

Boldness Behavior and Chronic Stress in Free-Ranging, Urban Coyotes (*Canis latrans*)

DISSERTATION

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By

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ABSTRACT

Human activity and the development of cities have major impacts on local wildlife. Some populations, however, have adapted their behaviors to successfully live in proximity to people. Within any given species, there is often behavioral variation. Some previous studies have suggested that individual variation is at least partly due to the presence of behavioral syndromes (i.e., suites of correlated behaviors in response to a common stimuli). One commonly studied set of behaviors are those that fall along a bold-to-shy spectrum. Bold individuals are often more risk-prone, more exploratory, and less sensitive to external stressors than their shy counterparts. Behavioral syndromes imply that individuals have innate, predispositions toward certain responses to external stimuli; behavioral plasticity is therefore limited under the behavioral syndromes paradigm. Limited plasticity can be beneficial in some situations, since it allows individuals to specialize in a particular response. Behavioral tendencies (e.g., boldness) are not necessarily efficient or safe in all situations, however. The environment may help to shape how prevalent certain behavioral syndromes are within a given population. In urban areas, the increased human activity, high level of habitat fragmentation and disturbance, and large quantities of novel resources (e.g., litter) may give bolder individuals multiple advantages. Shy individuals would likely have difficulty coping with the various stressors associated with urban life and would be less likely to find and benefit from novel, anthropogenic resources. In settings where coyotes are actively hunted, trapped, or hazed, however, bold individuals that are more comfortable around people may ultimately be more likely to get involved in a human-coyote conflict. In every environment, there is a tradeoff between potential benefits and potential risks.

To determine if behavioral syndromes are present in free-ranging coyotes and examine the possible relationships between urbanization, behavior, and physiology, coyotes in the Greater

Chicago Metropolitan Area were subjected to behavioral tests and tested for chronic stress. In my dissertation, I first provide an overview of some of the impacts of urban areas on wildlife and describe how wildlife sometimes respond to anthropogenic pressures. I also describe the possible link between behavior and physiology and highlight the need for more studies that incorporate both simultaneously.

My second chapter focuses on the results of flight initiation distance (FID) tests I conducted on free-ranging coyotes across Chicagoland's urbanization gradient. Coyotes in more developed areas tended to have shorter FID, indicating a greater degree of boldness towards human approachers. Additionally, the starting distance from the coyote, the distance from the coyote's resting place to the nearest road, and the average velocity of the approaching human were significant predictors of coyote FID. Flight initiation distances were consistent over time for individuals that were tested more than once, suggesting that coyote responses may reflect innate, individual variation in responses to risks rather than habituation over time.

In my third chapter, I report on novel object tests that I conducted on urban coyotes. A larger proportion of the coyotes in developed (i.e., urban and suburban) areas tended to be neophilic. A greater degree of neophilia is often associated with increased exploratory and bold behavior. Like FID, coyote responses to novel objects were influenced by the distance from the coyote to the nearest road. Individuals near roads may have been on the bold side of the bold-shy spectrum since, presumably, shyer individuals would have chosen to stay farther away from human activity in the first place. Alternatively, coyotes near roads could have been exposed to human presence and refuse along roadsides more frequently prior to testing and thus reacted less to our behavioral tests due to habituation. Further studies are needed to determine what role, if any, repeated exposures to human activity have on wildlife responses.

The fourth chapter discusses my finding from hair cortisol analyses that were conducted from coyote hair samples collected in the Chicago area. Contrary to our predictions, coyotes at highly urban sites (e.g., downtown Chicago) and coyotes in protected greenspaces outside of city limits (i.e., forest preserves) had similar cortisol levels. Coyotes in suburban areas had higher hair cortisol levels than coyotes in the other groups. It is possible that coyotes in the most urban areas tend to have bolder temperaments and have adapted so well to urban pressures that they exhibit attenuated hypothalamic-pituitary-adrenal (HPA) activity following exposure to each individual stressor. The combination of natural stressors and extra stressors from human presence and activity, however, may lead to urban coyotes being exposed to more stressors than forest preserve individuals. If urban coyotes are exposed to more stressors but respond less to each individual stressor, they may ultimately end up producing similar quantities of stress hormones as coyotes in more natural settings. The suburban animals were exposed to many of the same, or more, stressors as the urban individuals due to the types of human-dominated landscapes they were using. If suburban animals exhibit greater responses to stressors than urban animals and are exposed to more stressors than coyotes in natural areas, it follows that suburban animals may have greater hair cortisol concentrations overall. Other significant predictors of coyote hair cortisol concentrations included the coyote's age, physical condition (especially if mange was present), and social status.

Lastly, I summarize overall findings of the study, compare and combine results from the different tests, describe possible implications of the study, and suggest some areas to focus on in future research. Collectively, my research provides evidence for the presence of behavioral syndromes in free-ranging coyotes. It also suggests that human activity and urbanization may be altering coyote behavior, and specifically coyote boldness. While increased boldness does not

necessarily correlate to aggression, bolder coyotes could still contribute to greater incidences of human-wildlife conflicts. Learning more about the possible mechanisms behind coyote boldness behavior will be imperative for preventing and mitigating future conflicts as coyote behavior continues being shaped by urbanization.

In loving memory of my grandfathers, Jerry Lee Robertson, Sr. and Robert Graham Williams,
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Chapter 1

Surviving the City: a review of mammalian predator adaptations to anthropogenic landscapes

The loss of natural habitats to urban expansion in recent years has led to reductions of certain wildlife species and increases of others. While some predatory mammals are directly and indirectly eliminated from cities via anthropogenic means, other predators have adapted their behaviors to human activity and are currently thriving in urban settings. Through the vast number of observational studies that have been conducted, various urban carnivore behavioral trends have emerged. Most of the observed trends are ways that mammalian carnivores can presumably avoid negative interactions with humans and domestic animals while still successfully exploiting anthropogenic resources. For example, many predators exhibit greater degrees of nocturnal behavior to avoid moving around during hours of peak human activity. Such trends, however, do not always hold true. Behavioral adaptations can vary widely between and within species. Behavioral adaptation differences between species may be due to differences in life history traits and variations in the intensities of human-associated risks (e.g., larger carnivores are more likely to be detected and persecuted by humans). The observed behavioral differences within species, however, are more likely due to differences in the ways that individuals perceive and respond to stressors. Behavioral syndromes that correlate to stress perception and response have been documented in various taxa through mostly laboratory-based studies. Studies that thoroughly and simultaneously examine free-ranging, urban carnivore behavior and physiology are rare in the current literature, however. As such, though general changes to predator behaviors in urban areas have been documented, intraspecific variations within populations and potential, associated physiological mechanisms are poorly understood. Studies that combine behavioral and physiological measures are needed in order to fully

understand how urbanization is changing predator populations and altering the potential for human-wildlife interactions.

INTRODUCTION

Over recent decades, cities have expanded to accommodate rising human populations. The construction of roads and buildings has converted many once-natural landscapes into mosaics of relatively small vegetated areas and expanses of concrete (McKinney 2002; Hamer and McDonnell 2010). The alteration and fragmentation of natural habitats have greatly impacted wildlife community compositions and species distributions (Beissinger and Osborne 1982; Randa and Yunker 2006). Though some species are initially displaced when urbanization occurs, some adapt so well to urban settings that living within cities positively affects their survival and reproduction rates (Beckmann and Lackey 2008; Gehrt et al. 2009). The lack of large competitors and predators combined with an abundance of food makes cities particularly beneficial to many mid-sized and small species (Baker et al. 2007; Gehrt et al. 2009).

Not all species are suited to city life though. Among others, species that require large home ranges, are stress-sensitive, lack behavioral plasticity (e.g., specialists), and have low population densities, are unlikely to ever fully adapt to urban environments (Kaartinen et al. 2005; Baker et al. 2007). For mammalian carnivores, persecution from humans may deter them from settling in developed areas (McClennen et al. 2001). Many predators also require large areas for hunting and have relatively low population densities (George and Crooks 2006), making them more sensitive to habitat fragmentation than other taxa. Predators that are able to cope with human presence and disturbance tend to do well in cities, however. Adaptations seen in urban predators tend to include a variety of ways to avoid humans spatially and temporally, despite living in cities (Baker et al. 2007; Gehrt et al. 2009; Grindler and Krausman 2009).

The behavioral variation may be related to differences in stress perception and response, though it is unclear based on the current literature (Koolhaas et al. 1999; Lendvai et al. 2011; Atwell et al. 2012; Clary et al. 2014). By combining behavioral and physiological measures, it may be possible to identify the presence or absence of behavioral syndromes, determine what is driving behavioral changes in predator populations, and help to reduce future human-wildlife conflicts. The following review will synthesize some of the information known about urban predator adaptations and highlight the need for studies that provide support for or against human-induced changes to behavioral syndromes in free-ranging urban carnivores.

CITY LIFE TRADEOFFS

Though cities vary in many ways, such as in human density, urban areas present some consistent risks and rewards to predatory mammals. Such costs and benefits likely drive community composition and population-level behavioral changes.

Risks. With human activity comes environmental alteration. To create space for construction, native vegetation is often uprooted and removed. In many cases, non-native plants and concrete are then used to cover cleared plots, thus homogenizing the environment and drastically altering the composition of the terrestrial community (Beissinger and Osborne 1982). Additionally, the creation of roads, buildings, and other large structures fragment remaining habitats and promote exotic species invasions; thus, they often reduce the diversity of native vegetation and the prey species that depend on it (Blair 1996; Savard et al. 2000; Randa and Yunger 2006). Urbanization is also associated with increased noise, light, air, and water pollution, all of which can deter and harm native wildlife (Beissinger and Osborne 1982; Partecke et al. 2006; Birnie-Gauvin 2016).

In addition to environmental alterations, cities are sometimes associated with higher disease risks (Gosselink et al. 2007; Ditchkoff et al. 2006; Bateman and Fleming 2012; Birnie-Gauvin et al. 2016). The risk increase is partially due to the higher densities of animals in limited, available green spaces. Higher densities of animals and smaller habitat fragments may lead to higher frequencies of contact between individuals, as a result, increase the likelihood of disease exposure. Predatory mammals can contract and carry a variety of parasites and diseases, including some that are zoonotic (Riley et al. 1998; Grindler and Krausman 2001; Page et al. 2008; Kapil and Yeary 2011). In addition to being potentially dangerous to pets and humans, urban predator diseases and parasites can have direct impacts on the health and survival of wildlife populations. For example, a study conducted in Illinois estimated that sarcoptic mange, a mite infestation, was responsible for 40% of all juvenile urban fox (*Vulpes vulpes*) deaths as well as many adult fox deaths (Gosselink et al. 2007). Indirectly, even if diseases do not infect humans, they can still contribute to human-wildlife conflicts by causing public fear. People sometimes fear that diseases found in wild predators will make the animals aggressive and sickly animals may be less responsive to customary hazing attempts.

The fear of disease and physical attacks has led to some public mistrust of carnivores. To deter nuisance individuals from inhabiting populated areas and interacting with humans, combinations of non-lethal and lethal management techniques are often used (Howell 1982; Timm et al. 2004; Poessel et al. 2013; Bonnell and Breck 2017). If non-lethal methods (eg, hazing) do not correct the predator issue, wildlife conflict mitigation strategies can resort to trapping and shooting target individuals (Howell 1982; McClennen et al. 2001; Timm et al. 2004).

Lastly, urban predators are subject to road-related injuries and mortalities. Most urban coyote (*Canis latrans*) deaths are due to anthropogenic means, with vehicular collisions being the top cause (Grinder and Krausman 2001; Gehrt et al. 2009). Roads have also been previously found to be significant sources of mortality for other predatory mammal species, including bobcats (*Lynx rufus*), foxes, skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), martens (*Martes foina*), and black bears (*Ursus americanus*) (Gosselink et al. 2007; Beckmann and Lackey 2008; Bateman and Fleming 2012; Grilo et al. 2012).

Rewards. Despite the risks, city life does provide benefits to species equipped to navigate such hazards. Some species (e.g., coyotes, raccoons) even tend to live longer in urban environments (Riley et al. 2003; Gehrt et al. 2011; Prange et al. 2003). Similarly, some species are more reproductively successful in urban settings (Beckmann and Lackey 2008; Prange et al. 2003). Increased success in urban environments is often attributed to the abundance and variety of resources that some species can take advantage of within cities (Baker et al. 2007; Beckmann and Lackey 2008; Bourbonnais et al. 2013). Not only do predators have access to an abundance of small prey items (e.g., rats), but they also can scavenge for roadkill, consume pet food, and use various anthropogenic items found in garbage bins. Since there are so many resources that are readily available, urban predators often require smaller home ranges to survive (Gehrt et al. 2009; Gese et al. 2012). Urban predators can thus spend less time defending their territories and devote more time to foraging and breeding (Beckmann and Lackey 2008; Gese et al. 2012). Lastly, recreational hunting and trapping of wild animals in developed areas is generally greatly limited, if not completely prohibited. The lack of legal hunting and trapping opportunities in urban areas reduces or eliminates an important mortality source for many species (particularly

those classified as “furbearers”), thus allowing individuals of these species to survive longer when living in proximity to people (Gehrt et al. 2010; Batman and Fleming 2012).

BEHAVIORAL PATTERNS

In order to limit the risks of city life while increasing benefits, urban predators exhibit various behavioral adaptations (McClennen et al. 2001; Baker et al. 2007). Behavioral changes are often geared towards reducing human contact and can be spatial or temporal in nature (McClennen et al. 2001; Baker et al. 2007; Gosselink et al. 2007; Grubs and Krausman 2009).

Spatial use patterns. Human presence influences the sizes and locations of predator home ranges. Urban predators defend relatively small territories, preferentially in areas of low human activity (Gehrt et al. 2009; Gese et al. 2012). A study in the Nature Reserve of Orange County, California found that bobcats and coyotes were less likely to inhabit areas that frequently had bikers, hikers, and dog-walkers (George and Crooks 2006), indicating that some predatory mammals are sensitive to human recreation. That said, urban predators often choose to use green spaces within urban areas, including golf courses, parks, wooded neighborhoods, and nature preserves (Grubbs and Krausman 2009; Gese et al. 2012). Within green spaces, they tend to select habitats that have more vegetation cover, since cover can be used for foraging, stalking prey, and avoiding humans (McClennen et al. 2001; Way et al. 2004; Randa and Yunker 2006; Gese et al. 2012).

Some carnivores avoid travelling on impervious surfaces, such as concrete (Baker et al. 2007; Gese et al. 2012). Avoiding roads may hinder dispersal and mate-selection though (Baker et al. 2007), so most individuals only avoid high-traffic areas. Low-traffic roads and railways can actually serve as corridors that facilitate movement and provide prey-rich hunting grounds (Gehrt et al. 2009; Gese et al. 2012). Because busy highways are likely to deter many species and are

unlikely to be walked by humans, roadside culverts also can, in some cases, serve as protective den sites for small and medium sized predators (Gosselink et al. 2007; Grubbs and Krausman 2009). Roadside denning can result in more road-related mortalities, however, so it is a risky adaptation (Gosselink et al. 2007).

Temporal patterns. The other way that predators avoid human interactions is by changing temporal activity patterns. Predators use human landscapes when humans are least likely to be present (Grinder and Krausman 2001; Gese et al. 2012). For example, predators may be more likely to wander onto golf courses after the courses close for the evening. Similarly, predators are more likely to use roads during low traffic hours. Because less human activity occurs at night, urban carnivores tend to exhibit greater degrees of nocturnal behavior than their rural counterparts. The observation that predators in cities are more nocturnal has been previously documented in several species (e.g., coyotes, foxes, bobcats) and in multiple locations (Grinder and Krausman 2001; Grubbs and Krausman 2009; McClennon et al. 2001; Baker et al. 2007; Gese et al. 2012).

EXCEPTIONS TO THE PATTERNS

Interspecific variation. Though some behavioral adaptations can be observed across numerous predatory mammals, certain species are exceptions. For example, while many species (e.g., coyotes) often use roads as corridors and scavenging grounds (Way et al. 2004; Gosselink et al. 2007; Grubbs and Krausman 2009), wolves (*Canis lupus*) tend to be extremely wary of human-inhabited areas (Kaartinen et al. 2005; Shepherd and Whittington 2006) This may be partly because wolves have traditionally been persecuted more heavily than other species, thus they perceive humans as a greater threat. It also may be because, as pack-hunting carnivores, wolves are less likely to see human foods as desirable alternatives to large prey (Kaartinen et al.

2005). A study that designed a corridor for wolves along the edge of a golf course found that, though wolves did eventually use the wooded portion of the corridor, wolves never entered the golf course itself (Shepherd and Whittington 2006). The observed avoidance of the golf course, even during times of no human activity, was likely because the wolves were more interested in hunting elk rather than scavenging for human foods. They also may have been avoiding areas that had any level of human activity throughout the daytime.

Similar interspecific differences have been noted in other predators. For example, a study conducted in the Golden Gate National Recreation Area found that bobcats never left the forested park and rarely used the edge of the park that had an urban boundary (Riley 2006). Gray foxes within the same park, however, frequently left the park and spent large quantities of time in the adjacent urban area. Again, it was suspected that one species (bobcats) was less interested in anthropogenic resources than the other species (gray foxes). When species have little interest in anthropogenic resources, venturing into human-dominated landscapes may not be worth the associated risks of human-wildlife conflicts.

Interspecific interactions. Since some species are more human-tolerant and interested in anthropogenic resources, human activity has a strong potential to influence community compositions and interspecific interactions. For example, since wolves are sensitive to human activity and need large natural areas to hunt large prey, they tend to avoid developed areas (Shepherd and Whittington 2006; Bateman and Fleming 2012). As a result, coyote populations are able to persist without fear of intraguild predation (Kaartinen et al. 2005; Gehrt et al. 2009). Coyotes can become the top predators in anthropogenic landscapes and, regardless of location, the presence of coyotes can displace local fox populations (Harrison et al. 1989; Randa and Yunker 2006). To avoid being injured or killed by coyotes, urban foxes sometimes restrict their

activities to small woodlots, areas very close to human structures, and roadside culverts that are too small for coyotes to enter (Randa and Yunger 2006; Gosselink et al. 2007). The types of predators present in a given area then have the potential to drive further species interaction and community composition changes. Urbanization impacts on top predators in an ecosystem may, therefore, alter the frequencies of interspecific interactions between other species.

Differences within species. In contrast to behavioral differences between species that are likely due to differences in life history traits and interspecific interactions, behavioral differences within a single species may be due to behavioral syndromes. Behavioral syndromes are suites of associated behaviors that are exhibited in response to common stimuli (Sih et al. 2004). One commonly studied set of behaviors are those associated with the bold-shy spectrum. An individual animal is considered bolder if it is more proactive and likely to explore new objects and areas despite any associated risks (Sih et al. 2004; Darrow and Shivik 2009). Additionally, bolder individuals are believed to have reduced stress responses to stressors when compared with shyer individuals that are exposed to the same stressors (Koolhass et al. 1999; Laudenslager et al. 2011; Atwell et al. 2012; Frost et al. 2013; Clary et al. 2014). Multiple studies have found at least partial evidence of behavioral syndromes in predatory mammals (Wielebnowski 1999; Harris and Knowlton 2001; Darrow and Shivik 2009; Sinn et al. 2010; Young et al. 2015). For example, a study conducted on captive coyotes found that individuals responded differently to a motion-activated scare device; some individuals consistently were bold enough to approach it and others were too shy to ever approach (Darrow and Shivik 2009).

The idea of a bold-shy spectrum in coyotes and other predatory mammals may help explain some of the differences observed between individuals in urban settings. Some ‘nuisance’ coyotes spend time foraging in residential locations, whereas many coyotes simply pass through

populated areas in favor of more natural areas (Gehrt et al. 2009). In an urban context, bold individuals could be defined as those that are most likely to cross roads, use anthropogenic resources, or take other risks within the human-altered landscape. Relatively few studies, however, have attempted to examine how individual personalities of wild carnivores influence behavioral choices and could be influencing human-wildlife conflicts.

Closely linked to the idea of behavioral syndromes is the concept of differential stress responses. Studies in other taxa have found that individuals who behave the most proactively (i.e., bolder) are often the ones who exhibit the lowest hypothalamic-pituitary-adrenal axis (HPA) activation after being exposed to a stressor (Koolhaas et al. 1999; Lendvai et al. 2011; Atwell et al. 2012; Frost et al. 2013; Clary et al. 2014). Stress perception and response differences can be due to both genetic and experiential factors (Tsigos and Chrousos 2002; Lendvai et al. 2011) and may ultimately be drivers of different behavioral syndromes since stress can inhibit risk-taking and exploratory behavior (Laudenslager et al. 2011). One study conducted in California simultaneously examined the exploratory behavior and cortisol levels of urban-dwelling, dark-eyed juncos (*Junco hyemalis*), a small species of sparrow (Atwell et al. 2012). The major finding was that individuals with the greatest stress responses and therefore the highest levels of cortisol circulating in the blood were also the least exploratory individuals of the group. Such studies that combine behavior and physiology in wild animals are rare (Wikelski and Cooke 2006), especially for predatory mammals.

STRESS PHYSIOLOGY

To better understand mammalian predator ecology and the impacts that human activities are having on urban wildlife, relatively recent studies have begun examining cortisol concentrations in captive and free-ranging predatory mammals (Bourbonnais et al. 2013; Schell

et al. 2013). Cortisol can be extracted from different sources (e.g., blood, feces, hair), though each type of sample provides information about stress over a different time period. While blood cortisol can instantaneously change in response to new stressors, hair cortisol concentrations provide information about chronic stress since hair cortisol concentrations (HCC) are based on accumulations of cortisol throughout the total time that the hair was growing (Bourbonnais et al. 2013; Schell et al. 2013). For example, in species that shed and regrow their guard hairs on an annual cycle (e.g., grizzly bears), the HCC value obtained reflects the average stress level of the individual over the course of the previous year. Regardless of the type of sample used to examine stress hormones, higher glucocorticoid concentrations indicate higher levels of perceived and realized stress. In urban systems, chronic stress may be a reflection of the everyday risks, challenges, and environmental stressors that city-dwelling wildlife face (Bourbonnais et al. 2013; Dantzer et al. 2014).

Stress-food relationship. A concept that is found throughout urban wildlife physiology and behavior literature is the idea that food and other anthropogenic resources may help to mitigate some of the impacts of urban stressors (Randa and Yunger 2006; Riley 2006; Baker et al. 2007; Beckmann and Lackey 2008). In some cases, the temptation of anthropogenic food can even reduce stress perception so much that urban predators mistake hazardous locations for viable habitats (Beckmann and Lackey 2008). The quantities and types of resources that are necessary to induce a predator to gravitate towards a risky habitat over a safer one is likely dependent on the species and individual in question (Randa and Yunger 2006; Riley 2006). Gender may also be a factor that influences overall stress perception and makes anthropogenic resources more or less desirable in some species (Bourbonnais et al. 2013; Dowle et al. 2013). A study in Alberta, Canada that examined hair cortisol levels in free-ranging grizzly bears (*Ursus*

arctos) found that though males had similar cortisol levels in wilderness and urban locations, females had lower cortisol levels in urban settings (Bourbonnais et al. 2013). Regardless of gender, however, hair cortisol concentrations were relatively low when bears inhabited urban areas. A study conducted in Sydney, Australia found similar results when they examined fecal cortisol levels of two species of free-ranging bandicoots (*Perameles nasuta* and *Isoodon obesulus*) (Dowle et al. 2013). Though bandicoots are marsupials, they are another omnivorous predator that is present in urban systems. The bandicoot fecal samples were analyzed to determine if stress levels varied across the landscape. All urban bandicoots had relatively low fecal cortisol levels but males had lower cortisol levels than females. The study expressed a need for a larger sample size before they could draw any definitive conclusions. In both the grizzly bear and the bandicoot studies, however, low levels of cortisol were observed in urban predators (Bourbonnais et al. 2013; Dowle et al. 2013). If predators are sensitive to anthropogenic disturbances, as has previously been suggested (George and Crooks 2006; Schell et al. 2013), the lack of observed stress in free-ranging urban predators could be explained if anthropogenic resources (combined with a lack of hunting pressures) do indeed mitigate the influence of stressors.

ARE HUMANS BUILDING BOLDER PREDATORS?

As predators continue to be exposed to human activity, it is important to consider whether some behaviors may indirectly or directly influence predator fitness in urban systems. For example, assuming that ample food resources allow predators to be more fecund, live longer, and have reduced stress levels, individuals that are more exploratory will benefit most when such resources are present. In contrast, without stress mitigation in the form of new, abundant food and shelter resources, less exploratory individuals will likely experience greater levels of chronic

stress than their exploratory counterparts. High levels of chronic stress can lead to a “syndrome of distress” that includes lowered immunity to diseases, decreased reproductive output, and slower growth rates (Tsigos and Chrousos 2002) (Fig. 1.1). Individuals that cope with novel situations well, are more exploratory, and are more willing to utilize new resources will likely outcompete individuals that are shy and more neophobic. If bolder individuals are being selected for and less bold individuals are being selected against, constructing new anthropogenic landscapes may simultaneously be “constructing” bolder predator populations. Currently, the idea that humans are inadvertently selecting for specific urban predator personalities is only speculative. Further studies that address the relationship between behavior and stress physiology could, however, provide support for this hypothesis. If it is indeed true that predators in cities are becoming bolder, such studies could have major implications for human-carnivore conflict prevention and mitigation.

CONCLUSIONS & DISSERTATION OVERVIEW

As is the case in many disciplines, urban wildlife ecology studies have traditionally focused on either behavior or physiology. The lack of studies that directly compare behavioral responses and HPA activation responses to urbanization may be hindering our current understanding of predatory mammal adaptations to anthropogenic pressures. As humans continue to alter landscapes around the world, it will become increasingly important to recognize adaptations that are occurring and potential consequences that habitat alterations could have on wildlife. In cases where urban predator populations cannot adapt fast enough to human-induced environmental changes, losses of certain species and possibly entire trophic levels may occur. At the other extreme, in cases where predator populations actually benefit from human activity, urbanization may result in overabundances of predators. Nuisance individuals may also become

more common and may be more difficult to haze if they are already bolder than individuals found in more natural settings. Predators may behave more proactively in urban settings and exhibit lower stress hormone responses if, (a) lowered stress responses prevent inhibitions that would normally keep predators from being exploratory and successful in human-dominated landscapes, and/or if (b) resources found in urban environments are so abundant that they counteract some of the stress related to urban lifestyles. Either case would suggest that, by developing formerly-natural landscapes, humans may be indirectly driving the creation of bolder predator populations.

In my dissertation, I attempt to help fill the current knowledge gap between urban predator behavior and stress physiology. I do so by conducting two different behavioral tests on free-ranging urban coyotes (i.e. flight initiation distance tests and novel object tests) and measuring chronic hair cortisol concentrations of coyotes as an indicators of chronic stress. Afterwards, I provide a synthesis of my findings. Additional studies that simultaneously examine urban predator behavior and physiology could have important implications for broad-scale ecology, wildlife-conflict prevention, and future predator management regimes.

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TABLES AND FIGURES

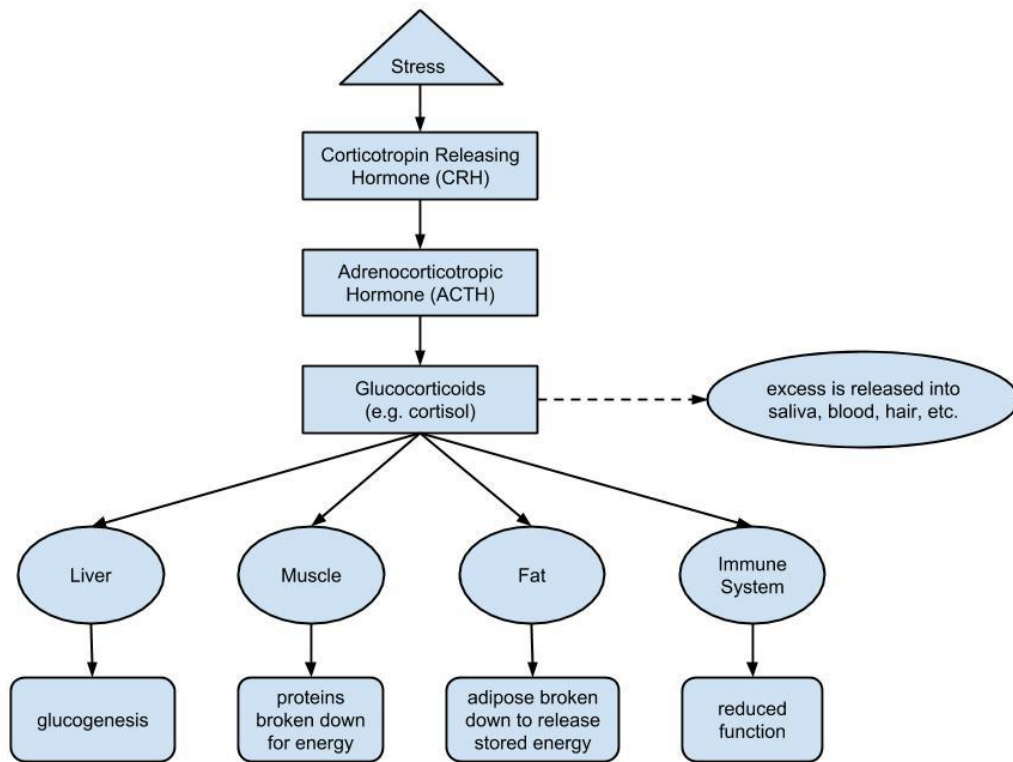


Figure 1.1. The sequence of events that occur when the hypothalamic-pituitary-adrenal (HPA) axis is triggered by a stressor. When an organism is exposed to a stressor, a chain reaction occurs, beginning with the release of various hormones and ending with metabolic/immunologic responses. Such responses are designed to maximize the amount of energy available to the organism in case it needs to fight, flee, or otherwise react to the external stressor. The release of energy stored in the muscles, adipose tissue, etc. comes at the cost of immunological function and overall body condition, thus chronic stress can be detrimental to an individual's overall health. To determine whether an individual has experienced acute and/or chronic stress, the amount of cortisol present in the saliva, blood, and hair of the individual can be analyzed via enzyme immunoassays.

Chapter 2

Flight Initiation Distance for Coyotes across an Urbanization Gradient

Urban expansion has led to alterations of natural habitats and animal communities. While some species have declined due to anthropogenic changes, other species have adapted and thrived in cities. Even within species, however, some individuals cope with change better than others. Intraspecific behavioral differences are often attributed to behavioral syndromes, such as those associated with the bold-shy spectrum. The bold-shy spectrum assumes a continuum of personality types that are consistent across time, ranging from bold (proactive) to shy (reactive). One species that has adapted well to urban settings is the coyote (*Canis latrans*). Coyotes thrive in cities throughout North America, including Chicago, IL. In coyotes, bolder behavior may allow individuals to better tolerate human activity and more efficiently locate novel resources when more natural habitats become fragmented. If increased boldness is beneficial to coyotes and contributes to their success in human-dominated landscapes, it is expected that coyotes in suburban and urban areas would, on average, behave more boldly than coyotes living in natural areas (e.g., forest preserves). To assess whether coyote boldness toward humans varied in the Chicago area, flight initiation distance (FID) tests were conducted. The top generalized linear models that were fit to the data support the hypothesis that coyotes in urban and suburban areas are bolder toward humans than those in less developed (i.e., forest preserve) locations. They also suggest that a coyote's distance to the nearest road and/or the approacher's starting distance are important factors in predicting a coyote's FID, though those two measures could not be differentiated in our study. Lastly, the velocity at which the coyotes were approached negatively influenced FID. Further research should be conducted to determine additional factors that may influence FID and other coyote boldness measures. If urbanization is driving coyote populations

to become bolder, on average, toward human activity, it could have major implications for the future urban coyote management.

INTRODUCTION

Urban areas have grown rapidly to accommodate the increases in their resident population. It has been estimated that by 2030, approximately 60% or more of all humans will be living in urban areas (United Nations Population Fund 2007). The construction of roads and buildings fragments formerly natural areas into expanses of concrete with only a few, small remnant vegetation patches (McKinney 2002; Hamer and McDonnell 2010). The average urban center tends to be < 20% vegetated land (McKinney 2002). The alteration and fragmentation of natural habitats typically alter wildlife community compositions and species distributions (Beissinger and Osborne 1982; McKinney 2002; Randa and Yunger 2006). Due to their loss of natural habitats, difficulties adapting to changing food sources, and low tolerance for human activities, many species are initially displaced when urbanization occurs (Randa and Yunger 2006; Hamer and McDonnell 2010). Over time, however, some adjust so well to urban settings that living within cities positively affects their survival and reproduction rates (Ditchkoff et al. 2006; Beckmann and Lackey 2008; Gehrt et al. 2009; Bateman and Fleming 2012). In particular, the lack of larger competitor species and predators combined with an abundance of food helps some small-to-mid-sized species thrive in cities (Baker et al. 2007; Gehrt et al. 2009).

For some mammalian carnivores, there is a high risk of persecution from humans when they enter developed areas (McClennen et al. 2001; Bateman and Fleming 2012). Predator persecution often stems from public fears about potential physical attacks on pets and children and, to a lesser extent, the risk of diseases being spread (Fox 2006; Bateman and Fleming 2012). Since many mammalian carnivores have low population densities, require large areas for

hunting, and are subject to persecution, they are usually among the most impacted by anthropogenic disturbances (McKinney 2002; George and Crooks 2006). Species with the ability to adjust to novel environments and human presence have thrived in cities, however. Predators often adapt by making spatial and temporal changes to their behavior to avoid human interactions altogether (Baker et al. 2007; Gehrt et al. 2009; Grinder and Krausman 2009; Murray and St. Clair 2015).

In contrast to behavioral differences between species that are likely due to differences in life history traits, behavioral differences within a single species may be due to behavioral syndromes. Behavioral syndromes are suites of associated behaviors that are exhibited in response to some common stimuli (Sih et al. 2004). Populations often contain individuals that exhibit different behavioral syndromes. One commonly studied set of behaviors are those associated with the bold-shy spectrum (Bell and Sih 2007; Reale et al. 2007; Darrow and Shivik 2009; Atwell et al. 2012). An individual animal is considered bolder if it is more proactive. In other words, bolder individuals are more likely to behave in risk-tolerant and exploratory manners than shyer individuals (Sih et al. 2004; Darrow and Shivik 2009).

Coyotes (*Canis latrans*) adapted well to urban environments and are, in fact, now found in major cities throughout North America (Howell 1982; Gehrt et al. 2009; Poessel et al. 2013). The coyote's success as a species may, in part, be due to its behavioral flexibility. Consistent with the behavioral syndromes theory, research on captive coyotes has shown substantial variation in boldness across individuals (Darrow and Shivik 2009; Young et al. 2015).

The idea of a bold-shy spectrum in coyotes and other wildlife may help explain some of the differences observed between individuals living in human-dominated and natural areas. While some individuals spend time foraging in locations near people (e.g., residential areas),

others simply pass through populated areas in favor of more natural ones (Gehrt et al. 2009). Typically, coyotes avoid paved, mowed, and highly developed locations in favor of less developed, natural or altered greenspaces (Grinder and Krausman 2001; Atwood et al. 2004; Gehrt et al. 2011; Gese et al. 2012; Poessel et al. 2016). Altered green spaces (e.g., golf courses, cemeteries) may offer urban wildlife an intermediate habitat that is developed but still vegetated enough for adequate cover, hunting space, and resting locations (Poessel et al. 2016). Temporally, successful urban coyotes tend to mainly venture into unnatural areas or cross roads at night (Grinder and Krausman 2001; Murray and St. Clair 2015; Poessel et al. 2016). This allows coyotes to navigate through highly developed areas with a reduced risk of interacting negatively with a human or vehicle.

Within an urban context, bold individuals could be defined as those that are most likely to use anthropogenic resources, use habitats in close proximity to humans, and react less to human activity in general (Lowry et al. 2013). Additionally, they may be more likely to find and benefit from novel resources associated with human activity (e.g., anthropogenic foods; increased rodent densities) due to their exploratory tendencies (Kark et al. 2007; Lowry et al. 2013). While one might expect bolder, urban individuals to cross roads more often and thus be at an increased risk for a vehicle-related mortality, previous studies have shown that the number of road crossings is not a good predictor of mortality (Riley et al. 2003; Murray and St. Clair 2015). Individuals that cross roads less frequently are actually more likely to be hit by a vehicle (Riley et al. 2003), likely because they are less accustomed to traffic patterns, are more hesitant to move quickly, and more likely to cross earlier in the day. Urban animals that are bolder and more likely to cross roads may, therefore, have a lower risk of road-related mortality than their rural and suburban counterparts. Another benefit of being bolder in an urban area is bolder individuals likely

experience less stress than shy individuals when human encounters occur or their habitats are altered (Reale et al. 2010; Lowry et al. 2013). Less activation of the hypothalamic-pituitary-adrenal axis will allow bolder individuals to be less impacted health-wise over time by exposure to frequent human disturbances. Lastly, while bolder animals are at a greater risk of being seen by people and subsequently persecuted in some locations, there is typically little or no trapping and hunting in highly populated areas. The benefits of boldness, combined with the reduced threat of lethal consequences of boldness in populated areas may ultimately lead urban coyote populations to become bolder than populations found in natural areas.

Assuming that bolder individuals fare better than their shy counterparts in human-dominated locations, it was hypothesized that coyotes living in urban and suburban areas of Chicagoland would behave, on average, more boldly toward people than coyotes living in natural areas (e.g., forest preserves) where there is less environmental pressure to behave a certain way. To test the hypothesis that urbanization is increasing coyote boldness behavior, flight initiation distance (FID) tests were conducted on coyotes from the Greater Chicago Metropolitan Area. FID tests have traditionally been conducted on a variety of taxa (e.g., birds, lizards, squirrels, ungulates), and are often used to assess animal risk responses, reactions to disturbance, and tolerance of human activity (Altmann 1958; Dill and Houtman 1989; Blumstein 2003; Boyer et al. 2006; Stankowich and Coss 2006; Groelle et al. 2014; Bonnot et al. 2017). FID testing involves locating a resting individual and having someone walk toward the individual to see how close a person can get before the animal flees. Shorter FID measures are associated with a greater level of tolerance for human activity. It was predicted that coyotes living in more urbanized areas would have shorter FIDs, thus indicating greater degrees of boldness toward humans.

STUDY SITE

This study was the continuation of a long-term, urban coyote research project in the Greater Chicago Metropolitan Area (GCMA). The GCMA contains parts of Cook, DuPage, Kane, Lake, Will, and McHenry counties in Illinois, as well as parts of Indiana and Wisconsin. Cook County, home to the city of Chicago, is alone estimated to contain over 5.2 million residents (US Census Bureau, 2017 population estimate). The GCMA is, therefore, highly influenced by human activity. Study sites could be classified as one of three major site types (i.e., urban, suburban, or forest preserve). Urban sites were those located within Chicago's city limits and included habitats such as railways, undeveloped lots, and cemeteries. Suburban sites were neighborhoods, parks, golf courses, cemeteries, and other matrix habitats located in cities surrounding Chicago. Forest preserve sites were county-designated, protected green spaces scattered throughout the GCMA. The preserves included a mixture of oak woodlands, savannas, open fields, riparian zones, and recreational areas. Though many natural areas are under government protection, urban sprawl is still advancing at a rapid rate in the Chicago area. A previous study estimated that there was a 49% increase in urban land cover in the GCMA from 1972 to 1997 (Wang and Moskovits 2001). All coyotes were captured within the GCMA. Coyote home ranges were then used to classify individuals into specific site types and define study site boundaries.

METHODS

Capture and processing. Coyotes were opportunistically captured from early autumn to late spring of each year from 2013 to 2017. Coyotes were captured by using relaxing cable neck restraints and padded MB-550 and MB-650 foothold traps (Minnesota Trapline; Pennock, MN, USA). All traps were checked every 12-24 hours, depending on the site location. Once captured,

coyotes were transported back to a lab for processing. Once at the lab, each coyote was immobilized with an intramuscular injection of Telazol (Fort Dodge Animal Health, Fort Dodge, IA, USA). Morphometric measurements, sex, age class (i.e., pup, subadult, or adult), breeding condition, and an overall condition rank (i.e., poor, good, or excellent) were recorded for each individual. Samples for other aspects of the coyote research (e.g., hair, whiskers, blood, fecal swabs, fecal samples) were also collected during the processing period. Each coyote then received a unique set of ear tags (NASCO Farm & Ranch, Fort Atkinson, WI, USA) for future identification in the field. Lastly, each coyote was fitted with a very high frequency (VHF) radio collar (Advanced Telemetry Systems, Isanti, MN, USA), a UHF collar (Lotek, Newmarket, Ontario, Canada), an iridium GPS collar (Advanced Telemetry Systems, Isanti, MN, USA) or a cellphone collar (Lotek, Newmarket, Ontario, Canada). Once the coyotes fully recovered from immobilization, they were released at their original capture locations. All trapping and handling was conducted in accordance with the trapping guidelines from the American Society of Mammalogists (Sikes et al. 2011) and the animal handling protocol was approved by The Ohio State University Institutional Animal Care and Use Committee (OSU IACUC #2010A00000113).

Tracking. Coyote locations in the field were obtained through a combination of radio telemetry and GPS collar downloads. For VHF tracking, daytime locations were recorded weekly for each animal. Night locations were recorded one or two nights per month, typically with five hourly locations recorded on each night. The GPS collars were configured to record either hourly or 15-minute fixes. All GPS collars were downloaded on a regular basis and final downloads were conducted upon recovery of the collars during recaptures, after the collars dropped off (for those collars which were equipped with a magnetic-based, timed, drop-off mechanism), or after

the coyote was found deceased. Coyote locations were plotted in ArcMap 10.4.1 software (Environmental Systems Research Institute, Redlands, CA, USA), so coyote home ranges and habitat use could be visualized.

Flight initiation distance testing. Coyotes were opportunistically located while they were resting during the morning or early afternoon (Li et al. 2011; Lin et al. 2012; Moen et al. 2012; Groelle et al. 2014). Resting individuals were identified by listening to the VHF signal sent out by the radio collars; a signal with a steady pitch, volume, and direction typically indicates lack of movement. Once a coyote was located, its resting point was triangulated. One person (i.e., the approacher) then walked steadily toward the animal while a second person listened to the VHF signal from the antenna-mounted truck. When coyote motion was detected through visual observation and/or a change in the signal, the approacher stopped walking and recorded his or her current location. The individual's FID was defined as the distance from the approacher's stopping point to the animal's initial resting point (Altmann 1958; Stankowich 2008; Engelhardt and Weladji 2011; Li et al. 2011; Lin et al. 2012; Moen et al. 2012; Groelle et al. 2014). We also recorded the animal's new location and whether the individual was resting or not shortly after the FID test was concluded; this provided us with a measure of how far coyotes typically fled before settling in one place again, post-disturbance.

To prevent causing excess stress to particularly vulnerable individuals, the breeding status and known health conditions of the coyotes were considered prior to testing. Breeding females and other individuals resting near known den sites were avoided during the beginning of the pup-rearing season (i.e., April-July) to avoid interfering with postnatal care of the pups. Similarly, any individuals identified as having compromised health due to suspected life-threatening diseases (e.g., distemper) or injuries (e.g., broken limbs) were excluded from testing.

Lastly, we considered the locations of the coyotes carefully before walking in; we approached from directions that would be least likely to push animals toward other people or vehicles.

Habitat measurements. Habitat measurements were collected from each coyote's initial resting location, immediately following the FID test. The presence of human activities, noises, vehicles, and structures were noted. The distance from the coyote's resting point to the nearest road was approximated by using ArcMap 10.4.1 GIS software, as anthropogenic disturbances have been shown to influence the wariness and activity levels of some species (Li et al. 2011; Tryjanowski et al. 2016). Additionally, the habitat type (e.g., forest, field), dominant substrate (e.g., dry leaves, tall grass, snow), current weather, temperature, wind speed, and wind direction were recorded. Canopy cover was estimated by using a concave, spherical densiometer at the resting site (Lemmon 1956). The first measurement was taken while facing the direction from which the person approached the coyote. Three additional measures were taken at 90°, 180°, and 270° from the first angle. The average of the 4 measures was recorded as the overall percent canopy cover. Lastly, horizontal visibility was measured by using a dot-gridded, white sheet (Boyer et al. 2006). One person held the sheet 12 m away from the resting point (approximately 0.3 m above the ground) while another person crouched at the resting point and counted the number of dots that were visible. The process was then repeated three additional times, at the same angles at which the canopy cover measures were collected. The average percentage of grid dots that were visible was recorded as the overall percent visibility.

Statistical analysis. To avoid introducing individual bias, only the first FID test for each coyote was included in the overall analysis. Flight initiation distance was compared across the sexes and study site types via Welch's two-sampled t-tests in the R statistical program (R Core Team 2016, v. 3.3.2). The FIDs were log-transformed prior to the overall analysis. The

transformed FID was analyzed by generating linear models in the R statistical program (R Core Team 2016, v. 3.3.2). The models included combinations of the coyote variables (e.g., sex, mange presence/absence), various habitat measures (e.g., temperature, canopy cover, visibility, habitat type), and location type (i.e., urban, suburban, forest preserve). The top model was selected by using Akaike's Information Criterion corrected for small sample sizes (AICc) and the Akaike weights (k) (Burnham and Anderson 2002). If models had a ΔAICc of < 2 , they were considered equally plausible. Lastly, we used the Spearman's rank-order method to compare FIDs from first and second trials conducted on the same individuals. This allowed us to assess whether FID was consistent within individuals over time.

RESULTS

Approximately 48 coyotes (21 males, 27 females) were already radiocollared at the initiation of this study in November 2013. Additionally, a total of 222 coyotes (n= 176 unique individuals; 104 males, 72 females) was captured between November 2013 and December 2017. One mortality occurred following a cable restraint capture, though the cause of death was not apparent, even through a formal necropsy. All other coyotes sustained minimal to no injuries and were successfully returned to the locations where they were captured.

Between March 2015 and December 2017, 90 FID tests were attempted (Fig 2.1). Of those, 78 tests (n=60 unique individuals, 34 males, 26 females; 18 repeated measures, 11 males, 7 females) were deemed to be successful and reliable. Tests that were excluded from the analysis included ones where outside factors may have triggered the coyote to move (e.g., a train passing by the resting point), the approacher may not have walked directly toward the animal (e.g., in cases of physical barriers or GPS failures), or the VHF signal change was not immediately apparent. The mean velocity of the approacher during successful tests was $0.756 \pm$

0.092 m/s. For the 60 unique coyote trials (excludes repeated tests), 35 coyotes settled back into a resting position while we were still in the vicinity. For 34 of the 35 that began resting again, we calculated the distance between their initial resting location and their new location. Coyotes, on average, fled 141.95 ± 48.56 m before resting again. The distance fled did not vary significantly by study site or with FID ($p > 0.05$).

The 95% confidence interval for the overall mean FID ($n= 60$) was $46.6 \text{ m} \pm 8.64 \text{ m}$ (Fig. 2.2). Urban coyotes had lower mean FIDs ($n= 11$; mean= $19.60 \pm 5.65 \text{ m}$) than suburban ($n=21$; mean= $30.84 \pm 9.56 \text{ m}$) or forest preserve individuals ($n=28$; mean= $65.73 \pm 15.36 \text{ m}$) (Fig. 2.3). There was no significant difference between male ($n=34$; mean= $37.80 \pm 8.94 \text{ m}$) and female ($n=26$; $54.57 \pm 17.96 \text{ m}$) FID ($t=1.71$, $df= 54.385$, $p= 0.093$) (Fig. 2.4).

We conducted 65 unique, linear models and assessed them with Akaike's Information Criterion (AIC) to determine which variables were significant predictors of the log-transformed, coyote FID (Table 2.1; Table A.1). The top two models had $\Delta\text{AICs} < 2$ and contained similar variables. The first model included site type, log-transformed distance from the coyote's resting point to the nearest road, and the approacher's average velocity as predictor variables (Table 2.2). According to the model, forest preserve animals had higher FIDs than urban individuals ($p < 0.001$) and tended toward having higher FIDs than suburban animals, though not significantly ($p= 0.089$). Additionally, FID tended to be larger when the coyotes were farther from a road ($p= 0.003$) and when the approacher's velocity was lower ($p= 0.019$). The overall model had an adjusted R^2 of 0.46 ($f= 13.73$, $df= 4, 55$, $p < 0.001$).

The second model predicted that $\log(\text{FID}) = 2.626 - 0.638(\text{suburban}) - 1.016(\text{urban}) + 0.352(\log(\text{approacher's starting distance})) - 0.490(\text{velocity})$. The model supports the idea that forest preserve coyotes have longer FIDs than suburban ($p= 0.006$) and urban ($p < 0.001$)

coyotes. Also, like the relationship seen with distance to the nearest road in the first model, the approacher's starting distance from the coyote was positively associated with coyote FID ($p=0.006$) and the approacher's velocity was negatively associated with FID ($p=0.030$). The overall model's adjusted R^2 was 0.45 ($f=13.2$, $df=4$, 55 , $p<0.001$)

To determine if coyote FIDs were consistent within individuals over time, 18 (11 male, 7 female) coyotes were successfully tested a second time for comparison (Fig. 2.5). On average, second trials occurred 278 ± 101 days after the first. No coyotes switched study site types between trials. When the Spearman's rank-order method was used to compare first and second FID tests, the correlation (r_s) between first and second FID tests was 0.825 ($n=18$; $S=170$; $p<0.0001$), indicating coyote FIDs were relatively consistent across trials.

DISCUSSION

Though sex differences in FID have been previously reported for other species (Cooper and Wilson 2007; Smith et al. 2012; Guay et al. 2013), we did not find a significant difference between male and female coyote FIDs in the Chicagoland region. Our findings are consistent with those produced FID tests conducted on captive coyotes at the Millville Predator Research Center in Utah, as the captive coyotes also did not show sex differences (Young et al. 2015). Male and female coyotes from a given area are likely exposed to many of the same potential stressors, including a certain level of human disturbance that ultimately helps drive coyote behavioral syndromes. As a social species that forms life-long pair bonds (Hennessy et al. 2012), males and females have similar home range sizes, dwell in the same locations, have similar social interactions, and are equally likely to avoid human activity (Andelt 1985; Gehrt et al. 2009).

Though we did not detect significant sex differences, coyote FID did vary across the urbanization gradient. Flight initiation distance variation in response to urbanization has been previously recorded for other taxa, including various birds (Evans et al. 2010; Atwell et al. 2012) and lizards (Groelle et al. 2014). Our urban coyote FIDs (mean= 19.60 ± 5.65 m) were similar to those previously reported for captive individuals (males= 17.5 ± 4 m and females= 20.7 ± 5.4 m; Young et al. 2015). Both the captive individuals in Utah and the urban coyotes in Chicago were exposed to human presence regularly. Because human activity is common in urban areas and fleeing is energetically costly, it may be more beneficial for urban individuals to wait longer to assess situations further before moving from their resting areas. Similarly, since green spaces are more fragmented in urban areas, allowing a human to approach closer may be less risky than fleeing, crossing roads, and trying to locate another safe, resting location. Lastly, because urban areas are often associated with high levels of disturbance and a variety of novel resources, individuals that are on the bolder end of the bold-shy spectrum may ultimately fair better in cities like Chicago. Bolder individuals cope better with exposure to stressors and tend to be more exploratory, thus they may ultimately tolerate human presence better, reap the benefits of city life more efficiently, and be able to adjust quicker to anthropogenic changes to the environment (e.g., construction) (Atwell et al. 2012; Lowry et al. 2013). Due to the lack of hunting and trapping in cities, there is also less selection pressure against being bold toward human approachers. All of these factors combined may result in coyote populations that are bolder, on average, in more urbanized areas.

In addition to urbanization level, other key variables that helped predict coyote FID were the resting coyote's distance to the nearest road and the distance that the human approacher started from the coyote. Because we typically tried to drive as close to the coyotes as possible

before beginning our approaches, distance to the nearest road and approach distance were not completely independent and had to be analyzed separately. Our top two models selected with Akaike's Information Criterion were similar, with the main difference being that one contained distance to the nearest road and the other contained approach distance as a predictor variable.

Coyotes closer to roads tended to have shorter FIDs. Animals resting closer to roads experience anthropogenic noises and smells more regularly, so they may be less likely to immediately detect and react to an approaching human (Bonnot et al. 2017). Additionally, coyotes that tend to be bolder in general may be more likely to rest near roads; shy individuals likely would not tolerate the increased level of disturbance and human presence along road edges. If bolder individuals are, indeed, closer to road edges than shy individuals, one would expect coyotes closer to road edges to have shorter FIDs. The pattern of decreasing FID as human-related disturbance increases has also been found in other species, like the yellow-bellied marmot (*Marmota flaviventris*) (Li et al. 2011).

Other studies have found the approacher's starting distance to be a significant predictor of FID (Blumstein 2003; Cooper 2008). In our study, the approacher's starting distance was positively associated with coyote FID. Starting farther away from the animal allows the animal more time to detect and respond to the human approacher (Blumstein 2003; Cooper 2005; Stankowich and Coss 2006; Bonnot et al. 2017). If animals detect an approaching human while the human is farther away, fleeing immediately may be less costly in the long run. The animal will be less likely to be detected if it is farther from the threat and it will not have to continuously monitor the threat for an extended period if it just leaves the area immediately (Blumstein 2003).

The final factor that influenced coyote FIDs in our study was the average velocity at which the approachers walked toward the coyotes. Higher approach velocities were associated

with shorter FIDs. This contradicts some other studies that found the opposite trend (Kitchen 1974; Cooper 1997; Cooper 2006). In our case, higher velocities may have given coyotes less time to assess the situation, thus they may have fled later than they would under a more optimal risk assessment timeframe. It is also possible that high-speed approachers could be viewed as more capable of pursuing a coyote, thus the coyotes may have chosen to use sit-and-wait strategies to confirm the person was indeed walking toward them before fleeing and drawing attention to themselves. Lastly, it is possible that an approaching threat that is moving rapidly causes greater confusion and indecisiveness in the animal being approached (Hutson 1982). Slightly longer hesitation while assessing a rapidly moving individual would result in a shorter FID.

No other habitat or demographic variables were significant predictors of coyote FID. Similar to the results of a crimson rosella study (Boyer et al. 2006), we did not find an effect of horizontal visibility on FID. Our study, however, contradicts other studies that suggest animals in more open habitats tended to have longer FIDs than those in areas with dense vegetation or more refuges (Altmann 1958; Dill and Houtman 1987; Moen et al. 2012; Li et al. 2011). Though not statistically significant in our study animals, horizontal visibility and other habitat characteristics that influence resting site safety may influence some animals' decisions to flee quickly or rest longer (Moller 2008; Engelhardt and Weladji 2011; Moen et al. 2012; Smith et al. 2012)

Overall, our findings suggest that urbanization does play a role in determining coyote FID. It is unclear if bolder coyotes are initially more likely to enter and establish themselves in urban areas or if urban habitat features prevent shy individuals from persisting over time and thus act as selecting forces for boldness. The current literature provides support for both arguments and ultimately there may be a combination of factors at play. Bolder individuals are

typically more likely to explore new areas and disperse farther, thus they may be the ones colonizing urban areas initially (Fraser et al. 2001; Reale et al. 2007; Reale et al. 2010). When and if shy individuals do enter urban areas though, the increased levels of human disturbance may cause too much stress for more sensitive, shyer individuals, to successfully survive long-term and reproduce (Lowry et al. 2013). Regardless of whether certain kinds of coyotes selected for specific environments or the specific environments selected for certain kinds of coyotes, more urbanized areas in our study tended to have coyotes with shorter FIDs. Short FIDs are an indicator that the urban coyotes are more complacent in the presence of humans than their non-urban counterparts.

While increased boldness is not always correlated with increased aggression (Bell and Sih 2007; Young et al. 2015), it may make coyote management more challenging in some ways. If this is a trend that has been occurring in Chicago over the last few decades, it could help explain the increase in the number of coyote-related sightings, news reports, and conflicts (White and Gehrt 2009). It is important to note that there have been few aggressive coyote encounters and no attacks on humans thus far in the Chicagoland region. Even if Chicago's coyotes are not behaving more aggressively, however, current populations may contain bolder individuals than in the past and thus coyotes may be more comfortable around people than they used to be. If coyotes continue to become more comfortable resting around people, they are more likely to be seen by members of the public, there are likely to be more human-coyote interactions (e.g., people feeding coyotes), and there will likely be increases in nuisance complaints. Most nuisance complaints on coyotes tend to be coyote sightings, not physical conflicts (Fox 2006; Poessel et al. 2013).

Managing bold coyotes that become true nuisance animals may be more challenging, especially in more urbanized areas. Responses to coyotes residing too close to humans often include non-lethal methods, such as hazing (Timm et al. 2004; Poessel et al. 2017). Hazing an animal involves walking toward a coyote, making noise, trying to look big”, and possibly throwing items in the direction of the animal to scare it off. For a bold individual, however, it may take more effort and more repeated attempts to get the animal agitated enough to leave an area permanently. Not only are bold individuals likely to have a reduced stress response to non-lethal hazing methods, but they also are more likely to have used anthropogenic resources that have positively reinforced their behaviors. Coyotes in urban areas, for example, often do eat some level of anthropogenic food (e.g, garbage, pet cats) (Howell 1982; Morey et al. 2007; Newsome et al. 2015). Once behaviors have been positively reinforced and coyotes have benefited from residing in a particular area, it is more difficult to effectively alter their behaviors through non-lethal means (Timm et al. 2004).

Further research is needed to determine whether coyotes are exhibiting bold behavioral syndromes or whether they are simply habituated to human activity. From a FID study alone, one can only determine that coyotes tolerate human presence better in urban environments. It is unclear whether the coyotes with short flight distances also exhibit bold and increased exploratory behavior in other situations or whether bold behavioral tendencies are innate or learned. Similarly, additional studies should be conducted in other regions to determine if the patterns we observed are consistent for other major metropolitan areas. This study, combined with other methods of testing for bold and exploratory behaviors, will help determine whether behavioral syndromes are present in urban coyotes and may ultimately help to inform future urban coyote management practices.

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TABLES & FIGURES

Table 2.1. Akaike’s Information Criterion (AIC) table comparing the top ten linear models of the log-transformed flight initiation distance. Predictor variables in the models below include, the site type (i.e., forest preserve, suburban, or urban), log-transformed distance to the nearest road (troaddist), log-transformed initial distance the approacher is from the coyote (tstartdist), average velocity of the approacher, sex of the individual, log-transformed % horizontal visibility (tvisibility), and the air temperature. All flight initiation distance tests included in the models (n=60) were conducted 2015-2017 in the Greater Chicago Metropolitan Area. For each model, k is the number of parameters, AIC is the Akaike Information Criterion value, AIC_c is the AIC value corrected for sample size, ΔAIC is the difference between the model and the top model’s AIC values, W. AIC_c is a weighted AIC_c, and Evid. Ratio is the evidence ratio. *See Table A.1 for the remaining models.*

Model	k	AIC	AIC _c	Δ AIC	W. AIC _c	Evid. Ratio
troaddist + sitetype + velocity	5	110.147	111.510	0.000	0.383	1.00
tstartdist + sitetype + velocity	5	111.305	112.669	1.159	0.215	1.79
troaddist + sitetype	4	114.163	115.052	3.542	0.065	5.88
tstartdist + sitetype	4	114.511	115.400	3.890	0.055	7.00
troaddist + sitetype + sex	5	114.794	116.157	4.647	0.037	10.21
sitetype + tstartdist + breeding + sex + velocity	8	112.783	116.295	4.785	0.035	10.94
sitetype + troaddist + breeding + sex + velocity	8	112.814	116.326	4.816	0.034	11.11
troaddist + sitetype + tvisibility	5	115.786	117.149	5.639	0.023	16.770
troaddist + sitetype + temperature	5	116.045	117.408	5.898	0.020	19.09
sitetype + sex + velocity	5	116.072	117.436	5.925	0.020	19.35

Table 2.2. The predictor variables that were included in the top model of log(Flight Initiation Distance) for coyotes in the Greater Chicago Metropolitan Area. The top model was selected using Akaike's Information Criterion Table (*see Table 2.1*). Flight initiation distance tests were conducted 2015-2018 and only the first trial was included for each individual coyote (n = 60). The estimates represent the coefficients of a linear model and the * denote statistically significant parameters in the model (* < 0.05, ** < 0.01, *** < 0.001).

Parameters in the Top Model of log(Flight Initiation Distance)

Coefficient	Estimate	SE	t-value	p-value
Intercept	2.863	0.499	5.736	< 0.001 ***
log(distance to the nearest road)	0.307	0.100	3.062	0.003 **
Site Type _{suburban}	-0.372	0.215	-1.733	0.089
Site Type _{urban}	-0.888	0.223	-3.989	< 0.001 ***
Velocity	-0.530	0.220	-2.409	0.019 *

Coyote Flight Initiation Distance Test Locations

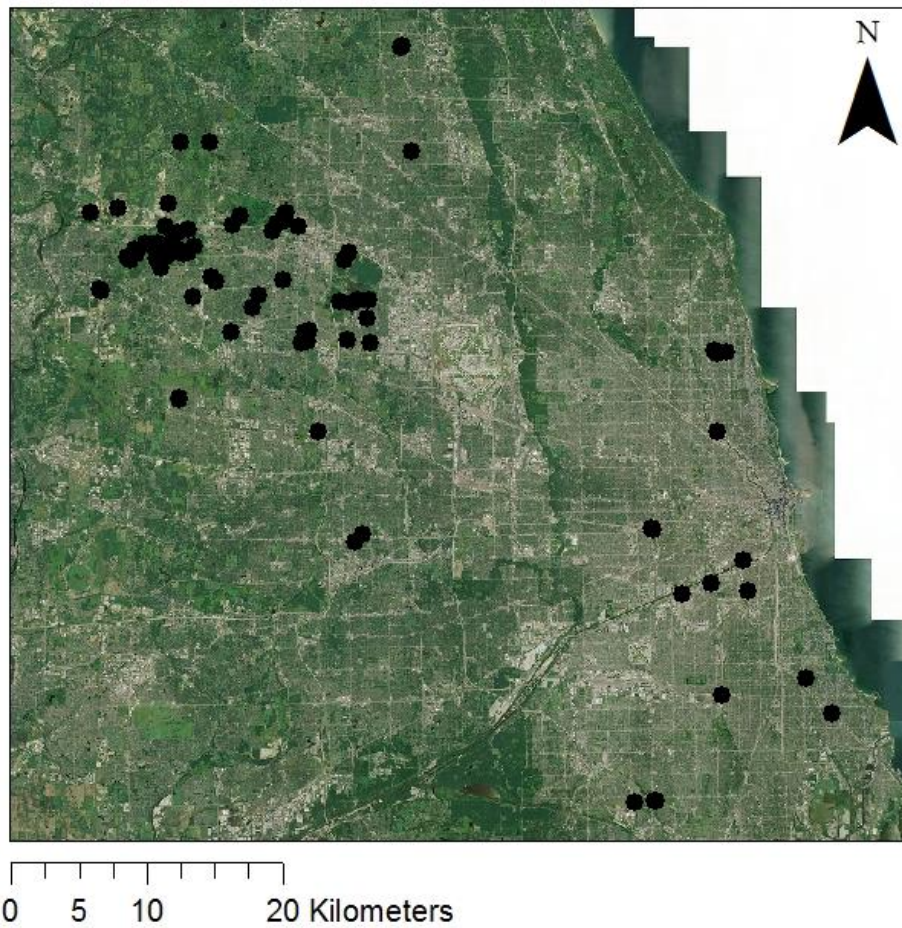


Figure 2.1. Initial locations of coyotes that were flight initiation distance tested (n= 90; 60 unique) in the Greater Chicago Metropolitan Area from March 2015 through December 2017.

Overall Distribution of Coyote FID

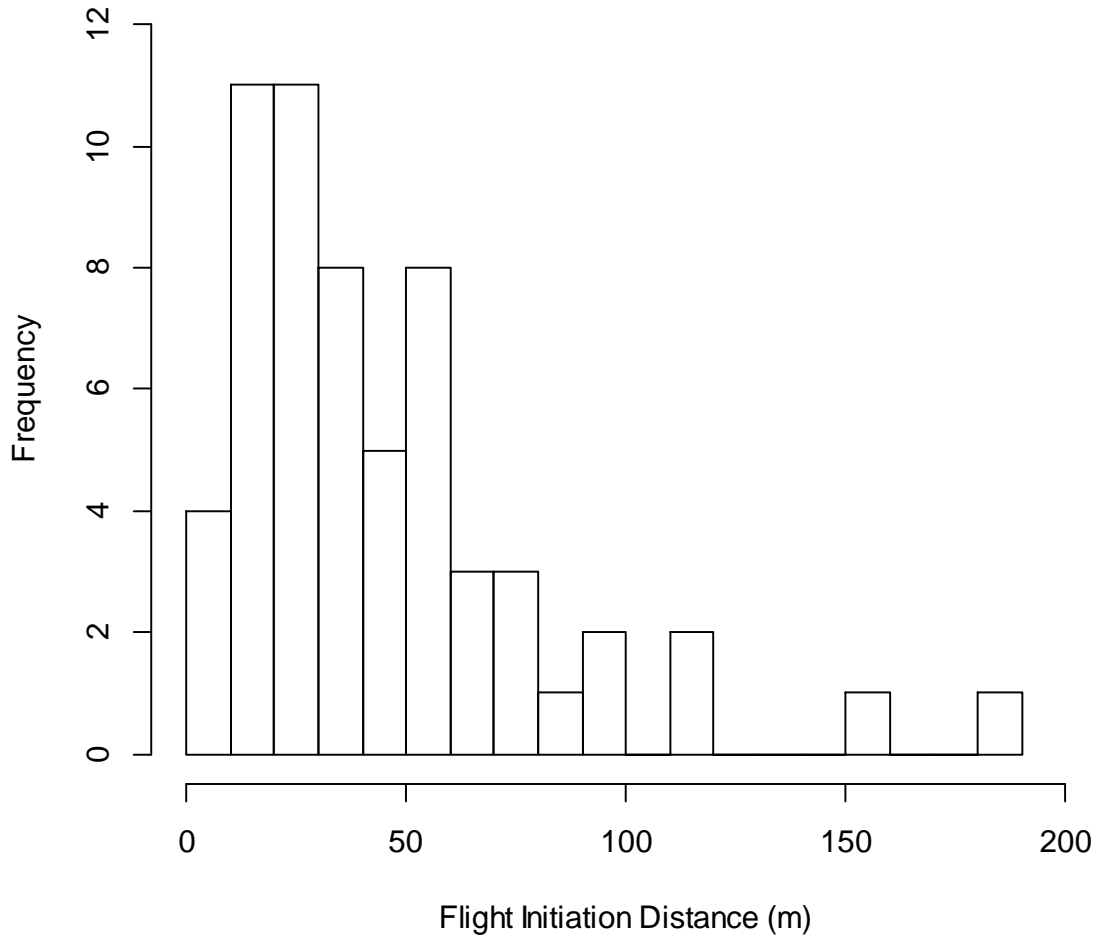


Figure 2.2. The overall distribution of flight initiation distance (FID) tests when all tests from the urban, suburban, and forest preserve sites (n=60; excludes repeated tests) were combined. All tests were conducted between March 2015 and December 2017 in the Greater Chicago Metropolitan Area.

Coyote Flight Distance v. Urbanization Level

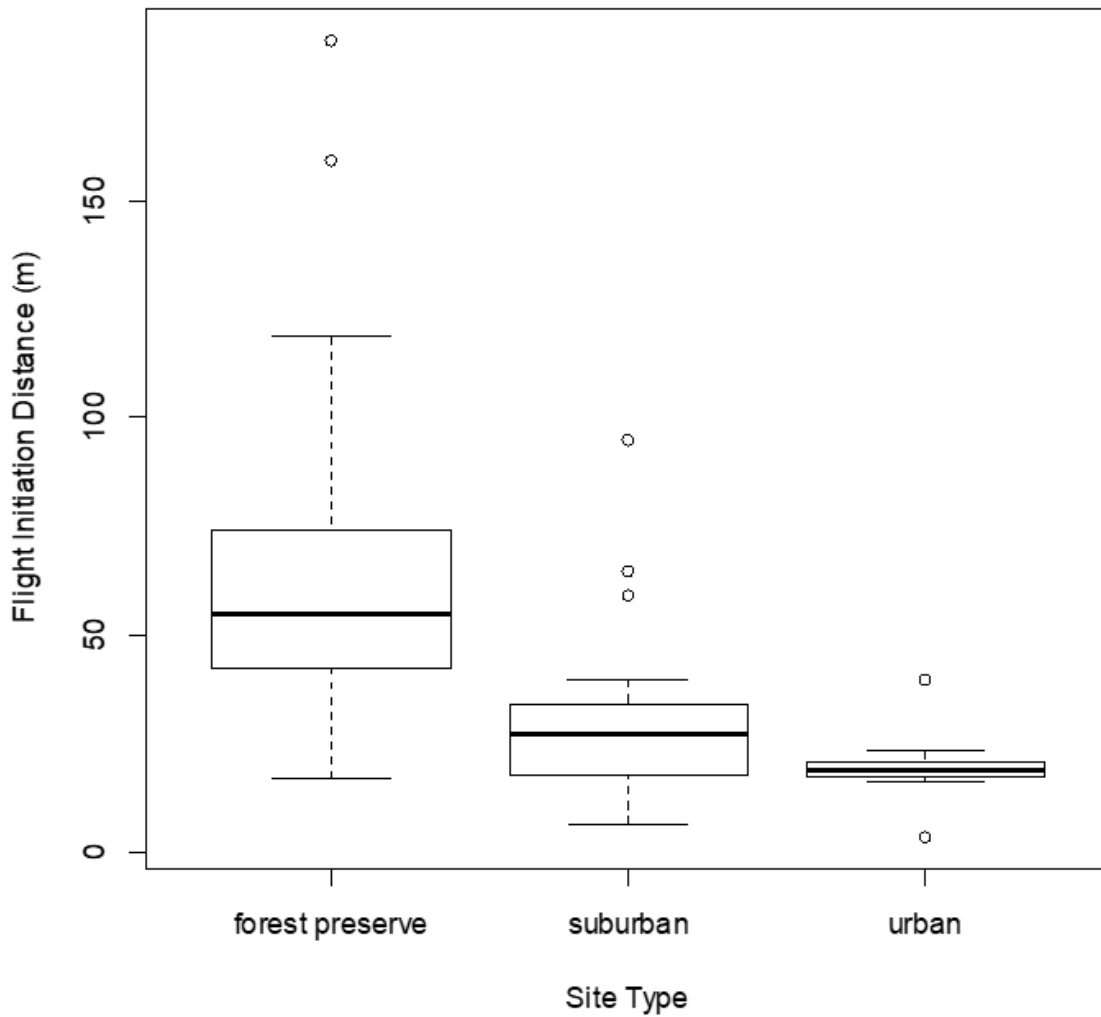


Figure 2.3. Coyote flight initiation distance distributions across the three site types (i.e., forest preserve (n=28), suburban (n=21), and urban (n=11)) in the Chicagoland area. All tests were conducted between March 2015 and December 2017.

Coyote Flight Distance vs. Sex

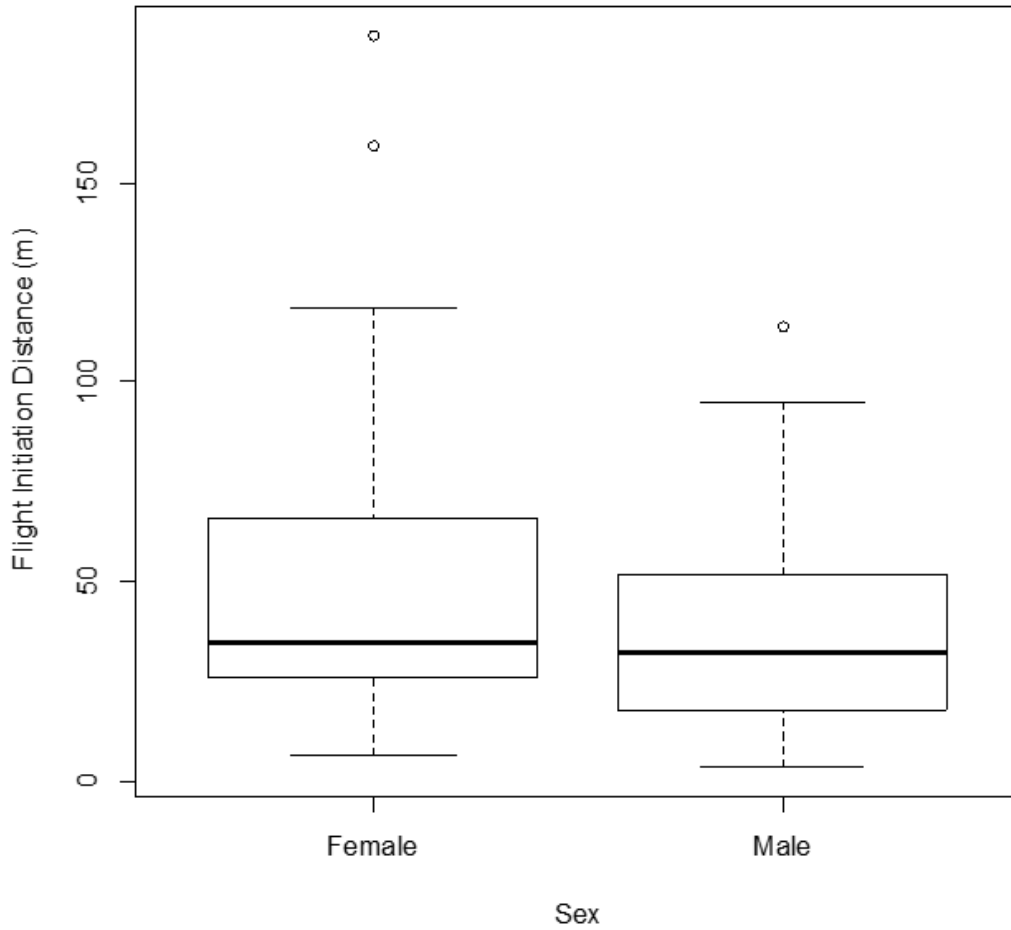


Figure 2.4. Flight initiation distance distributions for female (n=26) and male (n=34) coyotes when all sites were combined. There was no significant difference between the FIDs for the two sexes ($t=1.71$, $df= 54.385$, $p= 0.093$). All FID tests were conducted 2015-2017 in the Greater Chicago Metropolitan Area.

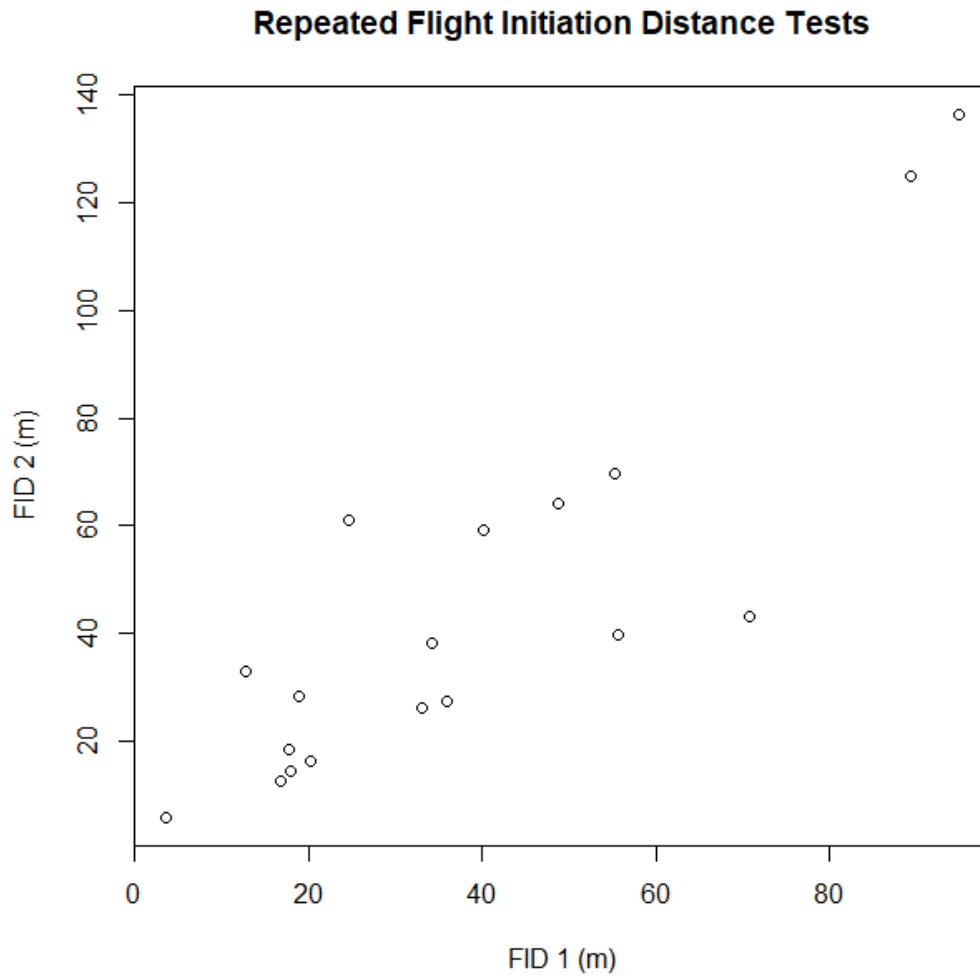


Figure 2.5. Flight initiation distance (FID) test results for first and second trials conducted on individual coyotes in the Greater Chicago Metropolitan Area (n= 18 coyotes; 11 males, 7 females) between July 2015 and December 2018. The Spearman’s ranked correlation coefficient (r_s) for first and second FIDs was 0.82 ($p < 0.001$).

Chapter 3

Examining Exploratory Tendencies of Free-Ranging Coyotes Via Novel Object Testing

As human influence has spread further into natural areas, some species have adapted their behaviors to live in proximity to people. The coyote (*Canis latrans*) has used its behavioral flexibility to ultimately thrive in natural, suburban, and urban settings. Individuals within populations can express suites of related behaviors that form the basis of behavioral syndromes, some of which may be beneficial for survival in certain environments. While some individuals exhibit reactive (i.e., shy) behavioral patterns and others exhibit proactive (i.e., bold) behavioral patterns, each pattern likely has associated costs and benefits. Oftentimes, bolder individuals also have increased exploratory tendencies. One method of examining the exploratory tendencies of individuals is through novel object testing. To determine if coyotes vary in terms of exploratory behavior across an urbanization gradient, we conducted novel object tests (n=50) on free-ranging coyotes in the Greater Chicago Metropolitan Area. Reactions (n=96) to objects were recorded via camera traps so coyote behaviors could be rated along a neophobic-to-neophilic scale. Distributions of reactions along the scale varied by location type, with developed (i.e., suburban and urban) areas tending to have more coyotes on the neophilic end of the spectrum than natural areas (i.e., forest preserves) ($p < 0.001$). A mix of neophobic and neophilic individuals were found in both developed and natural sites, however, suggesting there is some within-site, individual variation in coyote behavior, regardless of urbanization level. Coyote rank also varied by their distance to the nearest road, with animals closer to roads tending to have higher proportions of neophilic neophilic ratings ($F= 4.437$, $df= 1,93$, $p= 0.038$). Our findings support the idea that exploration-prone animals are more common in urban areas, possibly due in part to their ability to find and successfully use novel resources. Additional studies are needed to

determine if the increased neophilia we observed in developed areas are due to differences in behavioral syndromes or simply a result of habituation to novelty over time.

INTRODUCTION

Acquiring information about the local environment and surrounding conspecifics is vital for animal survival in the wild. Animals can learn information about their environments via watching other individuals or, more often, exploring their environments on their own (Day et al. 1998; Dall et al. 2005). During the exploration process, individuals can determine which areas are safe, where useful resources are located, and potentially what other species or conspecifics have been in the vicinity. Exploring can come at a cost, however. Exploring requires energy that could otherwise be used for foraging, eating, mating, denning, or interacting with other individuals (Greenberg and Mettke-Hofmann 2001). Additionally, investigating novel locations or novel items could be risky. There are no guarantees that novel locations or resources will be beneficial, and some may even be detrimental to an animal's health and fitness. Oftentimes, behaving in an exploratory manner requires reducing vigilance behavior as well, thus it leaves the animal vulnerable to predation or other negative interspecific interactions (Lima and Dill 1990; Greenberg and Mettke-Hofmann 2001).

Individuals frequently vary in terms of their behavior (Sih et al. 2004; Boogert et al. 2006; Young et al. 2015). Behavioral differences within a single species can be due to behavioral plasticity (Sih et al. 2004; Lowry et al. 2012). Being behaviorally plastic allows species to persist under a variety of environmental conditions and increases the adaptability of populations. Plasticity within individuals, however, can be limited (Sih et al. 2004; Dingemanse and Reale 2005). Increased exploratory tendencies and neophilia are often associated with high levels of boldness, higher activity levels, decreased behavioral flexibility, and attenuated hypothalamic-

pituitary-adrenal (HPA) axis responses (Drent et al. 2003; Sih et al. 2004; Cockrem 2007; Laudenslager et al. 2011; Dammhahn and Almeling 2012; Adriaenssens and Johnsson 2013; Frost et al. 2013). When groups of behavioral and physiological responses are commonly associated with one another and can be triggered by a single stimulus, they can be collectively referred to as a behavioral syndrome (Sih et al. 2004; Lowry et al. 2012). For example, individuals on the bold side of the bold-shy spectrum are often consistently proactive, risk-prone, and more exploratory than shyer individuals (Sih et al. 2004; Darrow and Shivik 2009; Cremona et al. 2015). Increased risk-taking activity may be at least in part due to lowered HPA activity. Since bold individuals do not experience high levels of stress in response to novelty or risky situations, they may be more likely to act with little or no caution. Individual differences can be found in many natural populations (Sih et al. 2004; Way et al. 2004; Gosselink et al. 2007; Grubbs and Krausman 2009). The dominant behaviors exhibited by populations may largely depend on the environment that the animals reside in. While it may be beneficial to be more risk-taking and exploratory in some locations, in others it may be safer to behave more cautiously.

Exploration is often associated with an animal's tolerance of novel stimuli. Neophobia (i.e., fear of new stimuli) is often tested as a proxy to examine animal exploratory tendencies. One commonly used method to test for neophobia is through novel object testing. In novel object testing, an unfamiliar object is placed in a familiar location. The subject's response to the object is then analyzed by using quantitative measures (e.g., latency to approach the object) and/or qualitative factors (e.g., behavior descriptions) that can be coded for and placed along a neophobic-to-neophilic scale. Responses to novel objects can be consistent for each individual (Boogert et al. 2006; Adriaenssens and Johnsson 2013), indicating the possibility of an innate response level. Past studies of neophobia have found, however, that various external factors can

also influence an animal's behavior toward a novel object. The size of the object can deter or attract some individuals, the presence of conspecifics when the object is encountered can reduce neophobia, and previous exposure to similar objects can alter behavioral responses (Fragaszy and Mason 1978; Windberg 1996; Heffernan et al. 2007; Darrow and Shivik 2009; Moretti et al. 2015). Additionally, an animal's sex (Berentsen et al. 2006), social rank within a group (Katzir 1982; di Bitetti and Janson 2001; Stahl et al. 2001; Darrow and Shivik 2009) and physical state (e.g., how hungry or stressed an animal is) (Day et al. 1998; Dall et al. 2005; Cockrem 2007) can influence risk-taking tendencies and responses to novel situations, especially if potential food resources are involved. Lastly, neophobia can be influenced by the location of the novel object tests; novel objects in familiar areas tend to elicit stronger neophobic responses (Cowan and Barnett 1975; Windberg 1996)

Urbanization may influence the prevalence of neophilic and neophobic individuals within wildlife populations. While exploratory individuals may be more likely to cross roads (i.e., risk being hit by vehicles), venture into areas near people (i.e., risk negative human-wildlife interactions), and investigate dangerous items (e.g., toxic foods; traps), the benefits may outweigh the risks. Individuals that are not as neophobic are likely able to find and benefit from human-associated resources more easily (Lowry et al. 2013; Tryjanowski et al. 2016). The success of some urban wildlife species is often attributed to the abundance and variety of resources present within developed locations (Martin and Fitzgerald 2005; Baker et al. 2007; Beckman and Lackey 2008; Bourbannais et al. 2013). In addition to natural resources found in remnant green spaces, small prey items (e.g., rodents) are often more abundant in areas where human refuse is present. Some species (e.g., raccoons, coyotes) also can scavenge for roadkill, consume pet foods, and eat a variety of human foods. When urban individuals are relatively

exploratory and neophilic, they can exploit such resources and may be able to maintain smaller territories than individuals found in more natural settings (Gehrt et al. 2007; Gese et al. 2012). The energy that neophilic, urban animals save by using readily-available resources and defending smaller territories may allow them to allocate more time to food consumption and breeding, thus increasing their overall fitness.

In addition to benefiting individuals in terms of resource acquisition, decreased neophobia may help individuals initially colonize urban areas and subsequently cope with human activity (Martin and Fitzgerald 2005). Urban areas are often highly dynamic in nature and even green patches within developed areas are subject to frequent disturbances. For an animal to locate an urban habitat and decide to reside in the area, at least some level of exploration would be necessary (Fraser et al. 2001; Reale et al. 2010; Lowry et al. 2013; Tryjanowski et al. 2016). Highly neophobic individuals would likely avoid developed areas, as the disturbances and novelties associated with humans would be stressful to them and inhibit exploration (Laudenslager et al. 2011). Once established in a developed area, bolder individuals that exhibit reduced levels of neophobia likely produce less cortisol in response to human encounters, exposures to novel items (e.g., litter), or habitat alterations. Reduced hypothalamic-pituitary-adrenal axis activity could lead to bolder, less neophobic individuals being less impacted health-wise by stress over time (Reale et al. 2010; Lowry et al. 2013; Birnie-Gauvin et al. 2016) and thus could result in them being more successful in terms of reproduction and longevity (Reale et al. 2010)

Consistencies in correlated behaviors have been previously documented in other coyote studies (Darrow and Shivik 2009; Young et al. 2015) and may help explain some of the behavioral variations observed and dealt with by wildlife managers on a regular basis. For

example, while most coyotes pass through populated areas in favor of natural habitats (Gehrt et al. 2009), some individuals show little or no fear of humans and spend large amounts of time foraging or resting in proximity to people. It was hypothesized that if bolder and more exploratory coyotes do benefit from novel resources and reduced stress responses following exposure to human activity, populations residing in highly developed locations (e.g., suburban and urban areas) would be more likely to contain higher proportions of neophilic individuals than natural areas (e.g., forest preserves).

To test the hypothesis that coyote populations in developed locations tend to contain more individuals on the neophilic side of the neophobic-neophilic spectrum, novel object tests were conducted in natural and developed areas throughout the Greater Chicago Metropolitan Area. The results of the novel object tests help provide information about how human disturbance and urbanization may directly and indirectly influence coyote behavior. Such information will be useful for future coyote management, as more humans and coyotes begin inhabiting similar areas.

STUDY SITE

This study was conducted as part of a long-term, urban coyote research project in the Greater Chicago Metropolitan Area (GCMA). The GCMA includes parts of Cook, DuPage, Kane, Lake, Will, and McHenry counties in Illinois, in addition to bordering areas in Indiana and Wisconsin. Among other towns and cities, Cook County is home to Chicago. Chicago alone is estimated to contain over 5.2 million people, thus parts of the GCMA are highly urbanized (US Census Bureau, 2017 population estimate). Other parts of the GCMA, however are less populated and are composed of natural landcover (Wang and Moskovits 2001). We classified our study sites into three categories along the urbanization gradient: urban, suburban, and forest

preserve. Sites within Chicago's city limits, some of which included railway edges, undeveloped lots, and cemeteries, were all categorized as urban locations. Any sites outside of the Chicago area but were still at least partially developed (e.g., neighborhoods, public parks, golf courses) were labeled suburban sites. Lastly, our least urbanized category was forest preserve. Within the Chicago suburbs, there are county-protected pockets of greenspace that are designated as forest preserves. The preserves include fields, savannas, riparian areas, oak woodlands, and multiple types of recreational areas. Within forest preserves, the public is allowed to participate in non-invasive recreation (e.g., hiking, picnicking at designated sites) but hunting and off-road driving is not permitted. Though some forest preserves exist and the majority of the area is not as developed as downtown Chicago, the GCMA is rapidly becoming more urban over time.

METHODS

Capture and processing. Coyotes were captured using relaxing cable neck restraints and padded MB-550 and MB-650 foothold traps (Minnesota Trapline; Pennock, MN, USA) were used to opportunistically capture coyotes from autumn through spring of each year from 2013 to 2017. The traps were checked every 12-24 hours, depending on the trapping site location. Once captured, the coyotes were transported to the Max McGraw Wildlife Fountain or the Cook County Forest Preserve District headquarters for processing. Immediately preceding processing, each coyote was immobilized with an intramuscular injection of Telazol (Fort Dodge Animal Health, Fort Dodge, IA, USA). Each coyote's morphometric measurements, sex, age class (i.e., pup, subadult, or adult), breeding condition, and overall health condition rank (i.e., poor, good, or excellent) were recorded. Samples for other aspects of the overall coyote project (i.e., hair for cortisol analysis, whiskers for stable isotopes, blood for genetics and disease, fecal samples for parasites, and fecal swabs for bacterial analysis) were collected during processing. All coyotes

received unique ear tags (NASCO Farm & Ranch, Fort Atkinson, WI, USA) for identification and a collar for tracking post-release. The collars were either very high frequency (VHF) collars (Advanced Telemetry Systems, Isanti, MN, USA) that had to manually triangulated, ultra high frequency (UHF) collars (Lotek, Newmarket, Ontario, Canada), iridium collars (Advanced Telemetry Systems, Isanti, MN, USA), or cellphone collars (Lotek, Newmarket, Ontario, Canada). After the coyotes fully metabolized the Telazol and were no longer immobilized, they were released at their initial capture locations. All trapping and handling was conducted in accordance with the trapping guidelines from the American Society of Mammalogists (Sikes et al. 2011) and the animal handling protocol that was approved by The Ohio State University Institutional Animal Care and Use Committee (OSU IACUC #2010A00000113).

Tracking. Each collared coyote was located at least one day per week during daylight hours and one or two nights per month. Day locations involved triangulating and recording a single location. Night tracking involved collecting 5 hourly locations per animal within a single night. Triangulations were manually conducted by using truck-mounted antennas. In addition to the manually triangulated locations, points were obtained from GPS collar fixes. The GPS collars were configured to record either hourly or 15-minute locations, depending on the location, time of day, the collar style, and the individual animal. All GPS collars were downloaded on a regular basis and were downloaded a final time upon recovery of collars (i.e., due to successful drop-off mechanisms, during recaptures when collars were manually removed, or when coyotes were found deceased). ArcMap 10.4.1 software (Environmental Systems Research Institute, Redlands, CA, USA) was used to plot all of the locations so coyote home ranges and habitats could be visualized. Coyotes were categorized as urban, suburban, or forest preserve based on the locations we collected for each individual.

Site selection. Novel object testing sites were selected based on a combination of factors. Maps of all coyote locations collected via VHF and GPS tracking were used to determine what areas collared coyotes were frequenting. Areas where multiple known individuals had visited were given priority. Once potential areas were determined by visually examining maps, each area was visited to look for coyote sign. Sites that included coyote sign or other game trails and that had at least one tree present were selected for testing. An ideal site was considered to be one that was located within or near a known animal's home range, in an area with limited human traffic (when possible), in a habitat with at least one tree for securing equipment, and on high enough ground that flooding would be unlikely. Once a specific site was selected the testing process took place for a 15-day period and was divided into three phases (i.e., pre-testing, novel object testing, and post-testing).

Pre-testing. During the pre-testing phase, a still-image, infrared trail camera (Reconyx Hyperfire) and a high definition, infrared video camera (Bushnell HD) were placed on trees, facing the direction where the object testing would occur in the next phase. Additionally, if any collared coyotes were suspected to be in the area, a data logger (Advanced Telemetry Systems) was placed discretely in nearby brush or behind a nearby tree. Prior to deployment, the data logger was attached to a pelican case, equipped with an antenna outlet and an external battery that both be attached to the datalogger. Based on prior testing in a controlled setting (Fig. B.2), using a small, UHF antenna while keeping the datalogger at a pre-determined gain level would allow us to detect coyote collar signals that were within ~20m of the datalogger. Programming the datalogger to search for up to ten coyote collar frequencies that were predicted to be in the area allowed collared coyotes to be detected and identified as they approached the site. Once the data logger was placed in the field and disguised by vegetation (when possible), the cameras and

data logger were turned on and allowed to run continuously without disturbance for 5 days. The pre-testing phase was used to identify which species were normally present in the area, determine how coyotes behave in a relatively undisturbed situation, and provide time for animals to adjust to the presence of the equipment before novel object testing.

Novel object testing. At the end of the pre-testing phase, a novel object (i.e., a garden gnome or ring stacker toy; Fig. 3.1) was staked to the ground in front of the cameras. No scent was added to the site or to the object and gloves were used to help prevent scent transfer. Additionally, when not in use, all objects were stored in a tub filled with cedar to prevent them from acquiring anthropogenic scents. After the object was placed at a site, the site was left undisturbed for another 5 days.

Post-testing. After leaving the object in the field for the duration of the novel object testing phase, the object was removed. The cameras and datalogger were left in the field for a final 5-day period that served as the post-testing phase. The post-test phase provided data on how animals behaved following the removal of a novel object.

Habitat measures. All habitat measures were collected at the end of the post-testing phase. The habitat type (e.g., forest, field), dominant substrate (e.g., dry leaves, tall grasses), % canopy cover, and % visibility were recorded. Canopy cover and horizontal visibility measures were collected from the point where the object had been previously placed. Canopy cover measurements were taken by using a concave, spherical densiometer (Lemmon 1956). Four canopy cover measures (one while facing each cardinal direction) were taken and averaged for the site. Similarly, for the horizontal visibility measure, a measure was taken in each cardinal direction. Visibility measures were collected by using a dot-gridded, white sheet (Fig. 3.2) (Boyer et al. 2006). One person (i.e., the counter) stood at the object site and another person held

the grid sheet 12 m away, approximately 1 foot off the ground. The counter then crouched and counted the number of dots that were visible. The horizontal visibility measures for each cardinal direction were averaged together to get an estimation for the site.

Rating coyote behavior. All photos, videos, and data logger detections were recorded and analyzed to determine how individuals reacted to the presence of a novel object placed in their natural environments. The identities of collared individuals seen in photos and videos were confirmed by examining the datalogger output and the amount of time each individual spent at the site was estimated. A six-category rating system was used to place coyotes along a neophobic (category 1) to neophilic (category 6) scale. The categories used were as follows:

Category 1: Neophobic (off-camera) and/or Oblivious. The coyote is not seen in any photos or videos but is detected by datalogger. Note that this category includes some animals that are too neophobic to walk within the frame of the cameras and some animals that are simply in the vicinity of the sites (< 20m) but do not notice the object).

Category 2: Neophobic (on-camera). The coyote looks at the object from a distance, jumps when it encounters the object, avoids the object by walking far around it, and/or runs away. Coyotes in this category likely also exhibit nervous posturing, such as tail tucking.

Category 3: Hesitant. The coyote hesitates to approach the object and may display nervous posturing initially, but eventually investigates the object (e.g., sniffs or marks near it).

Category 4: Indifferent. The coyote ignores the object. This may involve walking by it without stopping or glancing at it briefly before walking away. No hesitation toward or interest in the object is exhibited.

Category 5: Curious. The coyote immediately walks over to investigate (e.g., sniff) the object, but leaves shortly afterwards without marking or touching it. No hesitation or nervous posturing is shown, but no interest is shown beyond quickly examining the object

Category 6: Neophilic. The coyote immediately walks up to the object and either makes physical contact with it (e.g., bites or chews it) or marks on it (i.e., uses/claims it).

A combination of the photos, videos, and data logger output were used when determining coyote rating. Each visit was rated separately. A visit was defined as a period where no longer than 15 min passed between detections of the same animal.

Statistical analysis. All statistical testing was done using the R statistical program (R Core Team 2016, v. 3.3.2). The number of coyote visits per day, the number of collared coyote visits per day, and the number of unique, collared individuals that visited per day were recorded; for each of these groups, an analysis of variance (ANOVA) was run to determine if detection rates varied across the phases (i.e., pre-testing, object testing, post-testing). The amount of time coyotes spent on-camera was also quantified and the time spent in each phase of was compared via another ANOVA. Additionally, a linear model was run to determine if habitat variables (i.e., canopy cover, horizontal visibility, and distance to the near road) were significant predictors of the time coyotes spent on-camera at the sites. For coyotes that were collared and identifiable, a simple t-test was run to determine if male and female coyotes differed in the amount of time they spent on camera. After each coyote visit during the novel object test was categorized, the number of occurrences of each category was determined for each location type (i.e., forest preserve, suburban, and urban). The suburban and urban data were combined for further analyses and collectively referred to as the “matrix” location type. To compare the distribution of ratings in forest preserve versus matrix sites, a Fisher’s exact test was conducted using the R statistical program (R Core Team 2016, v. 3.3.2). Similarly, to compare the distribution of ratings for coyotes that were exposed to a garden gnome versus a ring stacker toy, another Fisher’s exact test was conducted. Lastly, two additional ANOVAs were run to determine if the time a coyote spent on camera and the distance to the nearest road varied by the behavioral rating of the coyote. All means are presented with \pm the margins of error for their 95% confidence intervals.

RESULTS

Approximately 48 coyotes (21 males, 27 females) from previous trapping sessions in the lab were already being consistently monitored at the beginning of November 2013. An additional 183 coyotes (n= 155 unique individuals; 97 males, 58 females) were captured between November 2013 and April 2017. One mortality occurred following a cable restraint capture, though the cause of death was not apparent, even through a formal necropsy. All other coyotes sustained minimal to no injuries and were successfully returned to the locations where they were captured.

A total of 50 trials were conducted from June 2015 to June 2017. Of those trials, 29 were in forest preserves, 13 were in suburban areas, and 8 were in urban areas (Fig. 3.3). A total of 23,657 still images and 11,925 videos were collected. Of those, 17,074 photos and 2,966 videos contained animals (Appendix 3.2). At 39 of the 50 sites, coyotes were detected during the 15-day period that the equipment was deployed. A total of 767 photos and 75 videos contained coyotes.

The number of coyote visits per day ($F= 0.525$, $df= 2$, 143 , $p= 0.593$), number of collared coyote visits per day ($F= 0.274$, $df= 2$, 144 , $p= 0.761$), and number of unique collared coyotes that visited per day ($F= 0.185$, $df= 2$, 144 , $p= 0.831$) did not vary significantly across the phases (i.e., pre-testing, object testing, post-testing) of the trial (Table 3.1). Similarly, average time an individual coyote spent on-camera during a single visit did not vary across the phases ($F= 2.188$, $df=2$, 190 , $p= 0.115$; Table 3.2).

Based on a linear model including percent canopy cover, horizontal visibility, and the site's distance to the nearest road (log transformed) as predictors of the time a coyote spends on camera (log-transformed), horizontal visibility ($t= 2.453$, $p= 0.015$) is a significant predictor but canopy cover ($t= 0.931$, $p=0.353$) and distance to the nearest road ($t= -0.403$, $p= 0.688$) are not. The overall model had relatively low predictive power ($R^2= 0.018$, $F=2.195$, $p=0.09$).

In addition to the habitat variables, we tested to see if the time coyotes spent on camera varied by sex for coyotes that we had collared and could identify. Females (n= 21) spent a mean of 15.90 ± 7.60 seconds on camera, whereas males (n= 34) spent 18.97 ± 19.52 seconds on camera. Based on a simple, t-test analysis, there was no significant difference in the time that the two sexes spent on camera ($t= 1.428$, $df= 46.551$, $p= 0.160$).

Each coyote visit was rated along the neophobic-to-neophilic scale, regardless of whether they were collared. A total of 50 forest preserve visits, 14 suburban visits, and 32 urban visits were categorized (Table 3.3). Due to the lower sample sizes in the suburban and urban categories, the suburban and urban categories were combined into a single “matrix” category for further analysis. To determine if the frequencies of the various ratings differed by site type, a Fisher’s exact test was used on the forest preserve and matrix data. Coyotes placed in category 1 were excluded from the analysis because it was not possible to differentiate the coyotes that were truly neophobic and off-camera from the coyotes that simply walked by the site without noticing the object. The distribution of coyote behavioral ratings (categories 2-6) did vary significantly between matrix and forest preserve sites, with matrix sites tending to have more coyotes on the higher (more neophilic) end of the spectrum ($p= 0.00058$). We were unable to analyze differences in ratings by coyote social status, since all collared coyotes that were present on camera during the novel object phase were presumed alpha coyotes (n=20). An additional 22 alpha, 4 subordinate, and 2 transient coyotes were detected by the datalogger but were not detected by either camera.

To test if the gnome and the ring stacker toy were similar in terms of novelty and the responses they generate from coyotes, a Fisher’s exact test comparing the proportion of coyotes in each behavioral category (excluding category 1) for each object was conducted. A total of 46

visits (n= 35 visits detected by cameras) were observed for the garden gnomes and 50 visits (n= 33 visits detected by cameras) were observed for the ring stacker toy. The distributions of coyote behavioral ratings (categories 2-6) did not vary by the object type ($p=0.1847$).

Lastly, to determine if a given coyote's behavioral rating may be related to the amount of time the coyote spends on camera or how close the coyote is to the nearest road, two additional ANOVAs were run. The amount of time coyotes spent on-camera did not vary significantly by behavioral rating ($F=0.057$, $df=1$, 59 , $p= 0.812$). The distance to the nearest road did vary by coyote rating, however ($F= 4.437$, $df= 1$, 93 , $p= 0.038$) (Fig 3.4).

DISCUSSION

The observed number of total visits, number of collared coyote visits, and number of known unique individual visits did not vary across the three phases (pre, object, and post) of the trials. Similarly, the time that coyotes spent on camera did not vary by phase. The lack of variation across the phases indicates that the cameras, datalogger, and objects used throughout the different phases were not enough of a deterrent to prevent coyotes from traveling in the vicinity of the site. Other novel object studies have used a wide variety of different objects, including plastic balls, black cubes and pyramids, juggling balls, gum with attached hair tufts, and plastic animal toys (Stevenson-Hinde et al. 1980; Harris and Knowlton 2001; Lendvai et al. 2011; Tryjanowski et al. 2016; Yuen et al. 2016).

When selecting an object for novel object testing, some key factors to consider are the novelty of the item (i.e., the object must be something the animal has not already encountered in the area it is placed), the durability of the item, and the size of the object (Windberg 1996; Harris and Knowlton 2001; Tryjanowski et al. 2016). The objects used to test the coyotes were a garden gnome and ring stacker toddler toy. Both objects are unlikely to have been experienced by

coyotes in forest preserve (i.e., natural) settings. Though garden gnomes are outdoor items and could potentially have been seen previously by suburban or urban coyotes who travel through neighborhoods, the gnomes should still have been novel in the locations where the tests took place. In other words, it is possible that a coyote may have seen a garden gnome in a front yard somewhere prior to the test, but the coyote likely had never come across one in the undeveloped lots or railroad edges where our tests took place. The gnome in a new location would still, therefore, serve as a novel item. Both the gnome and the ring stacker were relatively weather-proof, were able to be staked to the ground, could withstand most potential interactions with wildlife, and did not consist of any small or sharp pieces that could pose risks to the test subjects. The gnome and ring stacker were relatively equal in terms of novelty, as evidenced by the lack of difference in the categories of coyote responses to each one.

Our objects were under 30 cm each, making them smaller than those used in some coyote novel object tests (*90 cm*, Heffernan et al. 2007; *0.8 m*, Young et al. 2015), but slightly larger than those used in other coyote tests (*4, 8, and 16 cm*, Windberg 1996; *10 cm*, Harris and Knowlton 2001; *15 cm*, Heffernan et al. 2007). Some studies found that coyotes were less likely to visit sites while a large object was present (Windberg 1996; Heffernan et al. 2007), but they were more likely to visit sites where large objects had been previously removed (Heffernan et al. 2007). Coyotes did not appear to actively avoid the vicinity of our objects. In case our objects did generate interest after their removal, we continued running the cameras for 5 days post-testing. Again, however, we found no change in the number of visits per day before, during, or after novel object testing took place.

Another potential reason why we did not see changes in visitation rates across the phases is that we did not use any olfactory-based lures or foods to draw animals to the testing sites.

While some behavioral studies have used scent to lure animals to specific locations, increase detection probabilities, and test animal responses to different olfactory cues (Harris and Knowlton 2001; Cremona et al 2015), we attempted to limit the introduction of scent to our study sites as much as possible. Coyotes may rely on visual cues more than olfactory cues when approaching novel stimuli (Windberg 1996; Harris and Knowlton 2001), however scents may still influence individuals differently and ultimately confound novel object analyses. Similarly some novel object studies use food to lure individuals to specific sites for testing responses to novel stimuli (Darrow and Shivik 2009; Herborn et al. 2010; Tryjanowski et al. 2016). While providing a food subsidy may increase the number of individuals that arrive on-site and see the object and it is possible to measure how many individuals approach a food source with or without an object present, the food provided may alter the novel object test results. The risks associated with approaching a novel object may be outweighed by an animal's desire for food, particularly if it is in a less-than-optimal state (Dall et al. 2004). By avoiding the intentional use of scent or foods at our sites, we were able to observe coyote reactions that were based almost exclusively on visual cues.

Though we could not directly measure the latency for a coyote to approach the objects since we could not tell exactly when coyotes noticed the objects if they were off-camera, we did estimate how long each coyote that was detected by a camera was in the camera's field of view. We found no sex difference in the amount of time coyotes spent on camera. This finding is consistent with other studies that found male and female coyotes spend similar amounts of time approaching and investigating novel objects (Heffernan et al. 2007; Young et al. 2015). The amount of time spent on-camera was influenced, however, by horizontal visibility. As horizontal visibility increased, so did the amount of time that coyotes spent on camera. There are multiple

possible explanations for the pattern observed. First, coyotes in open areas may be able to see their surroundings better and escape more quickly in open areas, thus they may not be as likely to run immediately. Another potential reason open areas may be associated with increased time on camera is that objects stand out more in open areas and thus may catch and hold a coyote's attention longer than if an object was in an area with other distractions. One of the most likely factors that contributed to the observed pattern, however, is that the cameras would have larger fields of view in open areas. The larger the field of view, the longer a coyote can be detected as it is moving away from the site.

Though the visitation rates were similar across all three phases, we did detect differences in coyote responses to the objects during the novel object phase. Though we could not use traditional quantitative measures on Chicagoland's free-ranging coyotes (e.g., measure latency to approach), we were able to create a rating system that allowed us to categorize and quantify differences in the coyote's behaviors (Stevenson-Hinde 1980; Harris and Knowlton 2001; Andersson et al. 2014). Variations in coyote responses may indicate the presence of behavioral syndromes. Variations in response to novel objects have been reported in multiple species (*rhesus monkeys*, Stevenson-Hinde et al. 1980; *coyotes*, Harris and Knowlton 2001; *birds*, Herborn et al. 2010; *brown trout*, Adriaenssens and Johnsson 2013). Differences in coyote behavioral tendencies have also been previously reported in captive coyote studies (Harris and Knowlton 2001; Darrow and Shivik 2009; Young et al. 2015). Like the coyotes we observed in the Chicagoland area, the captive coyotes were reported to vary from neophobic to indifferent/neophilic, with some coyotes falling between the extremes (i.e., those that are initially anxious but eventually overcome their neophobia and investigate the object). Novel object tests can be correlated with other forms of boldness behavior and HPA activity (Drent et al. 2003;

Frost et al. 2013; Laudenslager et al. 2011). Typically, bolder individuals are more exploratory and less neophobic than their shy counterparts (Yuen et al. 2016).

The prevalence of the various behavioral rating varied by study site type. The matrix sites tended to have more coyotes on the neophilic side of the spectrum than the forest preserve sites. Similarly, the forest preserve sites had a greater proportion of neophobic individuals than matrix sites. Our findings are similar to those in a previous study that found urban birds were more likely to be neophilic or indifferent toward objects than rural birds (Tryjanowski et al. 2016). It is possible that neophilic and exploratory individuals may be more likely to colonize developed areas in the first place since they are more likely to seek out novel habitats and resources (Martin and Fitzgerald 2005). If neophobic individuals do enter urban areas, habituation to novel stimuli may be possible, as well. Coyotes have previously been observed to habituate to novel stimuli over time and repeated exposures (Darrow and Shivik 2009; Berentsen et al. 2006). Regardless, coyotes who are less neophobic likely do better in developed areas due to their abilities to find and use novel resources. Since exploration may be a heritable trait (Sih et al. 2004; Drent et al. 2013), the increases in coyote fitness associated with neophilia in urban areas would likely lead future generations of urban coyotes to contain even greater proportions of neophilic individuals. In the Chicagoland area, most of the coyotes, regardless of study site type, were placed in the indifferent category (category 4). This indicates that most coyotes were neither afraid of nor interested in the objects we used for the novel object test. Lastly but importantly, though the prevalence of certain rating categories varied by site type, both site types included coyotes from across the neophobic-neophilic spectrum.

The coyote's distance to the nearest road varied significantly by coyote rating, with coyotes closer to roads tending to be on the more neophilic end of the neophobic-neophilic

spectrum. Given that coyotes in matrix areas tended to be more neophilic than those in more natural areas and developed areas tended to have higher road densities, this result was expected. Coyotes that were less skittish around novel items (i.e., more neophilic) may also have been more comfortable travelling closer to roads than neophobic individuals. Alternatively, these findings could reflect habituation. Coyotes that spend more time near roads likely encounter more novel items (e.g., roadside garbage) than coyotes that spend more of their time in secluded, green spaces. Over time, exposure to novel items introduced by humans could dampen coyote responses to new, novel objects near roadways. Coyotes that previously exhibited neophobia or neophilia toward novel items may become indifferent toward such objects over time.

The time coyotes spent on camera did not vary by coyote behavioral rating. Overall there was a substantial variation in the time spent on camera for all ratings. Coyotes who were hesitant often spent just as much time investigating the object as the neophilic coyotes; the hesitant coyotes simply tended to observe the object at a distance for a longer period of time. Similarly, some coyotes ran away from the object immediately due to their neophobia, while others walked by immediately because they were simply uninterested in examining the object.

Several coyotes were detected by the datalogger but not by the cameras. Some coyotes may be warier of cameras and other novel objects than others (Sequin et al. 2003). A previous study by Sequin et al. suggested that coyote social status influences wariness toward cameras. We were unable to test for the effect of social status on detection due to the low number of subordinate ($n=4$) and transient ($n=2$) individuals that were detected during the novel object phase. Shy individuals, in particular, may be more difficult to detect due to their increased caution around traps, cameras, and other detection methods (Wilson et al. 1994). Individuals that we detected on the datalogger without camera footage may have been neophobic individuals that

were too nervous to walk in front of the cameras or they may have been individuals that simply did not notice the object through the surrounding vegetation.

In conclusion, though we observed a range of coyote responses to novel objects in both developed (i.e., matrix) and undeveloped (i.e., forest preserve) sites, developed sites tended to have greater proportions of neophilic individuals. Regardless of the mechanism by which coyotes in developed areas have become more neophilic, the finding is important for coyote management. To the extent that coyotes in developed areas are less wary of novel stimuli, scare devices will be less likely to deter resident, urban coyotes. Similarly, coyotes in urban settings may be more likely to reside near people and potentially use anthropogenic resources (e.g., refuse; concrete structures for denning). The increased tolerances of human disturbances and attractions toward anthropogenic resources that are shown by neophilic animals could potentially lead to more coyote sightings (and possibly more human-wildlife encounters) in the future. Further studies are needed to determine whether the differences in coyote neophilia in developed areas are due to personality differences or habituation. Though the coyotes in this study likely did not habituate immediately to the presence of our specific novel objects during the 5-day window, it is possible that previous exposure to novel items (e.g., litter) may have lessened their responses to novel stimuli in general. Similarly, if coyotes are exposed to anthropogenic resources that ultimately have a positive effect on them (e.g., if they learn to consume human foods), they may be more likely to behave in ways that allow them to gain more of those resources later on (i.e., they may be more exploratory in the future due to previous, positive reinforcement). Other facets of the overall Chicago coyote research project will provide further insight into whether behavioral syndromes could exist in the coyotes of the Chicagoland region.

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TABLES AND FIGURES

Table 3.1. Detection rates of all coyotes, collared coyotes, and unique (collared) individuals that visited the novel object test site per day during the pre-testing, object testing, and post-testing phases. Two cameras (Bushnell NatureView HD and Reconyx Hyperfire) and an Advanced Telemetry Systems datalogger were present at the site during all three phases. The novel object (i.e., a garden gnome or ring stacker toy) was only placed at the site during the object test phase. All novel object tests (n= 50) were conducted in the Greater Chicago Metropolitan Area (2015-2017)

Phase	Total Coyote Visits (per day)	Collared Coyote Visits (per day)	Unique Collared Coyotes (per day)
Pre	0.359 (\pm 0.120)	0.200 \pm (0.120)	0.126 (\pm 0.045)
Object Test	0.392 (\pm 0.171)	0.196 \pm (0.171)	0.114 (\pm 0.060)
Post	0.471 (\pm 0.185)	0.248 \pm (0.185)	0.138 (\pm 0.058)

Table 3.2. Mean duration of coyote visits (based on camera detections only; \pm margin of error for the 95% CI) to the novel object test sites. All novel object tests (n= 50) were divided into pre-test, object test, and post-test phases. Only two cameras (Bushnell NatureView HD and Reconyx Hyperfire) and an Advanced Telemetry Systems datalogger were at the site during the pre- and post- test phases. During the object phase, a novel object (i.e., a garden gnome or ring stacker toy) was added to the site so animal reactions to the object could be recorded.

Phase	n	Average Time Spent On-Camera (seconds)
Pre	53	15.23 (\pm 8.49)
Object Test	62	23.39 (\pm 20.04)
Post	78	17.62 (\pm 14.70)

Table 3.3. Number of coyotes that were classified in each of the neophobic-to-neophilic categories at forest preserve, suburban, and urban sites in the Greater Chicago Metropolitan Area (2015-2017). Note that, for statistical analyses, the suburban and urban categories were later combined to create a single, “matrix” site type.

Behavioral Rating	Forest Preserve (n= 50)	Suburban (n= 14)	Urban (n= 32)
<i>1</i>	19	6	3
<i>2</i>	11	0	2
<i>3</i>	2	1	0
<i>4</i>	17	6	16
<i>5</i>	0	2	6
<i>6</i>	1	0	4



Figure 3.1. Ring-stacker toy (~22.5cm tall) and garden gnome (~29.8 cm tall) that were used to novel object test coyotes in the Greater Chicago Metropolitan area (2015-2017).

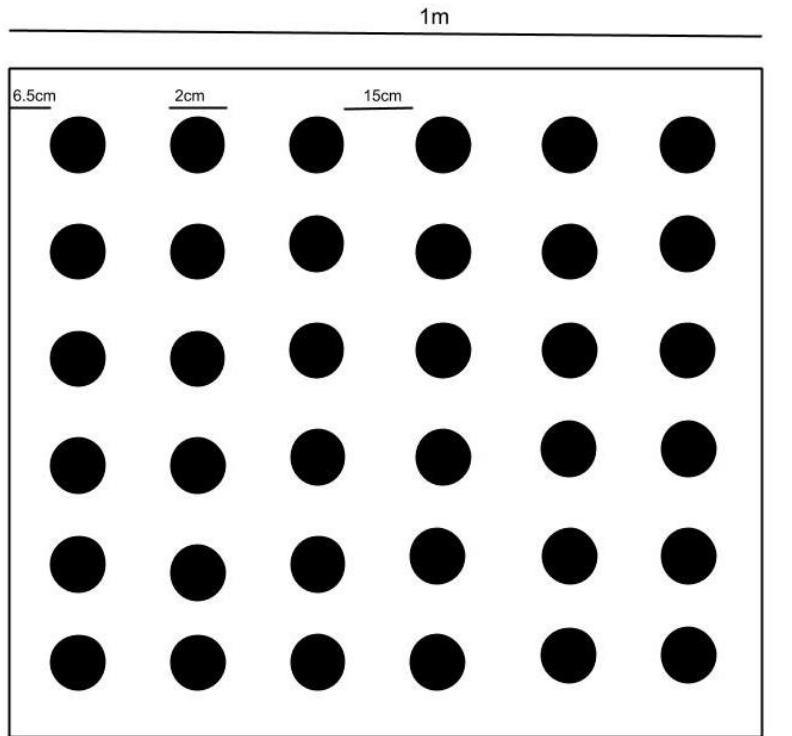


Figure 3.2. Diagram of the dotted, grid sheet used for measuring horizontal visibility at each novel object testing site in the Greater Chicago Metropolitan Area (n=50) from 2015-2017. The dots were painted on a 1-m² fabric sheet, which was then attached to a thin, PVC pipe for handling. To measure horizontal visibility, one person held the sheet 12m away while another person counted the number of dots visible through the vegetation.

Novel Object Test Locations

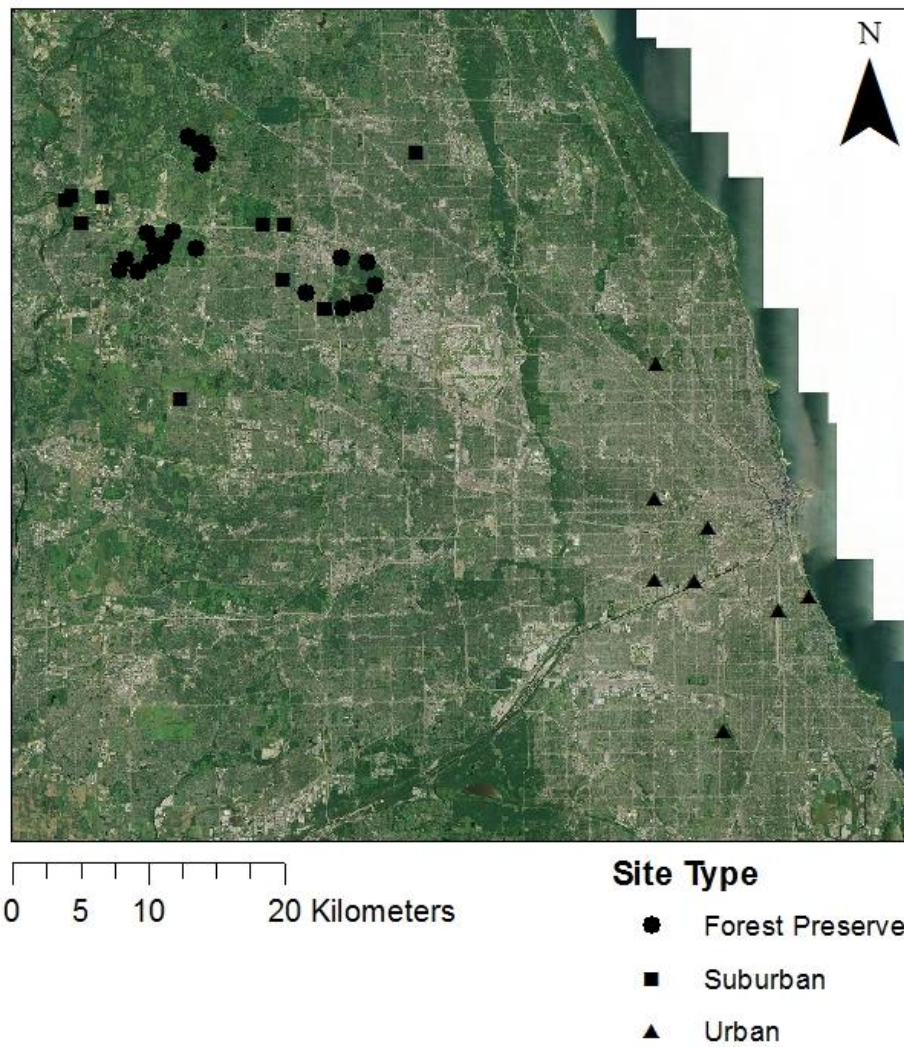


Figure 3.3. Locations where novel objects (i.e., garden gnomes or ring stacker toys) were placed to gauge coyote reactions to new stimuli in their respective environments. Novel object tests (n=50; 29 forest preserve, 13 suburban, 8 urban) were conducted in the Greater Chicago Metropolitan Area from 2015-2017.

Distance to the Nearest Road v. Neophobic-Neophilic Rank

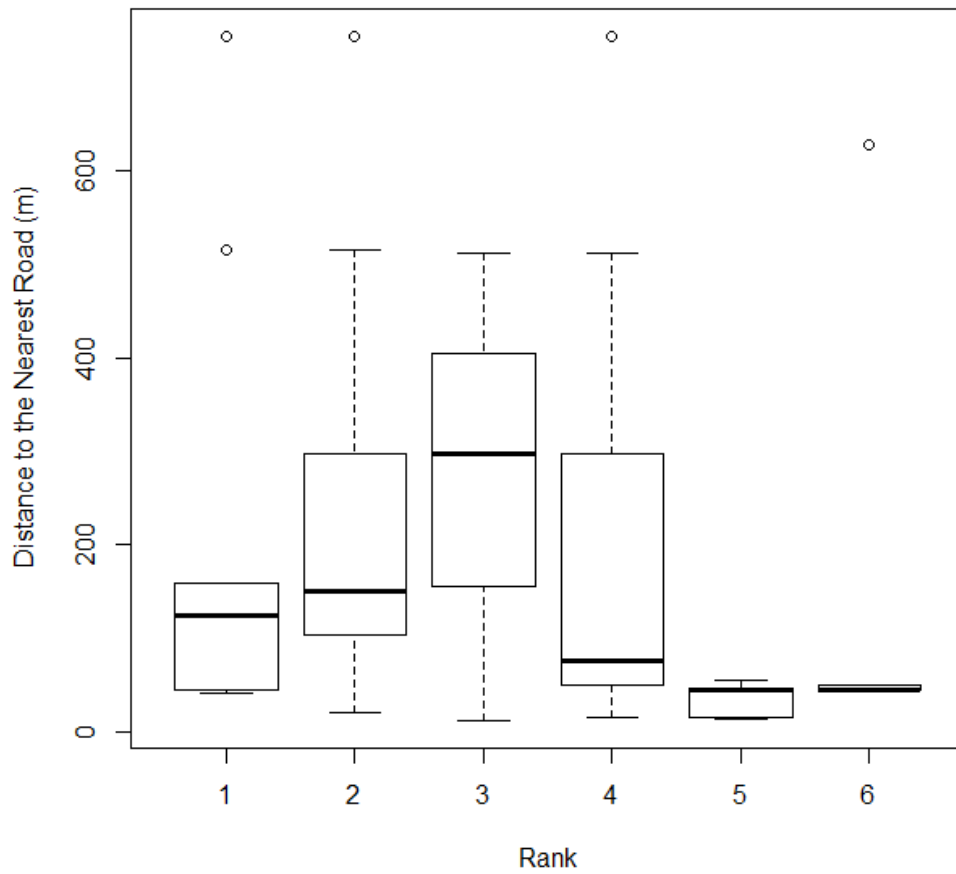


Figure 3.4. The behavioral ratings of coyotes that visited the novel object sites varied with the test sites' distances to the nearest road ($F= 4.437$, $df= 1$, 93 $p= 0.038$). Category 1 ($n=28$) included neophobic and/or oblivious individuals who did not show up on either camera but were detected by the datalogger, category 2 ($n=13$) included coyotes that were neophobic and did show up on camera, category 3 ($n= 3$) included coyotes that hesitated before approaching the novel object, category 4 ($n=39$) included coyotes that were indifferent toward the object, category 5 ($n=8$) included coyotes that immediately investigated the object, and category 6 ($n=5$) included neophilic coyotes that immediately approached, investigated, and make additional contact with the object (e.g., chewed it).

Chapter 4

The influence of demographic, social, and environmental factors on chronic stress in urban coyotes

ABSTRACT

All organisms regularly experience various forms of stress. While short-term stress can be beneficial or even vital for survival, chronically high levels of stress can negatively impact health and fitness. Exposure to stressors activates the hypothalamic-pituitary-adrenal axis and ultimately leads to the production of glucocorticoids (e.g., cortisol). Portions of the hormones that are produced are stored in keratinous tissues (e.g., hair) over time, thus chronic stress levels can be approximated by measuring the concentrations within such tissues. Assessing hormones through hair analysis can be especially useful for wildlife studies since hair cortisol concentration is robust against short-term stressors, including those that may be experienced by animals during capture and handling. Coyotes (*Canis latrans*) living in proximity to people are exposed to a combination of natural and anthropogenic stressors. To determine which demographic, social, and environmental factors may induce cortisol production in coyotes, we analyzed hair samples from forest preserve (n=100), suburban (n=64), and urban (n=34) animals throughout the Greater Chicago Metropolitan area. We found that coyote age, overall health condition, social status, and location along the urbanization gradient were all significant predictors of hair cortisol concentration. Coyote pups had a higher mean hair cortisol concentration than older individuals. Similarly, animals in poor physical condition tended to have higher hair cortisol concentrations than healthier individuals. Like the social status patterns seen in other canid species alphas were more stressed than subordinates. Transient individuals had substantially higher hair cortisol than coyotes in other social status categories. Lastly,

contrary to our predictions, coyotes living in suburban areas had, on average, higher hair cortisol concentrations than forest preserve and urban individuals. These findings will contribute to a greater understanding of urban wildlife endocrinology and may have implications for managing healthy wildlife populations.

INTRODUCTION

All living organisms experience stressors of varying degrees on a regular basis. Short-term stress responses are beneficial and, in some cases, even vital for survival. When stress becomes chronic, however, it can have harmful effects on the body (Davidson and McEwen 2012). Previous studies have shown that chronic stress can dampen the immune system, alter hormone levels, hinder reproductive output, and ultimately reduce the lifespan of the stressed individual (Romero and Wikelski 2001; Blas et al. 2007; Birnie-Gauvin et al. 2016).

Stress can come from a variety of sources, many of which are naturally occurring (Millspaugh et al. 2001). External disturbances, such as extreme weather events, can alter or destroy animal habitats and result in increased stress for wildlife (Wingfield and Ramenofsky 2011; Wingfield 2013). Seasonal fluctuations in temperature and food availability can also increase or decrease baseline stress levels (Saltz and White 1991; Millspaugh et al. 2001; Partecke et al. 2006). In addition to environmental factors, demographic and social factors like age, health (e.g., presence of diseases), social ranking, and breeding status may play roles in creating or mitigating stress (de Villiers et al. 1997; Creel 2001; Bales et al. 2006). Major life events, such as dispersal or the loss of a mate, likely increase stress even further.

In addition to natural stressors, urban environments impose unique stressors on wildlife (Birnie-Gauvin et al. 2016). First, the large number of people in urban areas can make it difficult for some wildlife to persist. It is estimated that over half of the world's population lives in urban

areas (United Nations 2014). Human activity can indirectly impact wildlife by producing noise, changing the habitat around them, producing litter, etc. or they can directly impact wildlife through hazing or removal (Blair 1996; Hamer and McDonnell 2010; Lowry et al. 2013; Birnie-Gauvin et al. 2016). Because of the potential for negative interactions with humans, many species fear people and will actively avoid being near them. In addition to the people present in cities, the lack of natural habitat can pose a problem for many species. While some have adapted to using unnatural green spaces (e.g., public parks), others are more sensitive and cannot thrive without remnant vegetation being present. Even for species that can persist in developed spaces, the lack of cover can be problematic; cover allows individuals to rest without worrying about being noticed by people. Many former vegetated areas become paved or become broken into small fragments (McKinney 2002; Hamer and McDonnell 2010). Typically < 20% of an urban area actually has vegetation (McKinney 2002), greatly reducing the value of these areas for some wildlife. Because of such changes to habitats, differences in food availability, and the presence of humans, some species are unable to cope and do not persist in more urbanized landscapes (Beissinger and Osborn 1982; McKinney 2002; Randa and Yunger 2006; Hamer and McDonnell 2010; Lowry et al. 2013).

Some species are more prone to experiencing stressors in urban areas than others. Partially because predators hunt and consume prey, some people fear mid-to-large-sized species. Fears about physical attacks on pets and children, the potential for diseases being spread, and concerns that predators will negatively impact other wildlife populations (e.g., deer) often result in predators being more persecuted than other groups of wildlife (McClennen et al. 2001; Bateman and Fleming 2012). In addition to being more likely to be viewed negatively than other groups, large predators are also more likely to require large spaces for hunting and denning.

Because of their large space requirements, some predator species may be even more impacted by the lack of connected green spaces in urban environments (McKinney 2002; George and Crooks 2006).

Some species of predators, including the coyote (*Canis latrans*), have mitigated urban stressors to a certain extent by altering their behavioral tendencies. For example, by becoming more nocturnal and avoiding sections of cities that are the most highly developed, some urban predators have been able to avoid people successfully and thrive in developed locations (Baker et al. 2007; Gehrt et al. 2009; Grinder and Krausman 2009; Murray and St. Clair 2015). By avoiding people and some of the human-associated stressors, wildlife can persist and sometimes even have greater fitness levels in human-dominated landscapes.

In cases where wildlife do have negative interactions with people or are unable to cope with environmental change, a stress response occurs when some stimuli triggers the hypothalamic-pituitary-adrenal axis (Fourie et al. 2015; Birnie-Gauvin et al. 2016). Once the HPA axis is triggered, a chain of events occurs within the body that ultimately leads to the production of stress hormones (e.g., glucocorticoids) (Cockrem 2007; Stalder and Kirschbaum 2012; Dowle et al. 2013). Excess glucocorticoids are sent throughout the body and can be found in a variety of fluids and tissues, including blood, saliva, urine, feces, toenails, and hair. To understand more about wildlife stress, cortisol levels in each tissue type can be measured, often through enzyme-linked immunosorbent assays (ELISAs). Liquid samples (e.g., blood, saliva) can provide information about instantaneous stress, digestive materials (e.g., feces) can provide information about the amount of stress experienced during the time it took the animal to consume and fully process their food, and keratinous tissues (e.g., hair, toenails, feathers) can provide information about the relative stress levels experienced by an animal over the time

period it took to grow the tissue being measured (Stalder and Kirschbaum 2012). While traditional studies focused more on instantaneous measures of stress or stress from fecal samples, those methods pose challenges for studying wildlife. For most wildlife species, obtaining samples from individuals requires, first, capturing them. The process of capturing and handling an animal that is not used to being approached, let alone touched, by a human could cause a significant increase in instantaneous cortisol (Wesson et al. 1979; Place and Kenagy 2000). The amount of time the animal spent in a trap or being handled, therefore, could bias the results of a glucocorticoid analysis. Some forms of non-invasive sampling do exist. Oftentimes, non-invasive sampling involves collecting what animals naturally leave behind (e.g., feces) and analyzing those materials. While non-invasive fecal sampling can provide some information about the animals in an area, it is often difficult to tell which particular individual a fecal sample came from., which creates difficulties when attempting to study factors impacting stress at the individual level. Studying feces without knowing who the feces came from, therefore, can make it more difficult to analyze fine details. Because hair cortisol analyses provide long-term stress information, they have relatively recently become the preferred method of studying chronic stress in wildlife populations. Particularly when hair can be directly shaved from individuals, factors that chronically elevate cortisol levels can be identified.

To determine what factors influence chronic stress in free-ranging coyotes along an urbanization gradient, we collected and analyzed coyote hair samples from across the Chicagoland area. Because urban coyotes are typically well-adapted to coping with human disturbances and have a wide variety of natural and anthropogenic resources available to them, we predicted that the baseline stress levels of urban coyotes would be lower than those in less developed areas. Additionally we predicted that, like in other canids, social status would

contribute to coyote stress levels. Finally, physical factors that have been known to influence stress in other species (e.g., age, physical condition) were predicted to be important factors for determining the overall stress level of each coyote. The results of this study will provide wildlife managers with a greater understanding of urban wildlife endocrinology and may have implications for maintaining healthy wildlife populations and preventing future human-wildlife conflicts.

STUDY SITE

This study was conducted in conjunction with and as a continuation of a long-term, urban coyote research project in the Greater Chicago Metropolitan Area (GCMA). The GCMA is comprised of parts of Cook, DuPage, Kane, Lake, McHenry, and Will counties in Illinois and parts of Indiana and Wisconsin. There is a gradient of human activity across the GCMA. The highest levels of human activity are in urban areas, and particularly in Chicago. Cook county, which encompasses downtown Chicago, is estimated to contain over 5.2 million residents (US Census Bureau, 2017 population estimate). Urban coyotes typically used altered habitats, such as railway buffer zones, undeveloped lots, and cemeteries. Outside of the city, there are lesser developed areas that are also inhabited by wildlife. In the suburbs, coyotes commonly roam throughout residential areas, golf courses, public parks, or other anthropogenic habitats. On the low end of the urbanization gradient, there are pockets of green spaces situated within the suburbs and labeled as county-designated forest preserves. The preserves include fields, savannas, riparian areas, oak woodlands, and multiple types of recreational areas. Though many of the remaining natural areas in the GCMA are legally protected, urbanization is still rapidly occurring in the Chicago area. All coyotes in our study were captured in the GCMA and were classified as urban, suburban, or forest preserve individuals. Classification of individuals was

conducted by examining known locations over a period of 4 months before or after hair samples were collected.

METHODS

Capture and processing. Coyotes were opportunistically captured from early autumn to late spring of each year from 2014 to 2018. Captures were accomplished with either relaxing cable neck restraints or padded MB-550 and MB-650 foothold traps (Minnesota Trapline; Pennock, MN, USA). The traps were checked every 12-24 hours. All captured coyotes were transported to either the Max McGraw Wildlife Foundation or the Cook County Forest Preserve District headquarters for processing. Processing involved, first, immobilizing the coyotes with intramuscular injections of Telazol (Fort Dodge Animal Health, Fort Dodge, IA, USA). For each coyote, the sex, age class (i.e., pup, subadult, or adult), breeding status, and various morphometrics were recorded. Age classes were determined by examining each coyote's teeth and genitalia. An overall condition ranking (i.e., poor, good, or excellent) based on a combination of palpable fat stores and visible injuries or illnesses was also given to each coyote. Additionally, if a coyote had visible symptoms of sarcoptic mange, we estimated the percentage of hair lost due to the infestation. To assess chronic stress, an approximately 2-in x 2-in square patch of hair was shaved from each coyote. According to a previous study on coyote hair cortisol, hair cortisol concentrations do not vary across the body of a single individual (Schell et al. 2017). For consistency, however, we shaved the hair from just above the base of each coyote's tail. We chose that particular location on the body because it is easy to locate, is less likely to have surface contaminants (e.g., mud), and typically is less likely to have guard hair loss than some other areas on the body (e.g., shoulders, which often lose hair during the denning season). Samples for other aspects of the overall coyote research project (e.g., whiskers, blood,

fecal swabs, fecal samples) were also collected during the processing period. After all data and samples were collected, each coyote received a unique set of ear tags (NASCO Farm & Ranch, Fort Atkinson, WI, USA) for future identification in the field. Lastly, the coyotes were fitted with very high frequency (VHF) radio collars (Advanced Telemetry Systems, Isanti, MN, USA), UHF collars (Lotek, Newmarket, Ontario, Canada), iridium GPS collars (Advanced Telemetry Systems, Isanti, MN, USA) or cellphone collars (Lotek, Newmarket, Ontario, Canada). Once the coyotes recovered from immobilization, they were transported back to their initial capture locations and were released. All trapping and handling was conducted in accordance with the trapping guidelines from the American Society of Mammalogists (Sikes et al. 2011) and the animal handling protocol that was approved by The Ohio State University Institutional Animal Care and Use Committee (OSU IACUC #2010A00000113).

Tracking. Coyote locations were determined through radio telemetry and GPS collar downloads. For all collars, day and night locations were via manual triangulations with a truck-mounted antenna. Day locations were recorded at least once a week for each individual. Night locations were recorded one or two nights each month, typically with five hourly locations recorded every night. GPS collars were configured to record either hourly or 15-minute locations. In addition to manual triangulations, GPS collars were downloaded on a regular basis and final downloads were conducted upon recovery of the collars. Collars were recovered when the same animal was recaptured at a later date, when the magnetic-based drop-off mechanisms allowed the collars to fall off animals in the field, and when GPS-collared animals were found deceased. All manually triangulated and GPS recorded locations were plotted in ArcMap 10.4.1 software (Environmental Systems Research Institute, Redlands, CA, USA). Coyote hair samples were labelled as urban, suburban, or forest preserve based on the locations that were collected for

the associated coyote. Classification was done by examining where the majority of each coyote's locations were collected during the 4 months prior to obtaining the hair sample. If no locations were available prior to the time of hair collection, we used the locations from 4 months after hair collection instead. Additionally, telemetry locations were used in conjunction with breeding condition data to determine the suspected social status (i.e., alpha, subordinate, or transient) of each individual.

Hair cortisol concentration analysis. Our hair analysis methods were derived from a combination of methods used in other coyote studies and methods used for other species (e.g., bears, dogs, chipmunks, monkeys) (Bourbonnais et al. 2013; Bryan et al. 2013; Mastro Monaco et al. 2014; Fourie et al. 2015; Schell et al. 2017). Approximately 50 mg of guard hairs from each coyote were washed in 5 mL of HPLC-grade methanol by adding it directly to the hair, shaking the vial constantly by hand, and removing liquid after 1 min (Schell et al. 2017). The washing process was repeated once to ensure that all exogenous sources of cortisol were removed. Each sample was dried at room temperature, minced with scissors, and re-weighed to determine the exact mass of the de-contaminated hair being used in the extraction. A blank (negative control) and standards (ELISA kit; Neogen Life Sciences, Lexington, KY) were created to internally validate the assay. Afterwards, a small amount (~9000 cpm) of radio-labeled cortisol was added to each sample and standard so sample recovery values could be assessed post-extraction.

To extract cortisol, 7 mL of methanol were added to each sample, both standards, and the blank vial. The vials were placed in a sonicating water bath for 30 min and then immediately moved to a shaking water bath. After being shaken overnight at 50°C (speed = 40 oscillations/minute), a vacuum filter was used to separate the hair from the supernatant. To ensure that all hormone was transferred in the supernatant, additional methanol was used to rinse

each vial twice (1.5 mL per rinse) and then was added to the supernatant. All methanol was subsequently evaporated via a stream of nitrogen gas while the tubes rested in a 50°C water bath. The samples were reconstituted with 1 mL of kit-provided extraction buffer (Neogen Life Sciences, Lexington, KY). To conduct the recovery analysis, 100 µL of each reconstituted sample, standard, and blank was added to scintillation fluid (5 mL) and run through a scintillation counter. A cortisol enzyme-linked immunosorbent assay (ELISA) kit (Neogen Life Sciences, Lexington, KY) was used to create a standard curve from a known solution of cortisol and measure the cortisol extracted from hair samples per kit instructions. The polyclonal antibody the kit relies on cross-reacts with cortisol 100%, prednisolone 47.4%, cortisone 15.7%, 11-deoxycortisol 15%, prednisone 7.83%, corticosterone 4.81%, 6β-hydroxycortisol 1.37%, 17-hydroxyprogesterone 1.36%, and < 1% with deoxycorticosterone, progesterone, bethamethasone, dehydroepiandrosterone, dexamethasone, d-aldosterone, testosterone, 17α-hydroxypregnenolone, androstenedione, cholesterol, estradiol, estriol, estrone, and pregnenolone. Hair cortisol concentrations were log-transformed prior to statistical analysis. Linear regression models were run to determine whether sex, social status, breeding status, season, site type, age class, overall condition rank, or percent hair loss due to mange were significant predictors of the log-transformed hair cortisol concentrations (R Core Team 2016, v. 3.3.2). Mean hair cortisol concentrations are presented with the ± margins of error for their 95% confidence intervals.

RESULTS

A total of 295 coyote hair samples from 230 unique individuals was collected from October 2014 through March 2018. Of those, 187 samples were collected from live individuals trapped for the project and 108 samples were collected opportunistically from deceased coyotes located within our study site boundaries. A subset of the hair samples (n=198; 174 unique

individuals), were successfully analyzed for hair cortisol concentration. All samples were included in the analysis since, even if samples were collected from the same individual more than once, they were collected at different time points and often after a change had occurred to the animal (i.e., developed mange, changed social status, etc.). To be considered a successful run, we required duplicate wells to have a coefficient of variation (CV) of less than 10%. Samples that did not meet the CV cutoff were removed and/or re-analyzed at a later date. For all hair samples combined (n= 198), the mean hair cortisol concentration was 5.68 ± 0.76 pg/mg, the mean recovery rate was $95.91 \pm 0.76\%$, and the mean intraassay CV was $2.99 \pm 0.31\%$.

Twenty unique, linear regression models were run to determine which variables were significant predictors of the log-transformed, hair cortisol concentrations (Table 4.1; see Table C.1 for all models). The top model was selected by using Akaike's Information Criterion (AIC). The top model's AIC value was over 2 points lower than the next best model, thus we considered it the best predictive model for our dataset (Burnham and Anderson 2002). The top model of the log-transformed HCC included coyote age class, health condition category, social status, and site type as significant predictor variables (Table 4.2). Sex was not a significant predictor of hair cortisol concentration in the top model. We also found no difference in male (n=121; 5.60 ± 1.06 pg/mg) and female (n=77; 5.8 ± 1.06 pg/mg) hair cortisol concentrations when they were analyzed with a Welch's two-sampled t-test (df= 164.49; p= 0.40) (Fig. 4.2a). Pups (n= 67; mean= 6.41 ± 1.54) had higher cortisol concentrations than adults (n= 87; mean= 5.89 ± 1.20 pg/mg), whereas subadults (n= 44; mean= 4.13 ± 0.75 pg/mg) did not (Fig. 4.2b). Similarly, coyotes in poor condition (n= 27; mean= 8.99 ± 3.12 pg/mg) had higher hair cortisol concentrations than those in excellent condition (n= 113; mean= 5.32 ± 1.02 pg/mg). Animals in good condition (n= 58; mean= 4.83 ± 0.731 pg/mg) were similar to the "excellent" condition

animals (Fig. 4.2c). In terms of social status, alphas ($n= 82$; 5.25 ± 1.08 pg/mg) had higher hair cortisol concentrations than subordinates ($n=75$; mean= 3.92 ± 0.51 pg/mg), but lower hair cortisol concentrations than transients ($n= 41$; mean= 9.73 ± 2.50 pg/mg) (Fig. 4.2d). Lastly, forest preserve coyotes ($n=100$; mean= 4.35 ± 0.66 pg/mg) had lower hair cortisol concentrations than suburban individuals ($n= 64$; 7.85 ± 1.95 pg/mg) and urban coyotes ($n=34$; mean= 5.48 ± 1.18 pg/mg) (Fig. 4.3). The overall model had an adjusted R^2 value of 0.32 ($f= 12.36$, $df=8$, 189, $p < 0.001$).

The second best linear regression model was similar to our top model. It included status, site type, and age, but it lacked the condition variable. Instead of the condition rank variable, it included the percentage of hair loss coyotes experienced due to mange. Since our overall condition ranks took into account the hair loss due to mange, the condition variable and percentage of hair lost to mange variables support similar patterns. According the second best model, as the percentage of hair lost due to mange increased, hair cortisol concentrations increased ($t= 3.243$, $p= 0.0014$). The trends for the other variables were the same as the first model as well.

DISCUSSION

The environment in which a coyote lives may play a role in determining how much cortisol is produced by the individual. Unlike the trend that was predicted however, we found that suburban coyotes had higher concentrations of hair cortisol than forest preserve and urban coyotes. Urban coyotes had only slightly higher hair cortisol concentrations than forest preserve coyotes. Forest preserve individuals are legally protected and thus are not subjected to hunting or persecution pressures. Additionally, forest preserve individuals have blocks of vegetation that are large enough for them to avoid people almost entirely while also being able to find plenty of

natural food and water sources for persistence. It is presumed, therefore, that forest preserve individuals would experience few stressors and thus have relatively low overall hair cortisol concentrations. Urban coyotes had relatively low baseline levels of hair cortisol concentration too, however. Though urban coyotes live in areas with frequent disturbance and human activity, urban animals tend to avoid people temporally and spatially, when possible. Even though they live within city limits, many urban coyotes spend most of their time in areas of low human activity; such areas include railroad edges, riparian buffer areas, and abandoned lots. They avoid the most highly developed land use types (Gehrt et al. 2011). Urban predators also tend to shift their activity patterns to become more nocturnal, thus allowing them to avoid times of peak human activity (Tigas et al. 2002; George and Crooks 2006; Gehrt et al. 2011; Bateman and Fleming 2012). Avoiding people through changes to their spatial and temporal activity patterns may help urban coyotes to circumvent some of the additional stressors they would otherwise encounter in urban environments. The presence of an abundance of natural and anthropogenic foods would also potentially help to counteract some of the stresses associated with living in a highly developed area. In the suburbs of Chicago, there are still many disturbances and high levels of human activity. Many of the green spaces that suburban coyotes tend to find and perceive as ideal resting areas, however, are much more prone to being used by people. For example, many of the suburban coyotes use backyards, parks, and golf courses as parts of their territories. If suburban animals are frequently encountering people and/or having more negative interactions with people, it could explain their elevated levels of hair cortisol. Animals in the suburbs may also have varying levels of exposure to human activity prior to establishing a territory. Coyotes that were born in forest preserves and ultimately dispersed into suburban

neighborhoods may not initially have known how to successfully navigate the human-dominated landscape and cope with associated stressors.

Previous studies comparing urbanization and human disturbances to glucocorticoid production in animals have had mixed results. In some studies, animals in areas with higher levels of human activity were found to have higher levels of stress hormones (Mastromonaco 2014; Fourie et al. 2015). Possible reasons for increased stress in more highly developed areas are increased disturbances that may stress sensitive species, more people that need to be avoided, and, for species that conflict with people, an increased likelihood of negative human-wildlife interactions. A study on grizzly bears found the opposite pattern, however (Bourbonnais et al. 2013). For species that can benefit from novel resources (e.g., anthropogenic food) in city environments, individuals in areas near people may be less stressed over time due to the ease of access to adequate food, shelter, and water resources. Though cities may be associated with an increased likelihood of mortality due to human-related causes, such sources of mortality are usually near-instantaneous and would not result in significantly increased hair cortisol concentrations. If predators are as sensitive to human activities as was suggested in Schell et al. 2013, the lack of observed stress in some free-ranging urban predators could be an artifact of anthropogenic resources mitigating the influence of other stressors. Anecdotally, at least one potential case of anthropogenic resources mitigating stress was documented during this study. Coyote 743 was a highly urban, adult coyote that resided entirely within the walls of a cemetery on the north side of Chicago. He was frequently seen wandering amongst the headstones and the taller vegetation along the cemetery edges. While one would expect a coyote living entirely in a human-altered landscape to be exposed to many stressors and potentially struggle to find places to hunt, he had one of the lowest hair cortisol concentrations on the project (HCC= 1.65 pg/mg).

One factor that may have led to his unusually low hair cortisol level is the abundance of anthropogenic food provided to him. Cemetery visitors knew of coyote 743 and, despite our instructions not to feed the coyote, some people consistently did. One particular member of the public claimed that she fed the coyote on a regular basis and could even sometimes get the coyote to come out for food if she honked the horn of her vehicle, almost like ringing a dinner bell. Though no incidences of aggression or altercations with the coyote were reported, the intentional feedings may potentially have resulted in a coyote that is was more relaxed (i.e., less stressed) than one should naturally be in such an urban setting. Providing food subsidies can simultaneously reduce an animal's need to find food (thus reducing their energy expenditure) and create a positive association with human presence. Other studies that have examined the relationship between baseline stress and urbanization found that there was no difference in baseline stress across habitats with varying degrees of development (Partecke et al. 2006; Atwell et al. 2012). In those cases, though the baseline was similar for urban and non-urban individuals, the urban individuals tended to respond to and recover from stressors more quickly than their non-urban counterpart when placed in the same situation. This suggests that even though the baseline levels of cortisol were the same when an animal was not under the influence of a stressor, the urban individuals were better equipped to cope with human disturbance and other stressors.

The presence of constant disturbance, novel resources, diverse stimuli, and many people in urban areas may favor individuals with attenuated stress responses (i.e., "bolder" individuals) (Atwell et al. 2012). In areas with high levels of resources, lowered stress responses are also favored in terms of fitness (Blas et al. 2007). Boldness and stress response tendencies have previously been found to be linked, typically with increased boldness and exploratory behavior

being associated with lowered stress responses (Cockrem 2007; Atwell et al. 2012; Raynaud and Schradin 2014). Individual variations in boldness and stress responses have also been previously reported in captive coyotes (Sequin et al. 2003; Darrow and Shivik 2009; Schell et al. 2013; Young et al. 2015), so it is likely that free-ranging coyotes vary as well. Due to an increased need to be able to cope with environmental disturbance and human activity, urban coyotes that are bolder may have higher overall fitness levels than shyer individuals. This would result in urban coyote populations becoming bolder (and responding less to stressors) than forest preserve populations over time. If urban coyotes are “bolder”, it could explain why forest preserve and urban animals had similar hair cortisol levels, even though there is more disturbance (and thus presumably more stressors) in the city. Suburban areas may contain populations that are somewhere between the forest preserve and urban populations in terms of boldness. While suburban areas likely favor bolder individuals to a certain extent for reasons similar to the urban areas, some suburban animals may be immigrants from the surrounding forest preserves. Individuals that move from forest preserves and into suburban sites may not be as equipped to cope with human activity and thus could have shyer behavioral tendencies. Individuals within suburbs that are on the shyer end of the bold-shy spectrum, likely respond to human activity and other disturbances more strongly, thus increasing the suburban population’s average stress output.

We found no relationship between coyote sex and hair cortisol concentration. This is similar to findings from previous studies that showed chipmunks, Chinese water deer, and captive coyotes do not show sex differences in baseline hair, plasma, and fecal glucocorticoid concentrations, respectively (Hastings et al. 1992; Schell et al. 2013; Mastro Monaco et al. 2014). Since male and female coyotes tend to share a home range, work together to defend a territory,

and raise pups together, their similar lifestyles likely result in them experiencing similar stressors throughout the year. This finding directly contradicts other studies, however. In some studies of other species, females had higher baseline cortisol concentrations than males (*North American clouded leopards*, Wielebnowski et al. 2002; *urban bandicoots*, Dowle et al. 2013). Cases where females may be more stressed include situations where females must defend their young or themselves from aggressive males. Since coyotes are monogamous and cooperative when rearing young, this is unlikely the case for our study species. In contrast, other studies found that males had higher baseline glucocorticoid levels than females (*vervet monkeys*, Fourie et al. 2015; *captive coyote pups*, Schell et al. 2017). Males may have higher baseline cortisol levels if they are competing with others on a regular basis and/or putting themselves in stressful situations more frequently. The findings from Schell et al. 2017 may also differ because of the age difference between their coyotes and ours. While they were examining 5-week-old individuals, even our “pups” were at least 3 months old and most were > 6 months old.

Our results indicated that within the Chicagoland coyote populations, pups (i.e., individuals < 1 year of age) had higher cortisol concentrations than older individuals. The first year of a coyote’s life is full of changes and challenges that could trigger additional hypothalamic-pituitary-adrenal (HPA) axis activity. In addition to the first year being a period of rapid growth, the pups must learn how to obtain food, they experience their first winter, and they explore many areas within and outside of their natal territories. Many pups also disperse from their natal territory within the first year (especially if one of the alphas is lost during that time frame), thus they must seek out a new place to live and, in the meantime, potentially experience negative interactions with individuals from other packs. Due to their inexperience and smaller physical size, it is unlikely that a pup would be able to actively take over a new territory alone.

Instead, lone pups may have to live on their own for awhile before locating a permanent home. Our findings contradict other studies of other species that have found no change in baseline cortisol levels as animals age (Hastings et al. 1992; Bales et al. 2006; Wilcoxon et al. 2011). A study of Florida scrub jays, however, did find that the birds decreased their stress responses to specific triggers with age, even though the baseline levels were similar when no stressors were present (Wilcoxon et al. 2011). Reduced maximum glucocorticoid values have also been reported in other species as they aged, potentially due to either habituation to everyday stressors over time or a lowering of HPA axis responsiveness as individuals age (Brett et al. 1983; Jessop and Hamann 2005).

As predicted, animals in poor physical condition had higher hair cortisol concentrations than healthy individuals. Particularly in wildlife with chronic conditions (e.g., sarcoptic mange), persisting with the side effects and immune system responses to them likely trigger the HPA axis on a regular basis and thus result in the production of more cortisol. In fact, our second-best linear model supported the idea that as hair loss due to mange increases (thus indicating a more severe, long-term infestation), hair cortisol concentration increases. For example, coyote 1084 was initially captured with only ~5% hair loss due to mange and, at that time, had a hair cortisol concentration of 3.80 pg/mg. Coyote 1084 was found dead approximately 10 months later in poor condition and with ~80% hair loss due to her mange infestation. When the post-mortem hair sample was analyzed, it was discovered that her hair cortisol concentration had nearly tripled (concentration= 12.89 pg/mg) since her initial capture, despite no recorded changes in her social status, age, or home range. It is likely that chronic, severe mange lead to the increase in cortisol and ultimately to her demise. Even coyotes that live through their mange often show increases in their cortisol levels. Coyote 1090 went from ~30% hair loss to ~70% hair loss within a span of

~9 months and exhibited a hair cortisol concentration change from 6.73 pg/mg to 9.34 pg/mg, despite still surviving the infestation at the time. Chronic diseases, reduced body conditions, or other long-term stressors have previously been associated with higher baseline cortisol levels, heavier adrenal glands, and altered brain structures in animals (Hastings et al. 1992; Romero and Wikelski 2001; Davidson and McEwen 2012). Additionally, animals with poorer body conditions may be slower to respond to stressful events and slower to recover from such events, thus they may have higher cortisol levels over a longer period of time than healthy individuals (Heath and Dufty 1998).

The relationship between social status and dominance has been debated frequently in past literature. Several studies have found that dominant individuals within social groups tend to have higher levels of glucocorticoids than subordinates (*alpine marmots*, Arnold and Dittami 1997; *African wild dogs*, de Villiers et al. 1997; *Japanese macaques*, Barrett et al. 2002; *chimpanzees*, Muller and Wrangham 2004; *gray wolves*, Sands and Creel 2004; *Ethiopian wolves*, van Kesteren et al. 2012). Higher-ranked individuals may produce more cortisol because they must constantly maintain their territories and be prepared to defend their positions within their social groups. For species with less rigid social groups, however, that trend does not hold true. In some species, subordinates are more stressed than dominants (*sparrows*, Rohwer and Wingfield 1981; *olive baboons*, Sapolsky 1992; *mice and rats*, Creel 2001) and in other species, there is no difference between subordinates and dominants (*male dwarf mongooses*, Creel et al. 1992; *mountain gorillas*, Robbins and Czekala 1997; *tufted capuchins*, Lynch 2002). Like the findings for other canid species (de Villiers et al. 1997; Sands and Creel 2004; van Kesteren et al. 2012), we found that dominant coyotes had higher hair cortisol concentrations than subordinates. Additionally, we compared individuals living in packs (i.e., alphas and subordinates) to

individuals that were not part of a pack (i.e., transients) at the time of hair collection. As expected, transient individuals had higher hair cortisol concentrations than pack members. As a social species, the lack of positive interactions with other coyotes along with the lack of a stable territory likely led to increased stress in transient individuals. Additionally, the events that led animals to become transient in the first place (e.g., the death of a mate) may have contributed to the elevated cortisol levels we observed in transient individuals.

Anecdotally, one particular pack of coyotes clearly illustrated the effects that social status can have on hair cortisol concentration. A female (coyote 874) and male (coyote 876) coyote were captured in March 2015. Coyote 874 and 876 were both previously unbred subadults that were in the process of taking over a territory in the Poplar Creek Forest Preserve. Their hair cortisol concentrations were 2.52 pg/mg and 3.27 pg/mg, respectively. They went on to produce healthy litters in 2016 and 2017. One of their pups from 2016 was captured as a subordinate in March of 2017, with a relatively low hair cortisol concentration (HCC= 1.93 pg/mg). In August of 2017, however, coyote 876 was killed by a vehicle. Less than 24 hours after the death of coyote 876, coyote 874 was also found dead, presumably due to another vehicular incident. Hair was collected post-mortem from both alpha coyotes. Coyote 874 had a post-mortem, hair cortisol concentration that was over double what it had been prior to her becoming an alpha, breeding female (new HCC= 7.09 pg/mg). Similarly, coyote 876's HCC had increased since his initial capture (new HCC= 5.76 pg/mg). With both alphas dead, their son (coyote 1054) was left without a stable pack. Over the weeks following the deaths of both his parents, he began wandering outside of his natal territory and became a transient in the forest preserve. Approximately 6 months later, in February 2018, coyote 1054 was hit by a car. His post-mortem hair cortisol concentration was 4.64 pg/mg, which was much higher than it was prior to the loss

of his parents and the loss of a stable pack. The combination of losing former pack members he may have bonded with, having no stable territory, and likely being exposed to negative interactions with coyotes outside of his natal pack as he traveled alone likely contributed to coyote 1054's elevated cortisol levels. The story of this single pack is only one of many that could be told and related back to coyote hair cortisol concentration changes.

Our low intraassay CVs and high recovery values, support our methods for analyzing hair cortisol concentration. Our raw hair cortisol concentration values differed from than those reported for captive coyote pups (Schell et al. 2017) and domestic dogs (Bryan et al. 2013). The calculated hair cortisol concentration can be influenced by multiple factors, however, including the fineness of the homogenized hair and the time allowed for extraction (Yamanashi et al. 2016). Our differences in hair cortisol could potentially be explained by differences in methodology (e.g., we only minced our hair with scissors so it would not be as fine as hair that was ground in a bead beater) and/or equipment (e.g., we used a different ELISA kit). On the other hand, there may truly be differences between captive, young animals and free-ranging, older coyotes.

Biologically significant variations in cortisol levels could have implications for future coyote management. While low levels of stress are necessary for survival, chronic stressors can be detrimental to the health of individuals. Additionally, though higher cortisol levels do not always lead to higher levels of aggression (Sands and Creel 2004), stress can alter animal behavior. When animals become too stressed, they may take risks they would not otherwise be willing to take (e.g., approaching human dwellings for food if food stress becomes too great) and they may be more likely to contract diseases due to their compromised immune systems (Bradley and Altizer 2007; Zuberogoitia et al. 2010). If urbanization does cause additional stressors, it

could play a role in shaping coyote behaviors and ultimately changing the prevalence of certain personality types in future populations. If the stressors associated with city life are able to be mitigated through behavioral modifications (e.g., becoming more nocturnal), it is likely that populations will exhibit more of those behaviors over time. Similarly, if coyotes that exhibit bolder behaviors are also the ones that experience less stress in urban areas and are better able to cope with human activity, one would expect future urban coyote populations to be bolder than their non-urban counterparts. Stress-induced changes in behavior at the individual and population levels could result in increased human-coyote interactions and conflicts. Knowing factors that contribute to chronic stress in coyotes, therefore, will be important for predicting urban coyote behavior and avoiding future human-coyote conflicts.

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TABLES & FIGURES

Table 4.1. Akaike’s Information Criterion (AIC) table comparing the top ten linear regression models of the log-transformed, coyote hair cortisol concentration. Hair cortisol concentrations were obtained from coyote hair samples (n= 198) collected 2014-2018 in the Greater Chicago Metropolitan Area. Predictor variables in the models below include coyote social status (i.e., alpha, subordinate, or transient), site type (i.e., forest preserve, suburban, or urban), age class (i.e., pup, subadult, or adult), overall condition rank (i.e., poor, good, or excellent), percent hair loss due to mange, breeding status, season, and sex. *See Appendix C, Table C.1 for the remaining models*

Model	k	AIC	AIC_c	Δ AIC	Weighted AIC_c	Evidence Ratio
status + sitetype + age + condition	9	326.863	331.363	0.000	0.682	1
status + sitetype + age + percentmange	8	330.465	333.977	2.615	0.185	3.70
status + sitetype + age + condition + breeding	11	329.232	336.180	4.817	0.061	11.12
status + percentmange + sitetype + season + age	11	331.401	338.348	6.985	0.021	32.87
status + percentmange + sitetype + age + breeding	10	333.652	339.293	7.930	0.013	52.73
status + sitetype + sex + age + condition + breeding	12	331.126	339.559	8.196	0.011	60.21
status + sitetype + sex + condition	8	336.998	340.510	9.147	0.007	96.90
status + season + age + condition + breeding	12	332.463	340.895	9.532	0.006	117.46
status + percentmange + sitetype + sex + season + age	12	333.091	341.524	10.161	0.004	160.83
status + sitetype + age	7	339.132	341.798	10.435	0.004	184.49

Table 4.2. The predictor variables that were included in the top model of log(hair cortisol concentration (pg/mg)) for coyotes in the Greater Chicago Metropolitan Area. The top model was selected using Akaike’s Information Criterion Table (*see Table 4.1*). Hair cortisol concentrations were analyzed from hair samples collected 2014-2018 (n= 198). The estimates represent the coefficients of a linear model and the *s denote statistically significant parameters in the model (* < 0.05, ** < 0.01, *** < 0.001).

Parameters in the Top Model of log(Hair Cortisol Concentration)

Coefficient	Estimate	SE	t-value	p-value
Intercept	1.208	0.090	13.450	< 0.001 ***
Status subordinate	-0.381	0.140	-2.727	0.007 **
Status subordinate	0.424	0.127	3.331	0.001 **
Site Type suburban	0.223	0.093	2.399	0.017 *
Site Type urban	0.220	0.112	1.959	0.052
Age pup	0.396	0.142	2.792	0.006 **
Age subadult	0.035	0.129	0.273	0.785
Condition good	0.059	0.090	0.663	0.508
Condition poor	0.485	0.122	3.983	< 0.001 ***

Chicagoland Coyote Study Sites

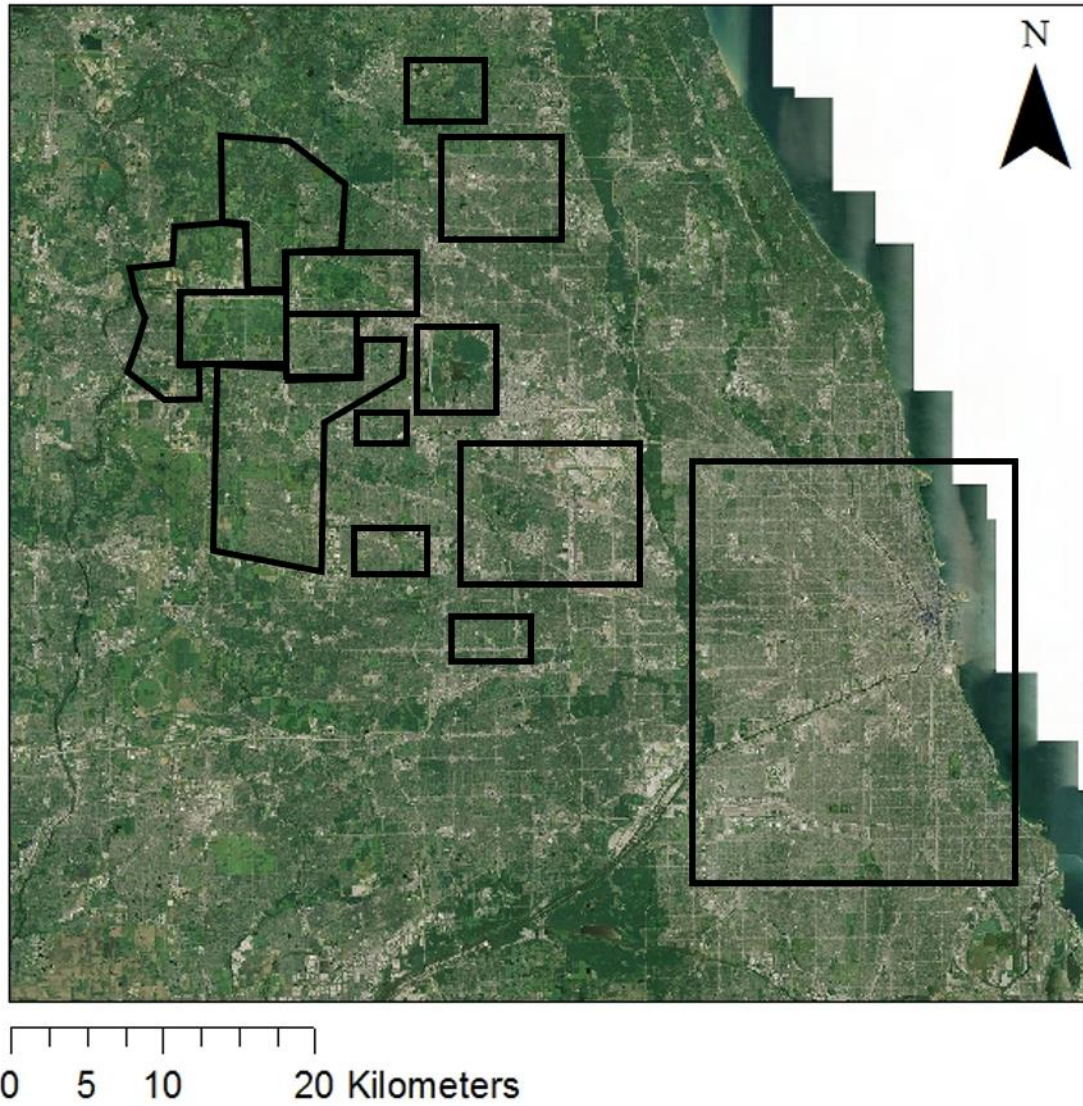


Figure 4.1. Study areas used to capture and monitor free-ranging coyotes ($n= 187$ coyotes) in the Chicagoland region from 2014 to 2018.

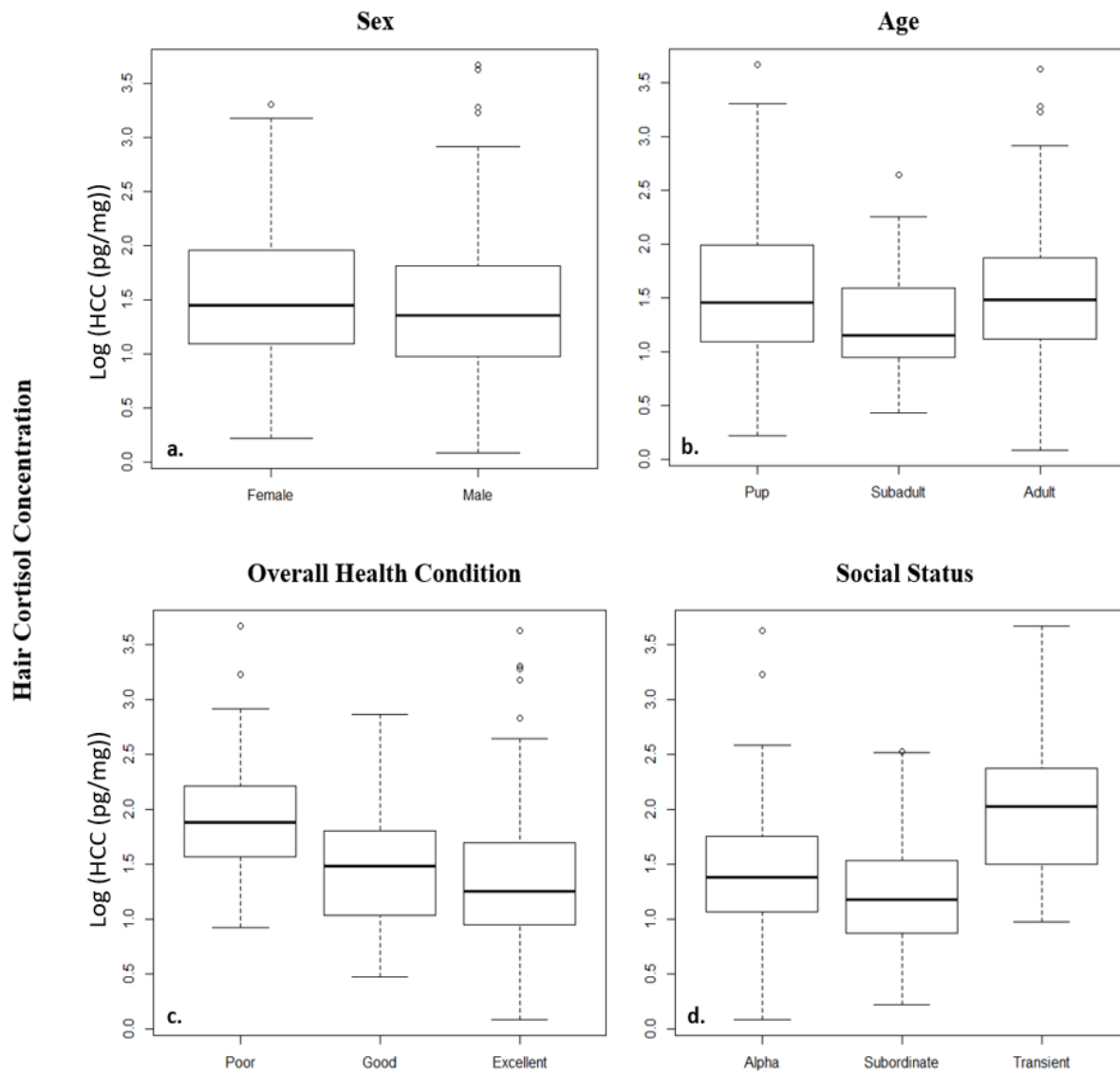


Figure 4.2. Log-transformed, hair cortisol concentration (pg/mg) distributions for coyotes when the coyotes are grouped by (a) sex (n= 77 females, 121 males), (b) age (n= 67 pups, 44 subadults, 87 adults), (c) health condition rank (n= 27 poor, 58 good, 113 excellent), and (d) social status (n= 82 alphas, 75 subordinates, 41 transients). All hair samples were collected from coyotes in the Greater Chicago Metropolitan Area, 2014-2018.

Hair Cortisol Concentration v. Urbanization Level

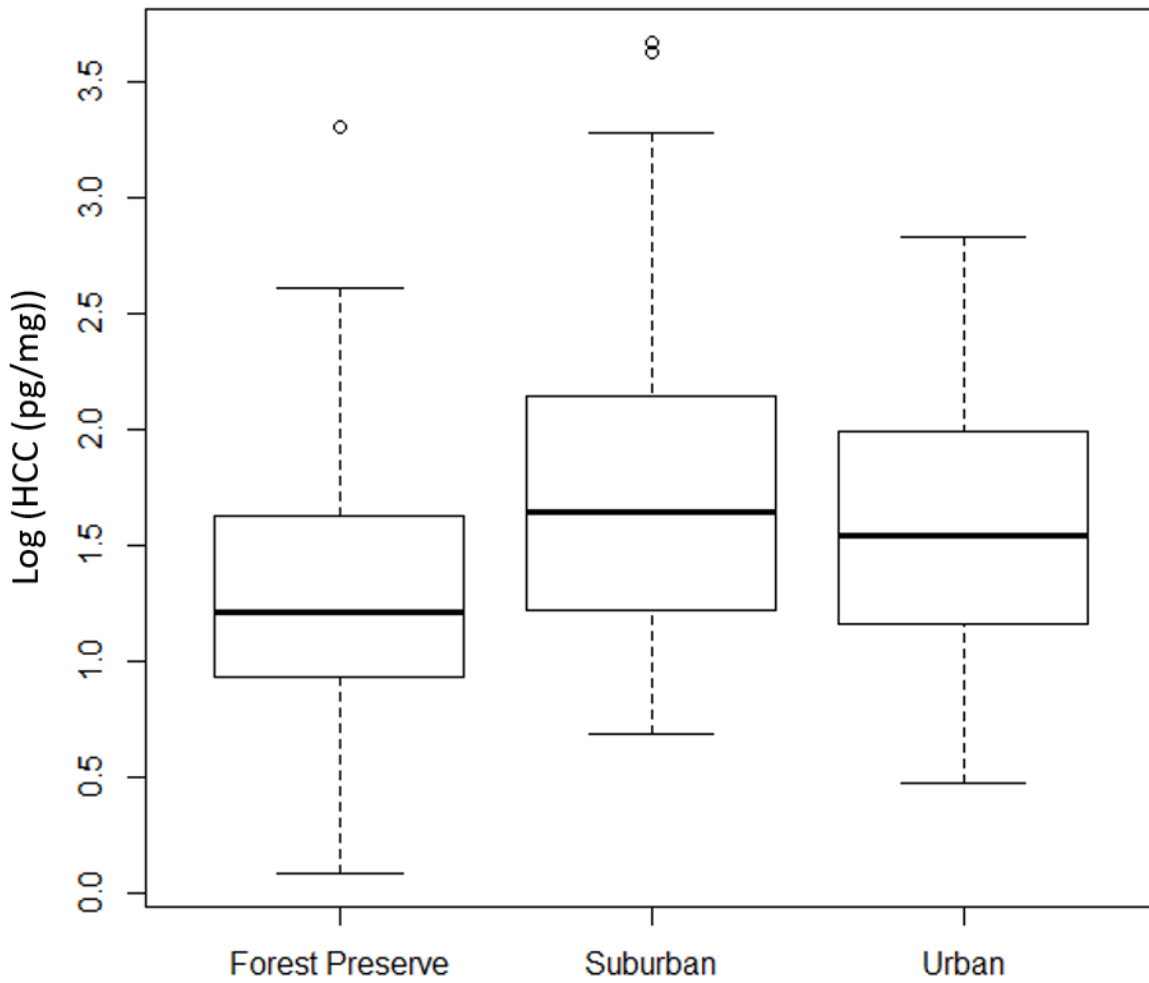


Figure 4.3. Log-transformed, coyote hair cortisol concentration distributions across the 3 site types (i.e., forest preserve (n=100), suburban (n=64), and urban (n=34) in the Chicagoland area. Coyote hair samples were collected 2014-2018 from free-ranging individuals.

Chapter 5

Could urbanization be generating bolder coyote populations?:

A case study from Chicago and its possible implications

Wildlife populations can contain individuals that exhibit different behavioral tendencies. Some studies have suggested that behavioral syndromes (i.e., suites of correlated behaviors in response to a common stimuli) are responsible for observed individual differences in behavioral patterns. The concept of behavioral syndromes implies that animals are predisposed to behave a particular way when exposed to various kinds of stimuli, rather than being completely behaviorally plastic. Having limited behavioral plasticity could be beneficial in situations where the “default” response is adaptive for the environment. The pre-determined responses may not be efficient or appropriate in all situations, however. Since some behavioral tendencies may be more beneficial than others in certain situations, environmental pressures may have the ability to indirectly select for individuals of a certain syndrome type (e.g., bold v. shy). In urban environments, high levels of disturbance, increased human activity, and large quantities of novel items may favor bolder, more exploratory, and less anxious individuals over shy individuals. If that is the case, one would expect to find a greater proportion of bold individuals in areas with increased development. Using the Chicago area as a case study location, free-ranging coyotes were subjected to two behavioral tests (flight initiation distance (FID) tests and novel object tests) to determine if coyotes in urban areas tended to be bolder and more exploratory than those in more natural settings. Chronic stress in the coyotes was measured via hair cortisol concentration analyses, as stress can also be correlated to behavioral syndromes. The results of the behavioral tests indicated that coyote boldness toward humans and novel objects was higher in more developed settings, supporting the prediction that bolder individuals may be better suited

to inhabiting urban areas. The hair cortisol concentrations of urban coyotes were similar to those found in more natural settings (i.e., forest preserves), however. Suburban coyotes had higher cortisol levels than the urban and forest preserve coyotes. Though strict conclusions cannot be drawn based on the available data, it is possible that the urban coyotes had adapted so well to human disturbances that, despite the increased number of human-related stressors in urban areas, they did not react as strongly to each individual stressor. Reacting less to each individual stressor, as is often the case in bolder individuals, but being exposed to more stressors may ultimately have led to the observed, limited difference between coyotes in urban and forest preserve settings. The findings from this study may have ecological and management implications, as they do imply that human activity and development may be generating bolder coyote populations over time. If coyotes are becoming bolder, their increased tolerance of human activities could lead to increased human-wildlife encounters and put more strain on wildlife management agencies. Additionally, controlling coyotes through non-lethal methods (e.g., hazing) may become more time-consuming and/or less effective. Further studies are needed to determine what mechanisms ultimately led to the observed increase in coyote boldness and examine whether increased coyotes boldness is a phenomenon found in other major metropolitan areas.

INTRODUCTION

Urban areas have expanded rapidly in recent decades. As more natural areas become developed and existing developed areas grow, increased human densities and anthropogenic disturbances often impact local wildlife populations (Beissinger and Osborne 1982; Randa and Yunger 2006; Markovchick-Nicholls et al. 2008; Birnie-Gauvin et al. 2016). While some species are unable to cope with human activity and are subsequently displaced from urban areas, other

species adapt to handle the challenges that come with city life (Prange et al. 2003; Gehrt et al. 2009; Rosatte et al. 2010; Bateman and Fleming 2012; Lowry et al. 2013). Even within species, some individuals can exhibit different behavioral tendencies and physiological responses that ultimately help them to succeed in proximity to humans. Previous studies have shown that behavioral syndromes (i.e., suites of correlated behaviors that occur in response to a common stimuli) exist in a variety of organisms and are often related to stress coping capabilities (Wilson et al. 1994; Sih et al. 2004; Wilson et al. 2010; Sih et al. 2012). Evidence from studies of captive coyotes has also suggested there is substantial individual variation in behavioral tendencies and hypothalamic-pituitary-adrenal (HPA) axis activity within the species (Harris and Knowlton 2001; Darrow and Shivik 2009; Schell et al. 2013; Young et al. 2015). If similar patterns of variation are found in free-ranging coyotes, it could help to explain how some individuals persist and thrive in highly developed landscapes. In this dissertation, behavioral tendencies and chronic stress in Chicagoland's coyotes were examined in the hopes of providing evidence for or against behavioral syndromes being present and important in free-ranging, urban wildlife.

BEHAVIORAL TESTING

To examine behavioral tendencies in coyotes, FID tests and novel object tests were conducted. All tests were conducted in the Greater Chicago Metropolitan Area (GCMA), along different parts of the urbanization gradient. Urban areas were defined as those in Chicago's city limits and suburban areas were locations outside of Chicago but still within the GCMA. Our most natural site type was the forest preserve designation. Forest preserves were county-protected greenspaces that were situated within the suburbs of Chicago. While they did allow for recreation and thus were not completely devoid of human activity, the relatively large blocks of

vegetation compared to the surrounding areas and the lack of hunting and trapping likely helped to buffer wildlife from some of the dangers associated with human presence.

Flight initiation distance testing. Flight initiation distance tests were conducted to measure coyote boldness toward approaching humans. Based on the results of the FID tests, a combination of testing-related variables and environmental factors influenced coyote FID. The velocity of the approacher had a negative influence on FID, possibly because a faster approach does not leave as much time for a coyote to make the decision to flee before the human gets closer. The distance an approacher started from the animal may have also influenced FID, though starting distance could not be differentiated from the coyote's approximate distance to the nearest road. Starting distance may play a role in FID since starting farther away provides coyotes more time to flee before the approaching human gets too close. Additionally, if a person starts farther away, animals may decide staying in one place is not worth the cost of monitoring an approaching human the whole time and will flee while farther away. Alternatively, distance to the nearest road is also a plausible factor. If coyotes are closer to roads, they may be less likely to detect an approaching human due to the already existing, increased level of human activity. Coyotes closer to roads may also already be bolder towards humans since, presumably, shyer individuals would rest farther from human activity (i.e., farther from roads) in the first place. Further studies are needed to tease apart whether starting distance or distance to the nearest road play a more important role. Lastly, the coyote's location along the urbanization gradient (i.e., urban, suburban, or forest preserve) played a major role in determining coyote FID. The more urban a site was, the lower the FID. Coyote FIDs were also found to be consistent over time when individuals were re-tested within the same general location and were exposed to similar testing conditions. The consistency of the tests over time provides evidence for behavioral

syndromes rather than habituation. If habituation was occurring, coyotes that were tested multiple times and had spent more time in proximity to people would have been expected to have shorter FIDs in subsequent tests.

Novel object testing. To examine coyote exploratory behavior and, more specifically, neophobia, novel object test sites were set up in the Chicago area. Similar numbers of coyotes visited during the pre-, object-, and post- testing phases of the trials and coyotes spent similar amounts of time on camera, regardless of whether the object was present. Coyote responses to the novel objects varied from neophobic (i.e., avoiding the objects) to neophilic (i.e., physically interacting with the objects), with developed (urban and suburban) areas tending to have greater proportions of neophilic coyotes than more natural (forest preserve) settings. Though there were not enough coyote visits to analyze suburban and urban coyotes separately, there was a slight trend of urban coyotes being more neophilic than suburban coyotes. The pattern of increasing neophilia as tests moved from forest preserve to suburban and then to urban sites, supported the hypothesis that neophilia would increase with human development. The responses of coyotes did not vary by object type (i.e., garden gnome or ring stacker toy), but did vary by the site's distance to the nearest road. Anecdotally, animals that were seen in multiple novel object tests did appear to be consistent in their level of neophobia/neophilia when experiencing a new object for the first time.

FID and neophobia comparison. The FID tests and the novel object tests produced similar findings. Coyotes tended to be bolder toward humans and more neophilic as urbanization level increased. Neither behavioral measure varied by sex, but both varied by the coyote's distance to the nearest road. Additionally, both were consistent across time and contexts. Only twelve coyotes were tested using both methods, so an accurate statistical analysis comparing the

two was not feasible. There was a slight trend, however, toward coyotes who were ranked lower (more neophobic) in the novel object tests having higher FIDs (Fig 5.1). A pattern of increasing FID with increasing neophobia was previously reported in a study of captive coyotes (Young et al. 2015). Both FID and novel object testing measure responses to some form of risk. In the case of FID testing, the risk is an approaching human. In novel object testing, the risk is a novel item that may or may not be harmful. The consistency in how willing coyotes are to expose themselves to risks over time and across contexts provides evidence for the possibility of innate, behavioral syndromes. If coyotes are born with predispositions to respond to stressors in a particular way, coyotes that immediately respond with fear and excessive caution would likely not fair as well in environments where novel stimuli are common but rarely dangerous. For example, in urban environments there is a high level of human activity, there are frequent habitat alterations, and there is an abundance of novel items (e.g., litter). Though human disturbance and novel items may cause a stress response in coyotes, humans and their associated objects are unlikely to detrimentally impact most urban coyotes. In fact, some items may actually prove to be useful novel food or denning resources (Fedriani et al. 2001; Prange et al. 2004; Otali and Gilchrist 2004; Newsome et al. 2015). It therefore may be to a coyote's benefit to behave in a more exploratory, risk-prone manner in an urban setting. Coyotes who are risk-averse would miss the opportunities to use novel resources and would find it more difficult to cope with human presence. The results of the FID and novel object tests support these predictions, as coyotes did tend to increase their boldness toward humans and novel objects as urbanization increased. It is possible, therefore, that human activity and disturbance associated with urbanization may play a role in shaping coyote behavioral tendencies.

CORTISOL ANALYSIS

Hair cortisol concentration. Behavioral patterns can sometimes be associated with differences in stress coping responses (Carere et al. 2010; Reale et al. 2010; Atwell et al. 2012; Baugh et al. 2012; Clary et al. 2014). Some individuals exhibit greater hypothalamic-pituitary-adrenal axis (HPA) activity following exposure to a stressor than others. Stress can be impacted by a variety of factors, however. To determine what factors influence chronic stress in free-ranging coyotes, the hair cortisol concentrations of individuals from throughout the Greater Chicago Metropolitan Area were analyzed. As expected, the physical health of the animals played a major role in their cortisol production. Animals that were in poor physical condition tended to have higher hair cortisol concentrations than healthy individuals. In particular, the presence of large quantities of hair loss due to mange appeared to correspond to high hair cortisol concentrations. The social statuses of the coyotes were also highly significant predictors of chronic stress (or lack thereof). Alphas were more stressed than subordinates, a pattern that has been previously reported in other wild canids (*African wild dogs*, de Villiers et al. 1997; *gray wolves*, Sands and Creel 2004; *Ethiopian wolves*, van Kesteren et al. 2012). Transient individuals (i.e., individuals living alone and without stable territories) were, by far, the most stressed. As a social species, consistent interactions with other individuals and stable access to resources are likely highly important for coyote wellbeing. Age was important, but to a lesser extent the other variables. Pups were more stressed than older individuals (i.e., adults and subadults). Lastly urbanization level was a significant predictor of coyote hair cortisol concentration. Contrary to the hypothesis that coyotes in urban areas would have reduced cortisol concentrations that corresponded with increased boldness behavior, urban coyotes and forest preserve coyotes had

similar cortisol levels. Suburban coyotes had higher cortisol levels than forest preserve or urban coyotes. Given the differences in the environments and the likely presence of different stressors at each site type, it was difficult to directly compare hair cortisol concentrations across coyotes from different site types.

Possible links between behavior and physiology. Though it was difficult to directly compare coyote hair cortisol to behavior across the urbanization gradient, it is possible there was a link between the two. Given the increased number of people, increased level of disturbance, and increased number of anthropogenic items found in urban landscapes, it is likely that urban settings contain more potential stressors than less developed settings. Seeing no difference in hair cortisol level between urban and forest preserve coyotes in the Chicagoland area is, therefore, biologically significant in its own way. The lack of observed difference between the two indicates that coyotes in urban Chicago have adapted to the urban environment and are able to cope well enough with the additional stressors associated with human settlements that they are no more stressed than a coyote in protected greenspaces. One possible explanation for the observed pattern is that, if the coyotes in downtown Chicago are relatively bold like the FID and novel object tests suggested, they may also exhibit attenuated responses to environmental stressors. Reduced HPA axis activity in response to single stressors but repeated exposures to more of those single stressors could result in the urban animals having similar cortisol levels as coyotes in natural areas. Suburban individuals had higher cortisol levels than coyotes in the urban or forest preserve locations. Many of the suburban individuals lived in areas with direct human contact, such as neighborhoods or golf courses. In some areas, suburban animals were exposed to just as much, if not more, human activity than urban animals. If the suburban animals were exposed to as many stressors as the urban animals, yet they are not as behaviorally adapted

to cope with anthropogenic stressors (as is evidenced by the results of the FID and novel object tests), they may ultimately respond more stressfully to human activity and, as a result, show higher hair cortisol concentrations. Further studies would need to be conducted to confirm the potential relationship between behavior and HPA activity. Based on a combination of the behavioral data and the hair cortisol analyses, however, it is highly plausible that behavioral syndromes do exist in at least some capacity in free-ranging coyotes.

ECOLOGICAL & MANAGEMENT IMPLICATIONS

The findings from the Chicagoland coyote study provide evidence that supports the possibility of behavioral syndromes being present in coyotes and variations in coyote behavior being present across the urbanization gradient. If bold and shy behavioral syndromes do exist and relate to stress coping capabilities, one would expect coyote populations in urban areas to become increasingly bold over time. Bold individuals may be more likely to disperse farther and colonize urban areas initially (Evans et al. 2010; Reale et al. 2010; Lowry et al. 2013). Additionally, once coyote populations are established in developed areas, bolder individuals will likely be more successful in terms of coping with stress, surviving, and reproducing. Increased reproductive fitness in bolder individuals in urban settings would lead in an increase in the proportion of individuals that fall on the bold side of the bold-shy spectrum.

If coyotes in urban areas are becoming bolder over time, it could have major management implications. First, if coyote populations are becoming bolder in developed areas, coyotes may become increasingly visible and live closer to humans than before. Anecdotally, there were some coyotes in the Chicagoland study that would rest in cemeteries during the day and simply watch people walking by. When FID tested, some of those individuals (e.g., coyote 743) were reluctant to move and, even once they did decide to move, they would slowly stand and walk away while

occasionally glancing at the approacher. They would then settle down in a new resting place relatively quickly and often within the same block where they were previously approached. Such coyotes showed little fear of humans or human-dominated landscapes. Other coyotes, including most of those found in more natural settings, immediately ran when they detected a human approacher and were never visible due to their use of cover. Increased coyote visibility in developed landscapes ultimately tends to lead to more nuisance complaints, since people sometimes fear coyotes and file reports when coyotes are sighted near people (Timm et al. 2004; Fox 2006; Poessel et al. 2013). Additionally, more coyotes living in closer proximity to human activity could lead to more incidences of vehicular collisions with coyotes and higher numbers of coyotes needing to be removed from airport properties, as coyotes present a significant strike hazard (DeVault et al. 2008; Biondi et al. 2014; Poessel et al. 2016).

Cases of coyote complaints that normally would benefit from simple, hazing techniques may also require more effort if coyotes become bolder. Non-lethal hazing is often one of the first techniques used to push coyotes out of areas where they are considered nuisances (Fox 2006; Schmidt and Timm 2007; Bonnell and Breck 2017). If coyotes in urban areas become bolder, however, the coyotes may be less likely to respond fearfully or exhibit strong stress responses when humans initially approach. It may take a greater intensity of hazing or more repetitions of the hazing process to successfully encourage bold individuals to change locations permanently. Additionally, if a bold individual has learned to exploit novel resources associated with a particular area (e.g., if it has eaten human foods from a local trash can), it may make it even more difficult or even impossible to handle the nuisance animal with non-lethal measures (Timm et al. 2004). In short, increasingly bold coyote populations in developed areas could lead to an increase in human-wildlife conflicts and an increased strain on wildlife managers and control

agencies. It is important to note, however, that boldness may not always correlate with aggression (Bell and Sih 2007; Evans et al. 2010; Scales et al. 2011; Young et al. 2015). Increased nuisance complaints likely come from increased sightings, not aggressive encounters. To date, despite the presence of relatively bold individuals in the Chicago region, no known coyote attacks have occurred on people in the Greater Chicago Metropolitan Area.

CONCLUSIONS

This study conducted on coyotes in the Greater Chicago Metropolitan area provides evidence that supports the possibility of behavioral syndromes existing in free-ranging coyotes. Additionally, it provides support for the idea that coyote behavior is being shaped by indirectly through anthropogenic disturbance and human presence. If urbanization does lead to shyer individuals being selected against and coyote populations in developed areas do become bolder, it will potentially impact the frequency of human-coyote encounters and potentially have wildlife management implications. Future studies need to be conducted in other locations to see if the patterns observed in the Chicagoland area are consistent in other developed landscapes. Similarly, more research is needed to determine the possible mechanisms behind coyote behavioral changes in developed areas (i.e., Is it genetic-based selection or is it simply habituation?). Though there is still more to learn about the relationship between coyote boldness behavior and physiology, the results of this study provide more evidence to support a possible link between the two and urban environments.

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TABLES AND FIGURES

Novel Object Rank v. FID

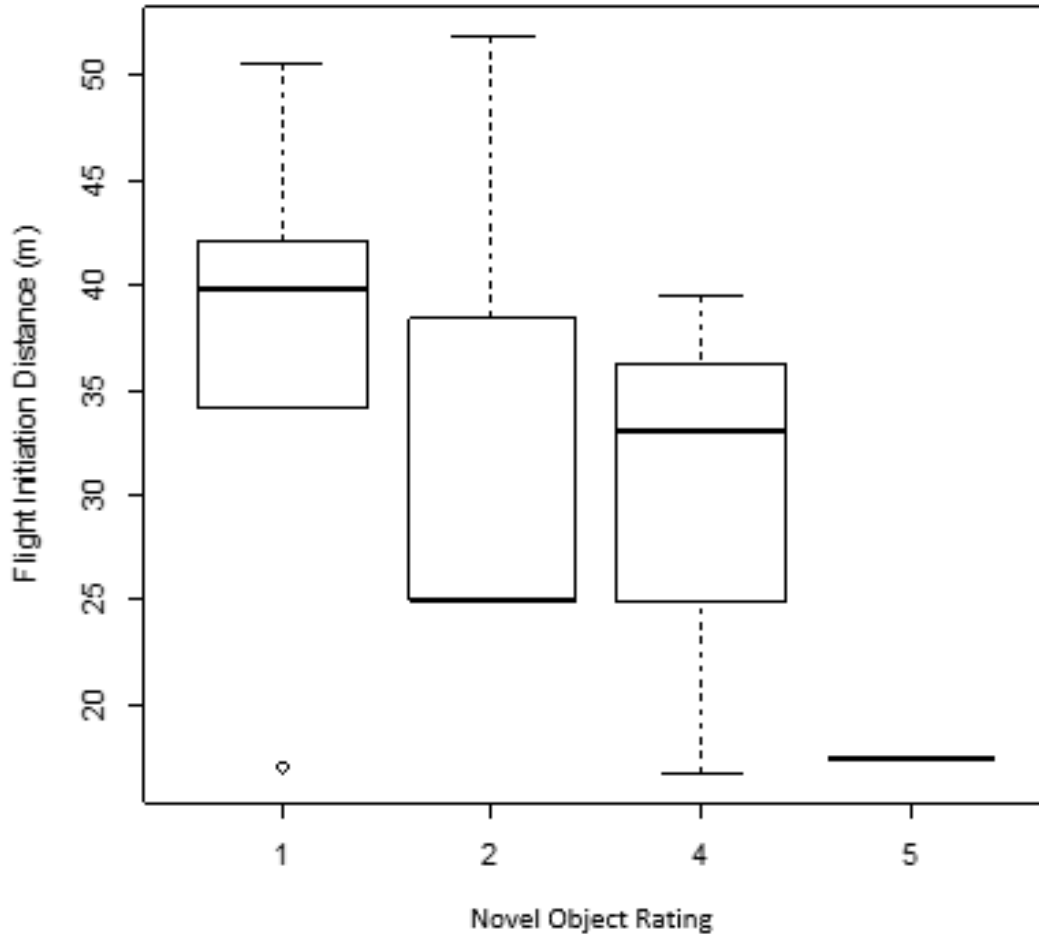


Figure 5.1. Coyote flight initiation distance values sorted by the behavioral categories the coyotes were given during novel object testing (n=12). Category 1 (n=5) corresponds to coyotes that were detected by an Advanced Telemetry Systems datalogger but were not seen on camera, indicating that the coyotes either were neophobic or oblivious to the object (i.e., garden gnome or ring stacker toy). Category 2 (n=3) includes neophobic coyotes that appeared on camera. Category 4 (n=3) is composed of coyotes who were indifferent towards the object. Category 5 is composed of coyotes who approached the object to investigate it (n=1). All behavioral testing was conducted 2015-2018 in the Greater Chicago Metropolitan Area.

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APPENDIX A: Supplementary Material for Chapter 2

Table A.1. AIC table of 54 linear models comparing the log transformed flight initiation distance of all coyotes (n= 60) to various biological and environmental factors. Factors included the coyote's sex, age, breeding status, site type (i.e., forest preserve, suburban, urban), velocity of the approacher, temperature, weather, dominant substrate, habitat type, % canopy cover, log-transformed % visibility (tvisibility), log-transformed distance to the nearest road (troaddist), and the log-transformed initial distance from the coyote's resting point (tstartdist). For each model, k is the number of parameters, AIC is the Akaike Information Criterion value, AIC_c is the AIC value corrected for sample size, ΔAIC is the difference between the model and the top model's AIC values, W. AIC_c is a weighted AIC_c, and Evid. Ratio is the evidence ratio.

Model	k	AIC	AIC_c	Δ AIC	W. AIC_c	Evid. Ratio
troaddist + sitetype + velocity	5	110.147	111.510	0.000	0.383	1.00
tstartdist + sitetype + velocity	5	111.305	112.669	1.159	0.215	1.79
troaddist + sitetype	4	114.163	115.052	3.542	0.065	5.88
tstartdist + sitetype	4	114.511	115.400	3.890	0.055	7.00
troaddist + sitetype + sex	5	114.794	116.157	4.647	0.037	10.21
sitetype + tstartdist + breeding + sex + velocity	8	112.783	116.295	4.785	0.035	10.94
sitetype + troaddist + breeding + sex + velocity	8	112.814	116.326	4.816	0.034	11.11
troaddist + sitetype + tvisibility	5	115.786	117.149	5.639	0.023	16.77
troaddist + sitetype + temperature	5	116.045	117.408	5.898	0.020	19.09
sitetype + sex + velocity	5	116.072	117.436	5.925	0.020	19.35
tstartdist + sitetype + tvisibility	5	116.135	117.498	5.988	0.019	19.97
sitetype + velocity	4	117.592	118.481	6.970	0.012	32.63
sitetype	3	118.043	118.565	7.054	0.011	34.03
tstartdist + sitetype + substrate	9	114.213	118.713	7.203	0.010	36.65
troaddist + sitetype + breeding	6	117.054	119.008	7.498	0.009	42.47
sitetype + temperature + sex + velocity	6	117.290	119.244	7.734	0.008	47.79
sitetype + age + sex + velocity	7	116.676	119.342	7.832	0.008	50.21
tstartdist + sitetype + sex + breeding	7	116.941	119.608	8.097	0.007	57.32
tstartdist + age + sex + sitetype	7	116.946	119.612	8.102	0.007	57.46
tstartdist + sitetype + tvisibility + temperature	6	118.123	120.077	8.566	0.005	72.47
troaddist + sitetype + sex + breeding	7	117.469	120.136	8.625	0.005	74.64
tstartdist + sitetype + weather	8	117.395	120.907	9.397	0.003	109.80
tstartdist + sitetype + tvisibility + substrate	10	115.934	121.575	10.065	0.002	153.30
sex + breeding + sitetype	6	119.962	121.916	10.406	0.002	181.79
troaddist + sex + velocity	4	121.388	122.277	10.766	0.002	217.72
tstartdist + sitetype + sex + breeding + tvisibility	8	118.849	122.362	10.851	0.002	227.17

Model (continued)	k	AIC	AIC_c	Δ AIC	W. AIC_c	Evid. Ratio
troaddist + sitetype + sex + breeding + substrate	12	117.882	126.314	14.804	0.000	1639.18
tstartdist + sitetype + weather + substrate	13	116.831	126.942	15.432	0.000	2244.05
tvisibility + weather + sitetype + substrate	13	119.838	129.949	18.439	0.000	1.01 x 10 ⁴
tstartdist + sitetype + tvisibility + weather + substrate	14	118.580	130.580	19.070	0.000	1.38 x 10 ⁴
temperature + troaddist + sitetype + sex + substrate + weather + breeding + age	19	105.719	131.053	19.543	0.000	1.75 x 10 ⁴
temperature + weather + sitetype + substrate + canopy	14	119.581	131.581	20.071	0.000	2.28 x 10 ⁴
troaddist + sex + breeding	5	131.121	132.485	20.975	0.000	3.59 x 10 ⁴
tstartdist + sex	3	134.265	134.786	23.276	0.000	1.13 x 10 ⁵
temperature + troaddist + sitetype + sex + substrate + weather + breeding + canopy	18	112.885	134.950	23.440	0.000	1.23 x 10 ⁵
tstartdist	2	134.952	135.207	23.697	0.000	1.40 x 10 ⁵
temperature + tstartdist + sitetype + sex + substrate + weather + breeding + age	19	111.168	136.501	24.991	0.000	2.67 x 10 ⁵
tvisibility + temperature + troaddist + sitetype + sex + substrate + weather + breeding + sex + age	20	107.580	136.545	25.035	0.000	2.73 x 10 ⁵
tstartdist + age + sex	5	136.248	137.612	26.102	0.000	4.66 x 10 ⁵
tstartdist + temperature + weather	7	139.834	142.501	30.991	0.000	5.36 x 10 ⁶
sex	2	142.743	142.998	31.488	0.000	6.88 x 10 ⁶
velocity	2	143.219	143.474	31.964	0.000	8.73 x 10 ⁶
tstartdist + temperature + season + age	8	139.966	143.478	31.968	0.000	8.74 x 10 ⁶
1	1	143.68	143.764	32.254	0.000	1.01 x 10 ⁷
season	4	144.215	145.104	33.593	0.000	1.97 x 10 ⁷
tstartdist + canopy + substrate	8	143.185	146.697	35.187	0.000	4.37 x 10 ⁷
tvisibility + canopy	3	146.961	147.483	35.973	0.000	6.47 x 10 ⁷
substrate	6	149.295	151.249	39.739	0.000	4.26 x 10 ⁸
tvisibility + temperature + tstartdist + sitetype + weather + mange + breeding + sex + age + season + canopy	20	123.841	152.807	41.297	0.000	9.28 x 10 ⁸
habitat	9	150.583	155.083	43.572	0.000	2.89 x 10 ⁹

Model (continued)	k	AIC	AIC_c	Δ AIC	W. AIC_c	Evid. Ratio
tvisibility + temperature + troaddist + sitetype + sex + habitat + substrate + breeding + sex + age	24	125.159	173.159	61.649	0.000	2.44 x 10 ¹³
tvisibility + sitetype + sex + habitat + substrate + mange + breeding + sex + age + season + canopy	27	127.258	195.985	84.475	0.000	2.21 x 10 ¹⁸
tvisibility + temperature + troaddist + sitetype + habitat + weather + mange + breeding + sex + age + season + canopy	28	126.318	203.651	92.141	0.000	1.02 x 10 ²⁰
tvisibility + temperature + troaddist + sitetype + habitat + substrate + weather + mange + sex + age + season	30	106.365	204.260	92.750	0.000	1.38 x 10 ²⁰
tvisibility + temperature + tstartdist + habitat + substrate + weather + mange + breeding + canopy	25	150.632	204.799	93.289	0.000	1.81 x 10 ²⁰
tvisibility + temperature + troaddist + sitetype + sex + habitat + substrate + weather + mange + breeding + sex + age + canopy	30	111.896	209.790	98.280	0.000	2.19 x 10 ²¹
tvisibility + temperature + troaddist + sitetype + habitat + substrate + mange + breeding + sex + age + season + canopy	29	126.642	213.642	102.132	0.000	1.51 x 10 ²²
tvisibility + temperature + troaddist + sitetype + sex + habitat + substrate + weather + mange + age + season + canopy	31	108.238	218.460	106.950	0.000	1.67 x 10 ²³
tvisibility + temperature + troaddist + sitetype + sex + habitat + substrate + weather + mange + breeding + sex + season + canopy	31	110.786	221.008	109.498	0.000	5.99 x 10 ²³
tvisibility + temperature + troaddist + sitetype + sex + habitat + substrate + weather + mange + breeding + sex + age + season	32	99.696	223.932	112.421	0.000	2.58 x 10 ²⁴
tvisibility + temperature + sitetype + habitat + substrate + weather + mange + breeding + sex + age + season + canopy	32	105.789	230.025	118.515	0.000	5.43 x 10 ²⁵
tvisibility + temperature + troaddist + sitetype + habitat + substrate + weather + breeding + sex + age + season + canopy	32	110.868	235.103	123.593	0.000	6.88 x 10 ²⁶

Model (continued)	k	AIC	AIC_c	Δ AIC	Weighted AIC_c	Evidence Ratio
tvisibility + troaddist + sitetype + sex + habitat + substrate + weather + mangle + breeding + sex + age + season + canopy	32	112.174	236.409	124.899	0.000	1.32 x 10 ²⁷
tvisibility + temperature + troaddist + sitetype + sex + habitat + substrate + weather + mangle + breeding + sex + age + season + canopy	33	101.042	241.292	129.782	0.000	1.52 x 10 ²⁸
tvisibility + temperature + troaddist + sitetype + sex + habitat + substrate + weather + mangle + breeding + sex + age + season + canopy + velocity	34	83.625	242.292	130.782	0.000	2.51 x 10 ²⁸
tvisibility + temperature + tstartdist + sitetype + habitat + substrate + weather + mangle + breeding + sex + age + season + canopy	33	107.186	247.436	135.926	0.000	3.28 x 10 ²⁹

APPENDIX B: Supplementary Material for Chapter 3

Table B.1 Quantities of photo and video detections, by species/taxa (June 2015 – June 2017) during the novel object tests (n=50) conducted in the Greater Chicago Metropolitan Area, 2015-2017.

Species/Taxa	# of Still Image Detections	# of Video Detections
Coyotes	767	75
Foxes	11	1
Raccoons	2138	329
Opossums	402	102
Skunks	213	45
Weasels	4	4
Mink	3	
Feral Cats	141	22
Feral Dogs	38	2
Deer	9561	432
Rabbits	1196	255
Chipmunks	100	65
Flying Squirrels	12	6
Other Squirrel spp.	2263	614
Other Rodent spp.	24	161
Birds	215	883
Bats	0	1
Frogs/Toads	6	5
Unknown	1	1
Total	17,095	3,003

Protocol B.1. Designing and Testing a New Datalogging Method

Prior to the beginning of the novel object testing trials, a method was designed for using an Advanced Telemetry Systems (ATS) R4500 datalogger/receiver to detect coyote presence within ~20 m of the datalogger unit (Advanced Telemetry Systems, Isanti, MN, USA).

Typically, dataloggers are used to determine animal presence in general and within a relatively large area. Rather than using a traditional very high frequency (VHF) antenna, an ultra high frequency (UHF) antenna that was sold as part of Lotek's UHF HCU (Handheld Command Unit) as a way to remotely download UHF GPS collars was used (Lotek, Newmarket, Ontario, Canada). The UHF antenna was attached to the datalogger with a coaxial adapter (BNC female to N male right angle) (Fig. B.1). An external battery was also attached to the datalogger to prolong its battery life in the field.

Once the antenna was attached, the datalogger was manually tested by holding coyote-sized VHF collars at various distances (i.e., 0, 10, 20, 30, 40, 50, 60, 75, and 110 m away from the datalogger) for approximately 2 minutes per distance. Testing was conducted in a mowed field so no signal interference should have occurred. The collars used to test the datalogger's receiving capabilities under the setup included a new VHF collar, a VHF collar that had been deployed only for ~6 months but had been chewed (i.e., the end of the collar's antenna was frayed), and an old collar that had been previously deployed for 2+ years. The datalogger output for each collar was checked and the signal strengths were recorded and averaged for each distance (Fig. B.2).

Based on the signal strength output from the test collars under controlled settings, it was determined that the UHF antenna setup only detected signals from collars within 75 m of the datalogger; there were no signals recorded at 110 m. Additionally, any signal strengths of 90 or

above were highly likely to be within 20 m of the datalogger. While the signal strength cannot be used to pinpoint a coyote's exact distance from the datalogger, it can provide a conservative estimate of the number of collared coyotes that walk within the immediate vicinity of the study site where the datalogger is placed. The signal strengths can also be used to identify collared coyotes that appear on cameras near the datalogger.



Figure B.1. ATS datalogger setup with a Lotek UHF antenna, being used for detecting VHF-collared coyotes during novel object testing.

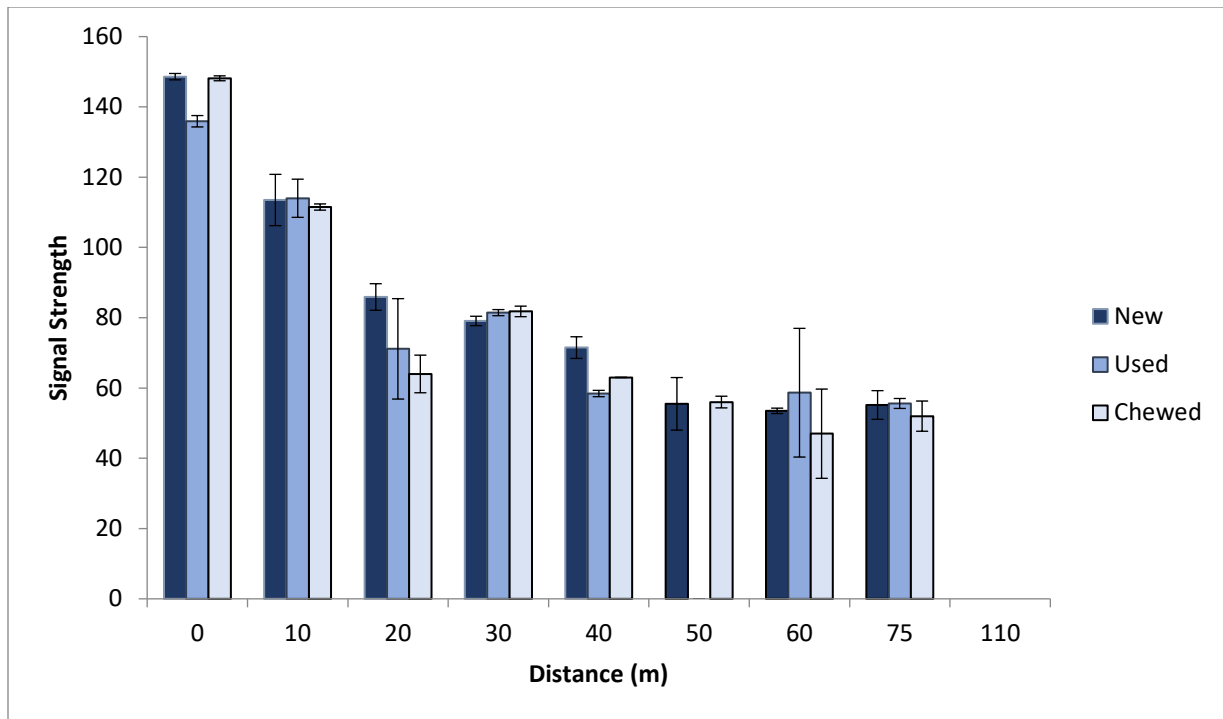


Figure B.2. Mean signal strengths (\pm margin of error for 95% CI) collected by an Advanced Telemetry Systems datalogger when testing new, used, and chewed Very High Frequency (VHF) collars at different distances from the receiver (June 2016 in Dundee, IL). An Ultra High Frequency (UHF) antenna attached to the datalogger/receiver was used to dampen the signal strength. Signal strength testing was conducted prior to deploying the dataloggers for novel object testing, so we could identify animals seen on camera and determine if other animals potentially were in the area, but off-camera.

APPENDIX C: Supplementary Material for Chapter 4

Table C.1. Akaike’s Information Criterion (AIC) table comparing 20 linear regression models of the log-transformed hair cortisol concentration. Hair cortisol concentrations were obtained from coyote hair samples (n= 198) collected 2014-2018 in the Greater Chicago Metropolitan Area. Variables in the models below include coyote social status (i.e., alpha, subordinate, or transient), site type (i.e., forest preserve, suburban, or urban), age class (i.e., pup, subadult, or adult), overall condition rank (i.e., poor, good, or excellent), percent hair loss due to mange, breeding status, season, and sex. For each model, k is the number of parameters, AIC is the Akaike Information Criterion value, AIC_c is the AIC value corrected for sample size, ΔAIC is the difference between the model and the top model’s AIC values, W. AIC_c is a weighted AIC_c, and Evid. Ratio is the evidence ratio.

Model	k	AIC	AIC_c	Δ AIC	W. AIC_c	Evid. Ratio
status + sitetype + age + condition	9	326.863	331.363	0.000	0.682	1
status + sitetype + age + percentmange	8	330.465	333.977	2.615	0.185	3.70
status + sitetype + age + condition + breeding	11	329.232	336.180	4.817	0.061	11.12
status + percentmange + sitetype + season + age	11	331.401	338.348	6.985	0.021	32.87
status + percentmange + sitetype + age + breeding	10	333.652	339.293	7.930	0.013	52.73
status + sitetype + sex + age + condition + breeding	12	331.126	339.559	8.196	0.011	60.21
status + sitetype + sex + condition	8	336.998	340.510	9.147	0.007	96.89
status + season + age + condition + breeding	12	332.463	340.895	9.532	0.006	117.46
status + percentmange + sitetype + sex + season + age	12	333.091	341.524	10.161	0.004	160.83
status + sitetype + age	7	339.132	341.798	10.435	0.004	184.49
status + sitetype + season + age + condition + breeding	14	331.292	343.292	11.929	0.002	389.33
status + percentmange	4	344.013	344.901	13.539	0.001	870.66
status + sitetype + sex + season + age + condition + breeding	15	333.177	347.294	15.931	< 0.001	2880.37
status + percentmange + sitetype + sex + season + age + breeding	14	336.032	348.032	16.669	< 0.001	4165.54
status + percentmange + sitetype + sex + season + age + condition + breeding	16	334.021	350.506	19.143	< 0.001	1.44 x 10 ⁴
status + percentmange + sitetype + sex + season + breeding	12	345.074	353.506	22.143	< 0.001	6.43 x 10 ⁴
status + sitetype + sex + season + age + breeding	13	345.100	355.212	23.849	< 0.001	1.51 x 10 ⁵
sitetype + age	5	377.018	378.382	47.019	< 0.001	1.62 x 10 ¹⁰
percentmange + sitetype + sex + season + age + breeding	12	379.913	388.345	56.983	< 0.001	2.36 x 10 ¹²
1	1	394.173	394.256	62.893	< 0.001	4.54 x 10 ¹³