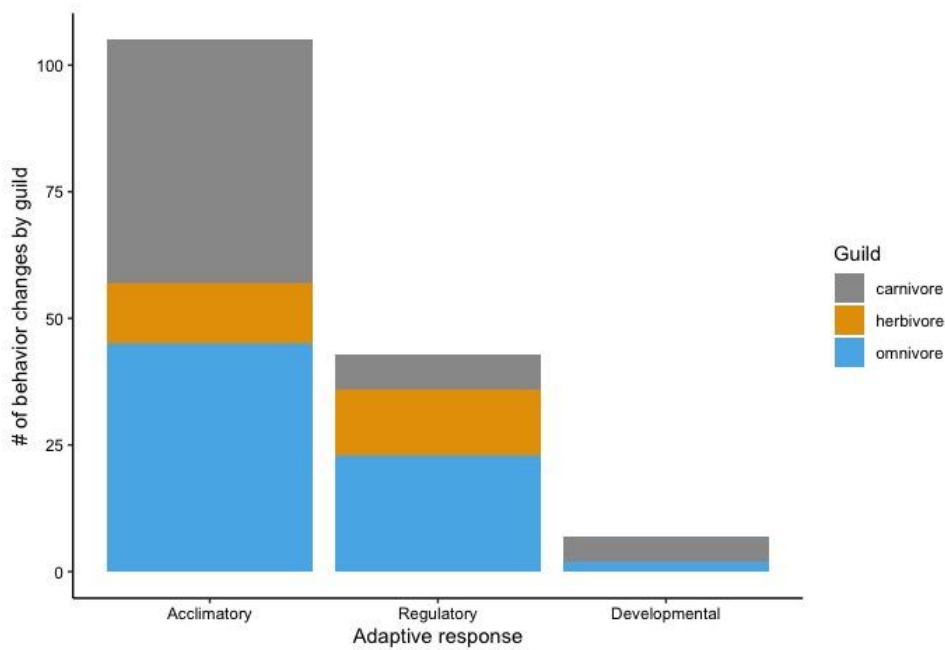


Figure 5. Number of behavior changes by guild in urban mammals from 1987-2020 categorized by type of adaptive response.

Discussion

My results clearly demonstrate that mammals are responding to the urban environment by changing their behavior. Much less clear is what these changes mean in terms of urban mammalian diversity, survivability, management, and conservation. Although the reported behavior changes reflect various types of adaptive response, the studies do not consistently discuss underlying mechanisms or their potential evolutionary implications. The vast majority of studies documented some degree of behavior change, but findings differed in terms of scale and direction – often depending on region, species, or resource availability. These results suggest there are varying mechanisms behind adaptive behavioral responses in urban mammals and that the nuances of these behavior shifts require further exploration.

Research extent

In-line with previous reviews, my results indicate that urban wildlife research is an emerging field and just recently gaining attention (Magle et al., 2019; Miranda et al., 2013). I found only 83 studies that explicitly studied mammalian behavior change in urban settings, and 50% of those studies were conducted in the last 5 years. Similarly, a previous review on overall urban wildlife behavior found 9 studies published between 1987 and 2012 that reported changes in alert and syndrome behavior in urban mammals (Miranda et al., 2013). That number increased to 50 in my review. Although this rapid jump is promising, the taxa remains significantly underrepresented, especially when compared to research on avian species in the urban environment (McDonnell & Hahs,

2015; Miranda et al., 2013; Sol et al., 2013). Given the negative impact that urbanization has on mammalian biodiversity (McCleery, 2010), and that the presence of mammals in urban areas often results in conflict with humans (Santini et al., 2019), it is important that future urban wildlife research reflects extant mammal populations in the respective region of study.

Taxonomic focus

Although mammals are an underrepresented taxonomic group in urban wildlife research, my review indicates a greater variety of mammalian species are being studied (n=45) as compared to previous reviews (Ditchkoff et al., 2006; McDonnell & Hahs, 2015; Miranda et al., 2013; Sol et al., 2013). Although the number of mammalian species has expanded, squirrel (n=12) and coyote (n=12) remain the dominate focal species, comprising almost a third of all studies. Likewise, herbivores were not well represented (n=31; 19%). Notably, deer (family *Cervidae*) and raccoon (*Procyon lotor*) made rare appearances in reviewed studies. Only one species of deer was represented (*Odocoileus virginianus*) in two studies (Gallo et al., 2019; Harveson et al., 2007) and I found only a single study (Prange, et al., 2004) assessing urban raccoon behavior change. As deer and raccoons are commonly associated with conflict in urban environment (Curtis & Hadidian, 2010; Hadidian et al., 2010; Westerfield et al., 2019), I were surprised at the apparent lack of interest in their behavior which does not align with on-the-ground management needs (Prange et al., 2003; Urbanek et al., 2011). These findings highlight the persistent gap between animal behavior research and management action, while underscoring the need for urban mammal behavior research that is responsive to

management and conservation concern (Caro, 1999; Curtis & Hadidian, 2010; Greggor et al., 2016; McDonnell & Hahs, 2015). Further, increasing taxa representation in this research will establish a foundational understanding of species-specific behavior change which can illuminate the degree and rate of urban-driven behavioral adaptation.

Changing behavior and adaptive response

The most common type of adaptive behavioral response observed was acclimatory. This is not surprising as the acclimatory category encompasses behaviors relating to movement, activity, and resource use, all of which were well represented in the reviewed studies. Urban mammals are widely adapting to the urban environment by acclimating their movement and resource use patterns. In every study assessing home range (n=25), a change was observed when compared to non-urban populations. The majority (76%) of studies on home range found that these decreased for urban mammals. However, the direction of effect was not consistent, even among the same species. As an example, the home range of urban lesser Asiatic yellow bats varied by sex: the home range of female bats increased in urban areas, while urban males decreased their home range (Atiqah et al., 2015). Conversely, 50% of studies on canids found that coyotes and fox (*Vulpes vulpes*) decreased their home range while 40% had an increased home range; the other 10% did not demonstrate a change in home range size per se, but a shift in terms of drifting territory or habitat type within the respective range (Doncaster & Macdonald, 1991; Grinder & Krausman, 2001; Grubbs & Krausman, 2009; Rosatte & Allan, 2009; Gehrt et al., 2009; Gese et al., 2012; Poessel et al., 2016; Ellington & Gehrt, 2019). One explanation for inconsistent changes in urban mammal home ranges could be the highly

variable nature of urban environments including inconsistent resource availability (Bateman & Fleming, 2014; Fitzgibbon et al., 2011; Van Helden et al., 2018; Wright et al., 2012). Urban mammals may selectively seek out natural prey, even among abundant anthropogenic resources which can drive increased home ranges in some mammals (Newsome et al., 2015). As population densities of mammals tend to be relatively high in urban areas, understanding behaviors that impact movement patterns and resource use can be key to successful management and conservation strategies (Curtis & Hadidian, 2010; Riley et al., 2010).

Although behavioral acclimations reveal much about mammalian adaptation to urban pressures, they do not reflect the full array of immediate behavioral response to urban stimuli, nor longer-term developmental change (McDonnell & Hahs et al, 2015). As examples, alert response and behavioral syndromes respectively provide insight into regulatory and developmental adaptations, both with important evolutionary implications (Dingemanse et al., 2010; Réale et al., 2010; Sih et al., 2004). Altered anti-predator behavior in the urban environment can significantly alter activity budgets and energy stores (Réale, et al., 2010). Consistent behavior modifications across different urban stimuli (i.e., behavioral syndromes such as increased boldness) can likewise impact mortality risk (Luttbeg & Sih, 2010). Each of the three types of adaptation (acclimatory, regulatory, developmental) offer useful clues as to how the urban environment affects mammal populations and how it may drive evolutionary change (Greggor et al., 2019; McDonnell & Hahs et al, 2015; Miranda et al., 2013). As such, increased research on behaviors that reflect a broader array of regulatory and developmental adaptations will

result in a more comprehensive understanding of the mechanisms behind urban mammal behavior change. Taking a collective look across the full temporal range of behavioral adaptation may help predict how urban mammal populations will fare in the face of continued urbanization. Beneficial behavior modifications by founder individuals can lead to increased fitness, whereas other adaptations may decrease survivability, both of which can result in higher-order effects on population dynamics among urban species (Alberti, 2015; Birnie-Gauvin et al., 2016; Lopez-Sepulcre & Kokko, 2012; Pelletier & Garant, 2012; Schell, 2018). Further, urban pressures and other drivers (e.g., anthropogenically provided food) that impact eco-evolutionary feedbacks appear to affect the distribution of behavioral traits (Alberti, 2015; Schell, 2018). Regulatory, acclimatory, and developmental adaptations all have the potential to alter processes that undermine healthy ecosystems and biodiversity, both of which are already fundamentally challenged in the urban environment (Alberti, 2015; McDonnell & Hahs et al, 2015, Palkovacs & Dalton, 2012). Continued research on how urban mammal behaviors are adapting across all timescales can yield important insights for conservationists, wildlife managers, city planners, and urban residents alike.

Modulating behavior

Because urban environments present such a dynamic mix of threats, it stands to reason that some changes in mammal behavior are multi-directional and perhaps, fluctuating. A particularly interesting finding among a small number of studies (n=7/166) is that some mammals demonstrate the ability to modulate adapted responses based on environmental cues. For example, two studies found variation in vigilance levels of

individual woodchucks (*Marmota monax*) based on the intensity of urbanization, possibly reflecting the variable nature of human pressures in highly urbanized areas (Watson, 2010; Lehrer et al., 2012). Likewise, fox squirrels (*Sciurus niger*) in Texas, USA demonstrated the ability to modulate anti-predator behavior to cope with constant stimuli created by humans in the urban environment (McCleery, 2009). Partan et al. (2010), found that eastern grey squirrels in western Massachusetts, USA modulated their alert behavior by increasing their reliance on visual signals versus audio signals in noisier environments. A study in New York, USA, found that 90% of urban grey squirrels increased their FID when approached by humans that veered off the sidewalk and looked at them, while squirrels from the same population did not increase FID if approaching humans remained on the sidewalk (Bateman & Fleming, 2014). Likewise, urban Eurasian red squirrels demonstrated the ability to assess risk levels of various approaching objects (e.g., humans and conspecific decoys) and modulated their FID accordingly (Uchida et al., 2019; Uchida et al., 2020). Finally, a study on Australian fur seals (*Arctocephalus pusillus doriferus*) found that seals modulated their alert response based on vessel type and whether or not vessels conformed with mandated approach distance thresholds – indicating that the seals learned the legal distance ships were able to approach (Speakman et al., 2020).

It is not readily apparent from these studies whether the modulations demonstrated are a function of inter-individual differences (behavioral plasticity) or consistent behavioral adaptations in response to repeated urban stimuli but they are all linked to risk assessment which has significant survival, and thus, evolutionary

implications (Bateman & Fleming, 2014; Lopez-Sepulcre & Kokko, 2012; Réale, et al., 2010). Although these represent a small sample size of reviewed studies, these apparent behavior modulations could begin to explain the behavior change pattern variation among certain urban mammal species. Seemingly, the majority of studies were designed to record discrete behavioral responses to specific stimuli and may have simply missed, or not considered, modulating behaviors. More research should focus on how urban mammals modulate their behaviors in response to variable urban pressures to better inform the drivers of urban-driven evolutionary behavior change. Understanding the mechanisms behind modulating adaptive behaviors, whether behavioral plasticity or contemporary evolution, can provide important insight into urban ecosystem ecology (McDonnell & Hahs, 2015; Miranda et al., 2013; Palkovacs et. al, 2012).

Limitations

I did not establish a specific definition of ‘urban’ for my review. Instead, I relied on the authors’ designation of the research setting as such. This inherently introduces limitations in capturing information about how varying levels of urbanization impact behavior change in mammals. Definitions of ‘urban’ in the reviewed studies, and elsewhere, are broad and may not consistently consider factors such as land use, structures, human population density, and impervious surfaces (McIntyre et. al, 2008; Ellington & Gehrt, 2019; Bateman & Fleming, 2012; Alldredge et al., 2019). Thus, I was unable to reliably relate specific features of urbanization to observed changes in behavior.

Recommendations for future research

As raccoon and deer conflict is relatively common in urban settings (Westerfield et al., 2019; Hadidian et al., 2010), it was odd to us that so little of the research focused on these species. Like McDonnell & Hahs (2015), I recommend future urban mammal research focus on delivering specific solutions to conservation and management challenges. Knowing how urban mammals are changing their behavior can improve mitigation strategies and conservation interventions (Caro, 1999; Greggor et al., 2016). Urban mammal researchers should continue to look at a host of behaviors that reflect various types of adaptive response (i.e., regulatory, acclimatory, and developmental) as they may be interrelated or lead to potential adaptive evolution over time (McDonnell & Hahs, 2015). Future research should highlight potential causes for observed adaptive responses to gain a better understanding of the mechanisms underlying urban mammal behavior change (Greggor et al., 2016; Palkovacs et. al, 2012). Conducting long-term, parallel studies on specific behaviors across a host of cities could likewise illuminate regional trends and help identify variable mechanisms driving behavior changes in the urban setting (Magle et al., 2019; Santini et al., 2019).

CHAPTER TWO

Introduction

Urbanization impacts wildlife through habitat degradation and loss (Lowry et al., 2013; Tuomainen & Candolin, 2011), modified resources and travel barriers (Barrett et al., 2013; Gese et al., 2012; Johnson & Munshi-South, 2017; Lowry et al., 2013; Prange et al., 2004; Tigas et al., 2002), increased noise and other pollution (Lowry et al., 2013; Tuomainen & Candolin, 2011), and shifting predator-prey dynamics (Fischer et al., 2012; Lowry et al., 2013; McCleery, 2009; Tuomainen & Candolin, 2011). These urban pressures can drive adaptations in wildlife behavior and alter resource use (Alldredge et al., 2019; Lowry et al., 2013; Newsome et al., 2015; Poessel et al., 2016), foraging tactics (Atiqah et al., 2015; Bowers & Breland, 1996; Sol et al., 2013), daily activity (Ellington & Gehrt, 2019; Jaman et al., 2013; Łopucki & Kiersztyn, 2020; Partan et al., 2010; Scheun et al., 2015), travel patterns (Barrett et al., 2013; Gese et al., 2012; Prange et al., 2004; Tigas et al., 2002), and anti-predatory strategies (Gallo et al., 2018; Lehrer et al., 2012; Ryan & Partan, 2014). These types of behavior change can ultimately affect species survival (Ditchkoff et al., 2006; Johnson & Munshi-South, 2017; Palkovacs & Dalton, 2012; Tuomainen & Candolin, 2011) and urban mammals are especially sensitive to these effects as changes in their behavior often precedes conflict with humans (McCleery, 2010; Greggor et al, 2016).

One such example is the widely distributed northern raccoon (*Procyon lotor*) which is one of the most abundant urban carnivores in North America and frequently

associated with human-wildlife conflict (Curtis & Hadidian, 2010; Hadidian et al., 2010). The raccoon's innate behavioral flexibility, high urban densities, and affinity towards anthropogenic resources make them particularly vulnerable to human-wildlife conflict in the urban setting (Daniels et al., 2019; Hadidian et al., 2010; Louppe et al., 2019; Prange et al., 2003). Additionally, raccoons are vectors for several diseases that pose a threat to public health including rabies, leptospirosis, and raccoon roundworm which has relatively high human mortality rates (Hadidian et al., 2010). Though raccoon behavior has been studied since the early 1800s (Hadidian et al., 2010; Zeveloff, 2002), surprisingly little is known about how wild raccoon behavior has changed as a result of urbanization (Ritzel & Gallo, 2020).

A generalist, both in terms of diet and habitat, raccoons can alter a wide range of behaviors in response to their environment (Daniels et al., 2019; Hadidian et al., 2010; Prange et al., 2004; Stanton et al., 2021). This ability affords a relatively high degree of 'behavioral plasticity' which can result in the adjustment of specific behaviors in response to environmental feedbacks (Breck et al., 2019; Dingemanse et al., 2010; Lopez-Sepulcre & Kokko, 2012; Lowry et al., 2013; Miranda et al., 2013; Palkovacs & Dalton, 2012; Tuomainen & Candolin, 2011). While studies specific to urban raccoon behavior are limited, research suggests that raccoons have a high degree of behavioral plasticity that allow them to persist and adapt in urban environments (Daniels et al., 2019; MacDonald & Ritvo, 2016; Stanton et al., 2021).

Behavioral plasticity may reveal itself in various ways including reduced fear of novelty (neophobia), increased boldness, and changes in exploratory and alert behavior,

sometimes referred to as behavioral syndromes (Lowry et al., 2013; Luttbeg & Sih, 2010; Sih et al., 2004; Young et al., 2015). Reduced neophobia may be an important factor in the ability of wildlife to adapt to urban environments through successful exploitation of anthropogenic resources (Barrett et al., 2019). Raccoons have been shown to demonstrate varying levels of neophobia, exploratory diversity, and persistence, all of which are likely important factors in the species' ability to thrive in urban areas (Daniels et al., 2019; Hadidian et al., 2010; Louppe et al., 2019; MacDonald & Ritvo, 2016; McCleery et al., 2014; Prange et al., 2003; Stanton et al., 2021). However, increased use of anthropogenic resources drives higher population densities and disease transmission among urban raccoons (Prange et al., 2003) which may set the stage for heightened conflict in the urban setting. Though there are several studies on captive and wild raccoon behavior, comparative behavior studies between urban and nonurban conspecifics are limited (Ritzel & Gallo, 2020). One such study found decreased dispersal and home ranges of urban raccoons, indicating urban-induced adaptation (Prange et al., 2004). Other examples of behavior adaptation in raccoons is limited, but unpublished data from MacDonald & Ritvo (2016) suggests that urban raccoons demonstrate higher levels of persistence, neophilia, and exploratory behavior when compared to rural counterparts.

Raccoons gather information from their environment largely using olfactory, tactile, and visual cues and may demonstrate a wide range of exploratory behaviors such as sniffing objects or the air and rubbing items between paws (Zaveloff, 2002). The number of distinct exploratory behaviors demonstrated by raccoons can vary at the individual level, as does the amount of time animals spend engaged in exploratory

behavior, sometimes referred to as “work time” or persistence (Amram-Benson & Holekamp, 2012; Daniels et al., 2019). Researchers working with captive raccoons found that levels of exploratory diversity, persistence, and neophobia predicted problem-solving performance (Daniels et al., 2019). As urban raccoons are routinely exposed to novel stimuli and rewarded for manipulating novel objects (e.g., household trash cans), one might expect urban individuals to demonstrate greater exploratory diversity and decreased neophobia when encountering a novel object.

Analyzing an animals’ reaction to novel objects *in situ* has been successfully used to assess behavior differences in wild mammals (Amram-Benson & Holekamp, 2012; Breck et al., 2019; MacDonald & Ritvo, 2016; Young et al., 2015). Further, past studies have shown that novel object tests are powerful tools for indicating behavior change among urban adapted species (Breck et al., 2019; Miranda et al., 2013). Differing responses to novel stimuli, such as reduced fear or avoidance, may indicate the development of behavior syndromes such as increased exploratory behavior and boldness which can contribute to increased human-wildlife conflict (Breck et., 2019; Dingemanse et al., 2010; Luttbeg & Sih, 2010; Sih et al., 2004). Similarly, response to novel stimuli can reflect maladaptive shifts in giving up density and anti-predator tactics, both of which can alter activity budgets and energy stores (McCleery, 2010; Partan et al., 2010; Réale, et al., 2010; Tuomainen & Candolin, 2011). Examining the ways in which urban raccoons react differently to novel stimuli can improve our understanding of the drivers and mechanisms behind urban-induced behavior change and adaptation (McDonnell & Hahs, 2015; MacDonald & Ritvo, 2016).

The goal of this study was to explore urban raccoon behavior change by comparing indicators of neophobic, exploratory, and alert behavior between urban and rural raccoons. I did this by analyzing individual raccoon response to novel stimuli using video data obtained from remotely triggered wildlife cameras at sampling sites throughout the Washington D.C. metropolitan area and rural Northern Virginia. I tested the effect of novel object treatment on raccoons in urban and rural study areas by assessing multiple response variables: latency to approach within an arm's length of sampling site center (bait location), time to make contact with bait location, exploratory and alert diversity, and time spent in exploratory and alert behavior states. I predict that urban raccoons will take less time to approach and contact the center of sampling sites, spend greater time at the site, and take up bait, thereby demonstrating reduced neophobia as previously seen in urban mammal populations (Barret et al., 2013; MacDonald & Ritvo, 2015). As reduced neophobia in raccoons has been linked to increased exploratory diversity and persistence, I predict urban raccoons will demonstrate higher levels of these exploratory behaviors (Daniels et al., 2019; MacDonald & Ritvo, 2015). The effect of urbanization on alert behavior among urban mammals is unclear. While some studies have observed decreased alert behavior in urban mammals (Bateman & Fleming, 2014; McCleery, 2009), others found that mammals in urban areas demonstrate increased alert response (Partan et al., 2010; Sarno et al., 2015). Notwithstanding the void of research on alert behavior among urban raccoons (Ritzel & Gallo, 2020), I predict that raccoons in the urban study area will demonstrate reduced alert behavior when compared to rural counterparts. Improving our understanding of these types of adaptations in raccoons, and

urban wildlife in general, can help us better predict how urban pressures will continue to impact biodiversity and evolutionary trajectories (Alberti et al, 2020; Greggor et al., 2019; McDonnell & Hahs et al., 2015; Miranda et al., 2013; Schell, 2018).

Methods

Study areas

I conducted this research in two distinct study areas: 1) the Washington D.C. metropolitan area (urban) and 2) northern Virginia (rural). The urban study area included Washington D.C. and surrounding urbanized areas of Virginia and Maryland adjacent to the district boundaries. Although the population density of Washington D.C. was 11,500 people/mi², the average population density for the greater urban study area was roughly 4,000 people/mi² (GGW, 2013; U.S. Census Bureau, 2019). The urban study area was comprised of a complex matrix of natural open spaces, waterbodies, and developed spaces with a mixed community of flora, fauna, and humans commonly reflective of urban systems (McCleery et al., 2014; Soulsbury & White, 2016). Washington D.C. was recognized as one of the top ten cities in America for wildlife with a relatively high percentage of parkland and ample opportunity for observing urban wildlife behavior (NWF 2019). I established 41 sampling sites in the urban study area (Fig. 6).

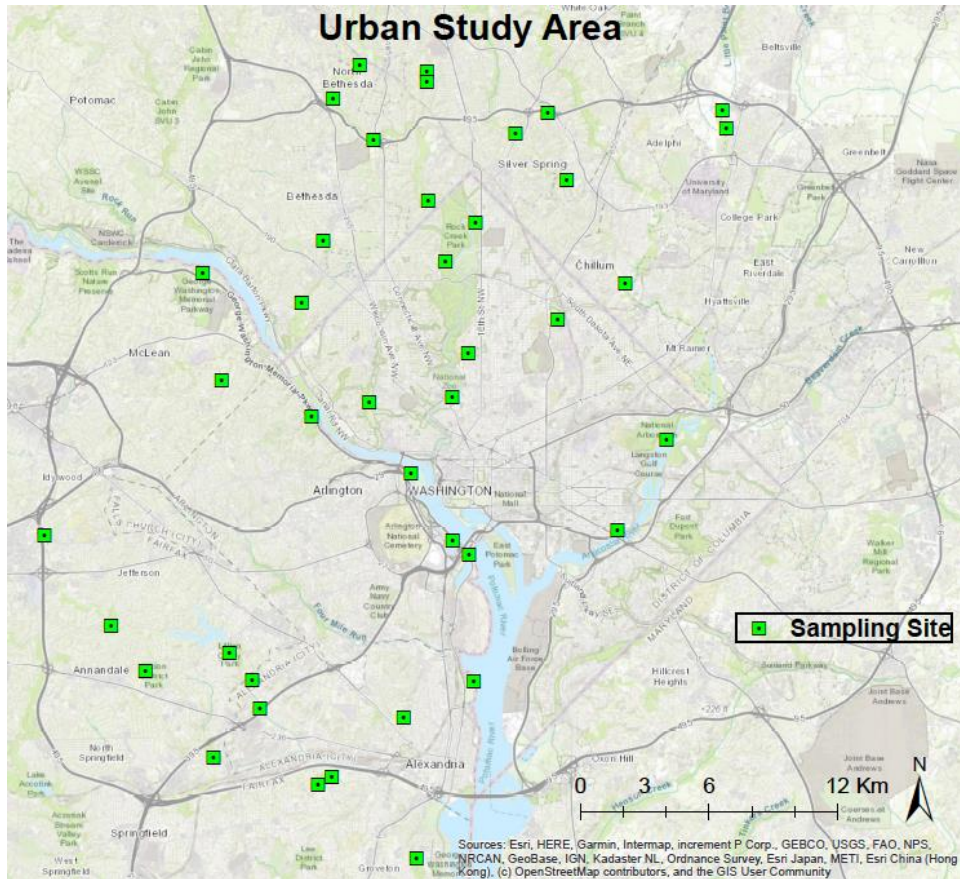


Figure 6. Extent of urban study area with example sampling site laydown. This map was created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved.

Sampling sites in the rural study area were spread throughout National Parks, Virginia State Parks, the Virginia State Arboretum, and Wildlife Management Areas (WMA). All rural sampling sites were located in Virginia (Fig. 7). The rural study area was comprised of primarily undeveloped, natural, and wild habitat that were protected by area boundaries with minimized built structures and relatively low human presence (DCR, 2021; NPS, 2021; UVA, 2021). There were 26 sites located in Shenandoah National Park which is surrounded by eight counties with an average population density of 101 people/mi² (NPS, 2021; U.S. Census Bureau, 2019). There were four sites situated

in Virginia Department of Conservation and Recreation (DCR) parks: Shenandoah River State Park located in Warren County (184 people/mi²) and Sky Meadows State Park located in Fauquier County (110 people/mi²) (DCR, 2021; U.S. Census Bureau, 2019). One site was located in the Virginia State Arboretum in Clarke County (88 people/mi²) (U.S. Census Bureau, 2019; UVA, 2021). There were nine sites spread throughout Virginia Department of Wildlife Resources (DWR) WMAs: C.F. Phelps WMA in Culpeper and Fauquier counties (122 people/mi² average); Merrimac Farm located in Prince William County (1,400 people/mi²); Rapidan WMA in Madison and Greene counties (83 people/mi² average); and Thompson and Weston WMAs both located in Fauquier County (110 people/mi²) (U.S. Census Bureau, 2019; DWR, 2020).

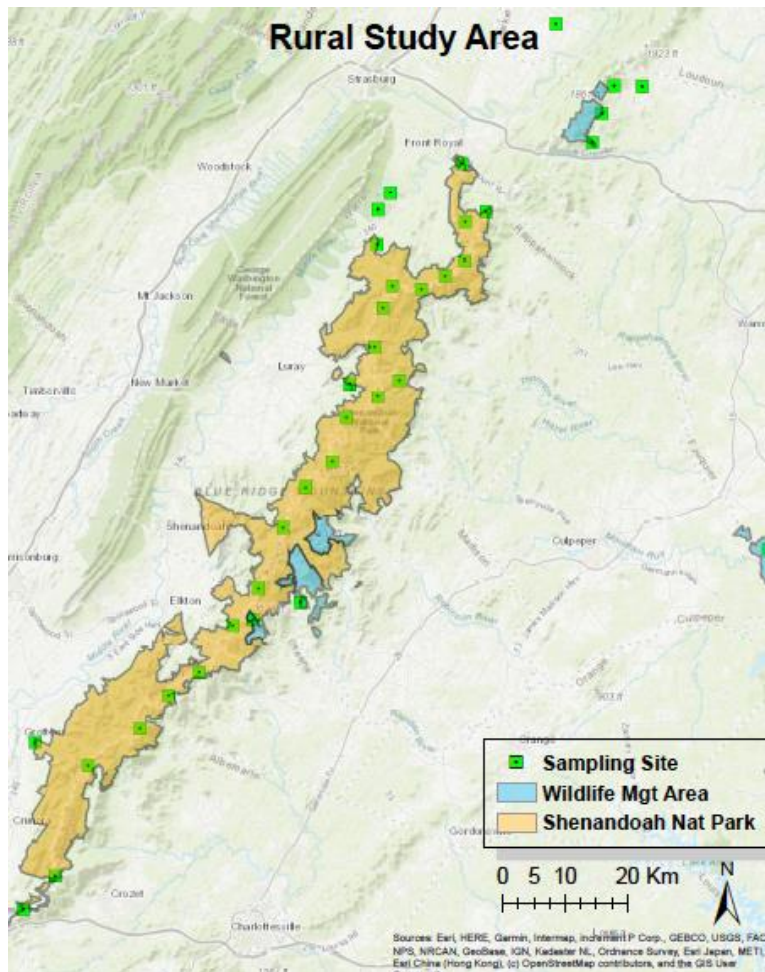


Figure 7. Extent of rural study area with sampling site laydown. This map was created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved.

Study design and data collection

The study design for my comparative analysis was based on the novel object test used by Breck et al. (2019) to compare bold and exploratory behavior of rural and urban coyotes. I used a similar design to gather and analyze data on raccoon behavioral response to novel stimuli. To establish individual sampling sites within my urban and rural study areas, I used ArcGIS ver. 10.7 (Esri, Redland, CA, U.S.A) to establish randomized cell grids with cell size set at the maximum raccoon home range for the

respective study area: 0.5 km² (urban) and 2 km² (rural) cells (Prange et al., 2004). For each grid, I randomly selected 50 individual cells to initially target as sampling site locations to ensure replication and minimize confounding factors. Locations within the urban study area variably included areas within or adjacent to parks, greenbelts, golf courses, arboretums, cemeteries, easements, nature preserves, public recreational spaces, and some areas that were subject to hunting pressure. Likewise, rural sampling sites included areas both near and far from public access points, recreational areas and trails with variable human traffic, campground/picnic areas, and areas subject to hunting pressure. I further refined these random locations to reconcile logistical and practical limitations (e.g., lack of trees, inadequate greenspace, or limited accessibility). I contacted landowners/managers for permission to conduct research at the remaining 90 locations. After obtaining permits for 81 locations, I numbered the final sampling site locations, then randomly assigned treatment or control to each: 41 urban – 22 control, 19 treatment; 40 rural – 20 control, 20 treatment.

At each sampling site, I secured one Bushnell motion-triggered infrared Trophy Cam (Bushnell, Overland Park, Kansas, USA) camera on a tree approximately 1m from the ground. Cameras were situated to record video of a location on the ground approximately 3.5m away where I placed 1 tbsp of Sweet Meat Predator Bait (Russ Carman, New Milford, Pennsylvania) and one 25mm diameter plaster disk impregnated with a fatty acid scent (Pocatello Supply Depot, Idaho) as an attractant. At treatment sampling sites, I installed 4 stakes made of processed wood at the corners of a 1m² area approximately 3.5m from the camera. These stakes were approximately 1m above the

ground with white paracord rope tied at the top of the stakes to form a square (Fig. 8). In the center of each treatment, I placed the bait in a shallow hole (approximately 5 cm deep), covered it with leaves, and placed the attractant on top. Each camera was set on the highest sensitivity setting to record a 30 second (day) or 15 second (night) video once triggered by a visiting animal. For each study site, I recorded latitude and longitude, set-up date, and take-down date. I visited study sites roughly every two weeks to download secure digital (sd) card footage, change camera batteries, and replenish bait and/or attractant as needed. I stopped sampling at each site once a raccoon visit was recorded (14 to 89 days). I collected data at the 81 sampling sites from 1 July 2020 through 20 October 2020.



Figure 8. Example of novel object used at treatment sampling sites.

Behavior analysis and ethogram

Raccoon behavior was assessed using a novel ethogram (Table 3) to code behaviors of individual raccoons visiting each study site. Each behavior was assigned a unique behavior code that fell into one of two behavior types indicating a behavior state, either exploratory or alert. Exploratory behavior state was one in which raccoons contributed the majority of their activity to investigating objects in their immediate vicinity. Exploratory behaviors included sniffing, touching, and otherwise investigating the novel object or ground at the sampling site. In an alert behavior state, raccoons generally paused and engaged in activity indicating the use of olfactory, auditory, and/or visual cues to gather information from the environment. Alert behaviors included sniffing the air with head lifted away from the novel object, a distinct pause in exploring, or other behavior to listen, sniff, or scan surroundings.

Table 3. Ethogram used to assess and code behavior observations.

Behavior	Definition	Behavior Code	Behavior Type
Back away	Approach novel object (within an arm's length), pause and reverse direction (still facing novel object)	BA	A
Bite	Open mouth and close teeth on novel object (stick or cord)	BI	E
Climb	Raise body vertically along novel object stick	CL	E
Dig	Use paws to penetrate the ground inside periphery of novel object/at attractant site	DI	E
Eat	Place predator bait or fatty acid tab into mouth and consume	EA	E
Groom	Scratch, clean, shake, or rub fur with paw	GR	NA
Hang	Use limbs to suspend body while holding on to novel object (stick or cord)	HA	E
Lick	Open mouth and move tongue on novel object (stick or cord)	LI	E
Jump	Hop or spring away from novel object or attractant site	JU	A
Look away	Distinctly pause and turn head away from novel object or bait/attractant	LA	A
Pace	Move back and forth repetitively within arm's distance of novel object/attractant site	PA	A
Pause	Approach novel object/bait/site on all fours, stop, and then continue in direction of object/attractant site	PS	A
Pick up	Take attractant/bait into paw(s)	PI	E
Pull/push	Use mouth or paw to wiggle or move novel object (stick or cord)	PU	E
Reach	Extend nose, neck, or paw toward object/attractant	RE	E
Rub	Move object/attractant back and forth between hands vigorously	RU	E
Sniff ground	Move nose back and forth along ground to detect scent; nose can be touching ground or within an arm's length	SG	E
Sniff object	Move nose along novel object (stick or cord) to detect scent, nose can be touching object or within an arm's length	SO	E
Stand	Stand on hind legs within body's distance from the object/attractant (not touching object)	ST	E
Stop	Pause movement, bring legs close together in a squatted position underneath body w/in periphery of novel object	SP	E
Turn away	Approach novel object/attractant, stop and proceed in a different direction	TA	A
Touch	Place nose or paw(s) on novel object (stick or cord)	TO	E
Walk by	Proceed past novel object/attractant on all fours not approaching site (within an arm's length)	WB	NA
Behavior type: A-alert; E-exploratory			

To code raccoon behavior, I recorded each demonstrated behavior, time engaged in each behavior, and total time spent in either an exploratory or alert behavior state. I annotated the number of raccoons visiting, whether or not they ate bait or attractant, time spent on video, time to approach the site center (baited area) within an arm's length, and time to contact site attractant or bait. Individuals that did not demonstrate exploratory or alert behaviors (e.g., raccoons walking by 'WB' or grooming 'GR') were not included in the analysis. I eliminated potential duplication of individuals by assessing the first raccoon visit to each study site. Videos in a continuous series (within 1 minute of each other) were considered the same visit/individual.

Data analysis

The independent variables for this study were 1) study area (urban or rural) and 2) the presence or absence of a novel object (treatment or control). I assessed the effect of these independent variables on response variables falling into one of three categories of behavior: neophobia, exploratory, and alert.

Neophobia

I used three response variables to assess neophobia. 1) latency to approach (LTA): the amount of time, in seconds, elapsed from the initial entrance of the raccoon into the video frame to when the individual was within an arm's length of the sampling site center (i.e., where the bait is located); 2) time to contact (TTC): the amount of time, in seconds, elapsed before the raccoon touched the site center; and 3) total time

at site (TT): the total time, in seconds recorded for each individual during a single visit (used as a proxy for total time spent at the site). Higher LTA and TTC times indicated increased neophobia, whereas higher TT generally indicated a higher comfort level, thus reduced neophobia.

Exploratory behavior

The response variables used to assess exploratory behavior were the number of unique exploratory behaviors demonstrated by visiting raccoons (exploratory diversity) and the total time, in seconds, raccoons were engaged in these behaviors (persistence).

Alert behavior

Similar to exploratory behaviors, alert behavior was assessed using the number of unique alert behaviors demonstrated by visiting raccoons (alert diversity) and the total time, in seconds, raccoons were engaged in alert behavior (alert behavior state).

Modeling approach

I analyzed response variables using generalized linear models and AICc model selection (Anderson et al., 2004). For each analysis, models within 2 Δ AICc of the top model were considered informative models. I used the top model in each analysis to make inferences about the effect of each treatment and study area on each response variable. I used Poisson regression to model latency to approach, time to contact, total time at site, exploratory diversity, persistence, alert diversity, and alert behavior state. For all Poisson models, with the exception of TT, I used an offset term $-\log(\text{Total_time})$ to account for the likelihood of increasing count data as a function of video length. For each response variable, I developed a competing model set that included univariate

models with each independent variable, an additive model of both study area and treatment, and a model that included an interaction term between study area and treatment, and an intercept only (null) model. All data analysis was conducted using R ver. 1.2.5033 (R Core Team, 2019).

Results

Within the urban study area, raccoons visited 33 of the 41 sites (80%). Of these, 15 were control and 18 were novel object treatment sites. In the rural study area, 34 of the 40 sites were visited by raccoons (85%) – 18 control sites and 16 treatment sites. I used the complete dataset of 67 observations (urban, n=33; rural, n=34) to assess neophobia indicators (LTA, TTC, and TT). As the behavior ‘Walking by’ (WB) was not reflective of either an alert or exploratory behavior state, I did not include these observations in alert and exploratory analyses. After I removed 16 WB-only observations, a subset of 51 observations remained to assess alert and exploratory behaviors of rural (n=30) and urban (n=21) raccoons.

Neophobia

Small sample sizes for latency to approach (LTA) and time to contact (TTC) (urban/treatment, n=7; urban/control, n=6; rural/treatment, n=6; rural/control n=9) hampered model convergence and I was unable to make inference about the significance of the effect. However, I found that when a novel object was present, both populations increased average LTA and TTC (urban LTA=14.3 ±14.1, TTC=22.8 ±20.3; rural LTA=10.0 ±11.9, TTC=13.0 ±11.7). Rural raccoons had lower LTA and TTC at sites without a novel object (LTA=7.0 ±4.2, TTC=8.2 ±4.1).

With respect to total time at site (TT), rural raccoons at control sites had the highest average TT (30.9 ± 4.5), while urban raccoons at control sites had the lowest average TT (12.1 ± 13.3). The top model for the analysis was the model with an interaction term between study area and treatment (Table 4). Results showed an overall decrease in TT in the urban study area ($\beta = -0.94$, 95% CI [-1.10, -0.77], $r^2 = 0.08$), but an increase in TT of urban raccoons when a novel object was present ($\beta = 0.88$, 95% CI [0.67, 1.09], $r^2 = 0.08$).

Table 4. Model selection results for the total video time (seconds) as a function of study area and treatment. Study area refers to either rural or urban; treatment refers to either control or novel object treatment; * indicates an interactive effect; + indicates and additive effect.

Response	Model	K	Δ AICc	Weight	LL
Total Video Time (TT)	Study area * Treatment	4	0.00	1.0	-1026.32
	Study area + Treatment	3	65.22	0.0	-1060.06
	Study area	2	70.38	0.0	-1063.74
	Treatment	2	133.41	0.0	-1095.25
	Intercept only (null)	1	135.67	0.0	-1097.44

Exploratory behavior

Urban and rural raccoons had similar average exploratory diversity scores (urban: 3.14 ± 1.90 ; rural: 3.07 ± 2.56). However, the average exploratory diversity of urban raccoons increased when they visited sites with a novel object treatment (3.50 ± 1.93) while exploratory diversity decreased in rural raccoons (2.5 ± 2.50). All models except the model with an interaction term were within 2 Δ AICc of the top model (Table 5). However, no model outperformed the null model. Although the presence of a novel

object increased exploratory diversity in urban raccoons and lowered it in rural raccoons, the (individual and additive) effects of treatment and study area were not significant.

Table 5. Model selection results for exploratory diversity as a function of study area and treatment. Study area refers to either rural or urban; treatment refers to either control or novel object treatment; * indicates an interactive effect; + indicates and additive effect.

Response	Model	K	Δ AICc	Weight	LL
Exploratory Diversity (score)	Intercept only (null)	1	0.00	0.33	-111.68
	Study area	2	0.98	0.21	-111.09
	Treatment	2	1.05	0.20	-111.12
	Study area + Treatment	3	1.14	0.19	-110.04
	Study area * Treatment	4	3.04	0.07	-109.81

Like exploratory diversity, average persistence among urban and rural raccoons was similar (urban: 0.66 ± 0.24 ; rural: 0.61 ± 0.31) and the average persistence of urban raccoons increased when they visited sites with a novel object treatment (0.67 ± 0.27), whereas it decreased in rural raccoons (0.59 ± 0.33). Similarly, top models included all models with the exception of the model with an interaction term (Table 6). Although the study area only model indicated that urban raccoons had lower persistence than urban raccoons, the effect was not significant as the model coefficient confidence intervals overlapped 0 ($\beta = -0.12$, 95% CI [-0.25, 0.01], $r^2 = 0.03$).

Table 6. Model selection results for persistence as a function of study area and treatment. Study area refers to either rural or urban; treatment refers to either control or novel object treatment; * indicates an interactive effect; + indicates and additive effect.

Response	Model	K	Δ AICc	Weight	LL
Persistence (seconds)	Study area	2	0.00	0.39	-163.75
	Intercept only (null)	1	1.33	0.20	-165.49
	Study area + Treatment	3	1.55	0.18	-163.39
	Treatment	2	1.67	0.17	-164.58
	Study area * Treatment	4	3.62	0.06	-163.25

Alert behavior

Average alert diversity was higher in urban raccoons (0.71 ± 0.90) than in rural raccoons (0.57 ± 0.77). Average alert diversity was highest in urban raccoons that visited sampling sites with a novel object (0.83 ± 0.94) and lowest in urban raccoons that visited control sites (0.55 ± 0.88). The top models included the intercept only (null) model and the study area only model (Table 7). The model that included only study area indicated that urban raccoons had higher alert diversity, but the effect of study area was not significant as model coefficient confidence intervals overlapped 0 ($\beta = 0.38$, 95% CI [-0.31, 1.08], $r^2 = 0.01$).

Table 7. Model selection results for alert diversity as a function of study area and treatment. Study area refers to either rural or urban; treatment refers to either control or novel object treatment; * indicates an interactive effect; + indicates and additive effect.

Response	Model	K	Δ AICc	Weight	LL
Alert Diversity (score)	Intercept only (null)	1	0.00	0.45	-64.29
	Study area	2	1.01	0.27	-63.71
	Treatment	2	2.03	0.16	-64.22
	Study area + Treatment	3	3.27	0.09	-63.71
	Study area * Treatment	4	5.23	0.03	-63.51

On average, urban raccoons spent less total time in an alert behavior state (0.07 ± 0.11) than rural raccoons (0.11 ± 0.22). Urban raccoons that visited sites without a novel object treatment (control) spent the lowest average time in an alert behavior state (0.05 ± 0.08). Rural raccoons that visited control sites, on average, spent the most time in an alert behavior state (0.13 ± 0.23) though rural observation data was disproportionately affected by outliers (Fig. 9).

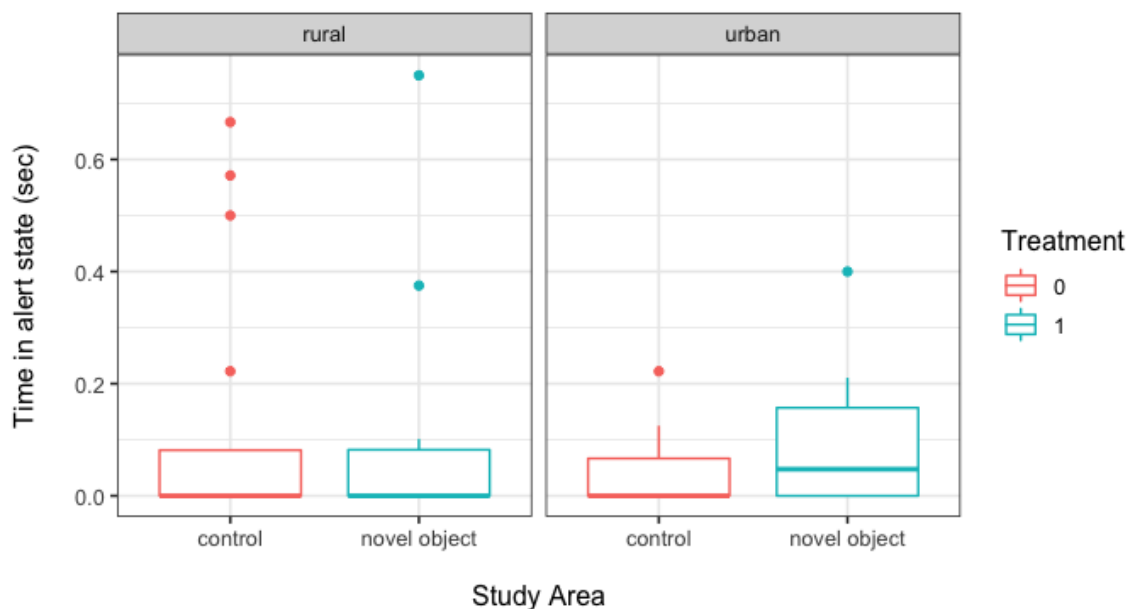


Figure 9. Boxplots of time (seconds) raccoons spent in alert state by study area and treatment. Study area refers to either rural or urban; treatment refers to either control or novel object treatment; bold horizontal line = the median value; bottom and top of box = 1st and 3rd quartiles; dots = outliers in the data.

Top models included all models with the exception of the treatment only model (Table 8). The top model (study area only) indicated a slight increase in time spent in alert state among urban raccoons, though this effect was not significant as model

coefficient confidence intervals overlapped 0 ($\beta = 0.38$, 95% CI [-0.02, 0.78], $r^2 = 0.02$).

The model that included the interaction term between study area and treatment showed a significant effect increase in the time urban raccoons spent in an alert behavior state ($\beta = 0.83$, 95% CI [0.20, 1.47], $r^2 = 0.04$).

Table 8. Model selection results for alert behavior state as a function of study area and treatment. Study area refers to either rural or urban; treatment refers to either control or novel object treatment; * indicates an interactive effect; + indicates and additive effect.

Response	Model	K	Δ AICc	Weight	LL
Alert Behavior State (seconds)	Study area	2	0.00	0.35	-132.19
	Study area * Treatment	4	0.80	0.23	-130.28
	Intercept only (null)	1	1.31	0.18	-133.93
	Study area + Treatment	3	1.98	0.13	-132.05
	Treatment	2	2.35	0.11	-133.37

Discussion

Although humans have been studying raccoons for over two centuries, there has been a lack of research specifically on urban raccoon behavior. With abundant urban populations, the behaviorally flexible, urban-adapted raccoon serves as an ideal focal species to assess urban-induced behavior change (Daniels et al., 2019). Through a comparative analysis of urban and rural raccoon behavior, I explored whether or not urbanization has affected the behavior of raccoons in terms of neophobic, exploratory, and alert behavior. Results indicate that behavioral response to novel stimuli differs among urban and rural raccoons, particularly in exploratory and alert behavior. In urban environments, novelty is routinely introduced through anthropogenic disturbance which leads to changes in wildlife behavior that affect their ability to persist in urban systems

(Breck et al., 2019; Lowry et al., 2013; Greggor et al., 2014). If urban raccoons are less fearful of novelty (i.e., less neophobic) than those in urban areas, there may be an elevated potential for conflict with humans in urban settings (Barrett et al., 2018; Prange et al., 2003). Likewise, changes in alert behavior may compromise fitness by altering activity budgets and avoidance tactics (Lowry et al., 2013; Sih et al., 2004). Although the results of my comparative analysis on raccoon behavior were not definitive in terms of neophobia, they suggest that urbanization has influenced the behavior of raccoons by affecting their response to novelty.

Neophobia

Changes in fear of novelty (neophobia) among wildlife can result in maladaptive behavior and present challenges to survival, particularly in human-dominated systems (Barret et al., 2019; Greggor et al., 2019; Lowry et al., 2012). To assess changing levels of neophobia in raccoons, I used total video time assuming that higher total time indicated reduced neophobia. Total time was lower for urban raccoons overall, but their time at sites increased significantly with the presence of a novel object. Urban raccoons may be desensitized to novel objects appearing in their home range and may associate the introduction of novel objects with exploitation opportunities (e.g., food). Urban raccoons were also more persistent when a novel object was present which leads me to believe that time spent at site is more closely linked to exploratory behavior rather than fear of novelty. Given the dynamic nature of the urban setting, along with its shifting resources and additive pressures, urban raccoons may move more quickly through the landscape and invest their energies where they perceive

potential for reward. In retrospect, I believe that total time spent at a sampling site was not an appropriate indicator of neophobia and was likely confounded by the presence (or absence) of bait – many sites were visited by various other species that took bait from the site prior to raccoon visits. To better assess neophobia in urban raccoons, a more robust dataset is needed along with fine-scale analysis of avoidance behaviors such as latency to approach (Daniels et al., 2019) and giving up density (Stephens et al., 2008).

Exploratory behavior

Much like its effect on total time, the presence of a novel object increased exploratory diversity and persistence in urban raccoons. Although I predicted that urban raccoons would demonstrate higher levels of exploratory behavior, I did not foresee the variable effect of treatment on these indicators across study areas. That is, when a novel object was present, the exploratory behavior of urban raccoons increased whereas the exploratory behavior of rural raccoons decreased. These results suggest expanded exploratory plasticity among raccoons in general and may lead to selection for increased exploratory behavior in urban settings. Likewise, urban and rural raccoons may differ in their ability to discriminate and classify cues from the environment – an ability that underlies how animals perceive, and adjust to, novelty (Barrett et al., 2019; Greggor et al., 2014). Although I did not assess specific elements of cognition or perception in my study, many rural raccoons appeared not to notice the novel object whereas urban raccoons typically stopped to explore it before moving towards the bait. It is possible that increased exploratory behavior in urban raccoons when a novel object is present reflects an ability to categorize the object as a potential resource opportunity. Whereas, the novel

object may not be similarly categorized by rural counterparts. Differences in categorization, and cognition in general, among urban raccoons should be further investigated.

Alert behavior

My results suggest that raccoons may be able to modulate alert behavior in response to environmental cues as seen in other mammals (Ritzel & Gallo, 2020). Although I predicted alert behavior in urban raccoons would be lower than rural raccoons, my results showed the opposite to be true – average alert diversity was higher in urban raccoons and highest when a novel object was present. Conversely, urban raccoons spent less total time in an alert behavior state though this nearly doubled when a novel object was present. Modeling results indicated a significant interactive effect of novel object presence and urban study area which may partially explain this shift in alert behavior. Urban raccoons may associate the appearance of novel objects with anthropogenic disturbance and perceive it as either a threat or as an opportunity to exploit a novel resource. Modulating alert behavior may be a response that urban raccoons use to navigate these unknowns. This ability may be an example of fully expressed behavioral plasticity in urban raccoons or, as suggested by previous research, may indicate microevolution in the urban population (Miranda et al., 2013).

Broader implications

To promote sustainable urbanization, continued research that focuses on understanding and monitoring urban-induced changes in animal behavior is important (Alberti et al., 2020). Such change may variably impact the fitness of specific urban

species (Dingemanse et al., 2010; Réale et al., 2010; Sih et al., 2004). The differing behavior among urban raccoons in this study suggest the need to further explore the causal mechanisms behind urban wildlife behavior change, levels of adaptive response, and possible evolution on a contemporary scale (Alberti, 2015; McDonnell & Hahs, 2015). Uncovering the specific mechanisms causing behavior adaptation, evolutionary or otherwise, can inform every enterprise involving urban wildlife – from conservation to conflict management (Johnson et al., 2017; Sol et al., 2013; Tuomainen & Candolin, 2011).

The behavioral flexibility allowing certain species such as raccoons to adapt to selective pressures in the urban environment (i.e., phenotypic plasticity as discussed in Lowry et al., 2013) is an important consideration for urban development and wildlife conflict management. Unfortunately, as emphasized by Honda et al. (2018), there is an ongoing gap between human-wildlife conflict management practices and scientific understanding of urban wildlife behavior. This is especially pertinent as research suggests that an increased tolerance of certain urban species to anthropogenic disturbance may simultaneously increase the potential of conflict encounters (Alberti et al., 2020; Johnson et al., 2017). Knowing the strength, direction of effects, and outcome of different behavior changes can lend vital insight into urban-induced adaptation and allow practitioners to make informed and predictive decisions regarding the management of urban wildlife. Additional comparative behavior studies among urban and non-urban mammalian conspecifics are needed to build this knowledge.

Limitations

Because I assessed only one raccoon visit at each sampling site, I did not consider consistent behavior differences among individuals, sometimes referred to as temperament (Réale et al., 2007). To gain a comprehensive understanding of behavior change in wildlife, comparative behaviors should be studied at the level of the individual while also investigating related processes at the ecosystem scale (Shochat, 2006). Exploring individual differences in behavior, especially in terms of neophobia and temperament, can offer insight into inter-individual differences and the mechanisms behind behavior change (Greggor et al., 2019; Lowry et al., 2013; Réale et al., 2007). Comparative analyses would therefore benefit from long-term observation of marked individuals to assess type and degree of change over time.

Possible confounding factors present with this study include the introduction of novel stimuli without controls and camera limitations. Raccoons are highly sensitive to olfactory stimuli and the fatty acid scent tab likely served as a secondary novel stimulus. As I did not control for the fatty acid tab (i.e., olfactory stimuli), I was unable to assess its effect on behavior. Additionally, camera limitations were tied to camera field of view, and at times, camera malfunction. I was only able to record and assess behavior captured within the frame which excluded the full gamut of approach and exit behaviors demonstrated by visiting raccoons. This was a necessary trade-off as tightening the frame allowed more granularity in terms of assessing specific behaviors and the behavior state of each visiting raccoon. In terms of malfunction, cameras intermittently failed to capture

raccoons entering the site. For similar research, I would recommend using a different camera model with higher sensitivity and a faster trigger time.

Conclusion

As humans continue to alter the habitat and resources available to urban wildlife, their ability to persist is inherently linked to how they adapt their behavior (Ryan & Partan, 2014; McDonnell & Hahs, 2015; Soulsbury & White, 2016). The findings from Chapter 1 demonstrate that urban mammals are exhibiting widespread acclimatory behavioral response to urban pressures. Likewise, my comparative analysis of urban and rural raccoon behavior (Chapter 2) revealed differing behavior along the urban-to-rural gradient. Yet, the long-term effects of these changes are unknown. My findings suggest a need to better understand the mechanisms behind urban mammal behavior change and the eco-evolutionary impacts that may result. Urban mammal research requires a shift to align priorities in a way that contributes to the growing body of knowledge on changing behavior while supporting real-time management and conservation efforts. To fully understand changing urban mammal behavior, long-term studies across multiple cities will better inform local wildlife management solutions, establish baselines of species-specific behavior change, and promote the mutually beneficial co-existence of all urban residents.

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