Assessing Coyote (*Canis latrans*) Boldness in Urban and Rural Environments of New York State



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ABSTRACT

Coyotes (*Canis latrans*) evolved on the plains of the Pleistocene as medium-sized mesopredators. In the past century, anthropogenic landscape changes (such as agricultural production and urbanization) have drastically altered environments in the eastern United States, and once dense deciduous forests now appear more similar to the grasslands and deserts of the Pleistocene. Also, humans' eradication of wolves and other apex predators produced open niches for the coyotes' rapid population growth and territorial expansion. Coyote territories now extend from the West Rockies to the East Coast and include urban spaces such as Chicago and New York City. News reports emphasize many cases of boldness and aggression in urban coyotes, and the temperament of coyotes appears to vary as determined by geographic location and proximity to humans. By analyzing behavioral and spatial responses of coyotes in New York City and the Hudson Highlands, I aim to help quantify how coyotes vary in boldness across urban and rural territories. For this analysis, I deployed 20 camera traps at rural sites in the Hudson Highlands with controls (n=10) and treatments, or novel objects surrounding attractants, (n=10) from July to October 2019. My data was augmented by data from 18 camera traps with controls (n=9) and treatments (n=9) deployed by the Gotham Coyote Project (2020). Approaching coyotes were recorded by motion-activated cameras at each site; after reviewing the footage, I coded coyote responses into spatial and behavioral data. I found that region (urban vs. rural) did not have a statistically significant effect on the duration of time coyotes spent in front of the camera. However, coyotes at sites treated with novel objects spent significantly more time in front of the camera than coyotes at baseline sites without the novel object treatment. Studying spatial responses and behavioral patterns of coyotes will contribute insight to our understanding of a species that has historically been persecuted through both federally sanctioned bounty programs and negative press in the United States. This study will help us to better understand if coyotes adapt and change their behaviors to suit the ecological niches available to them in territories densely populated by humans. Hopefully, through this study and others like it, a more nuanced understanding of the bold and trepid behaviors of coyotes will pervade America's cultural narrative of the coyote. This insight could guide the policies surrounding coyote-human interactions and inform how humans and coyotes can best coexist peacefully in both long-standing western territories and recently populated eastern territories.

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INTRODUCTION

The Effects of Urbanization on Biodiversity

Anthropogenic changes impact local climatic conditions, alter water balances, and increase the dispersal rates of environmental pollutants. Landscape fragmentation is one type of anthropogenic change that describes the separation of an environment by the construction of roads, the creation of dams, the expansion of agricultural areas, the expansion of urban spaces, and other alterations. Fragmentation can have devastating effects on the diversity of native wildlife species and on the ecology of affected regions (Jaeger, 2000). Urbanization is an especially complex type of landscape fragmentation that leads to a loss in native species by dividing and diminishing available plant and animal habitat through the increasing development of impervious surfaces such as roads and buildings. Increasing urbanization also leads to landscaping and residential yard upkeep, which both involve the removal of unwanted native plants and the introduction of nonnative species. This artificial selection increases urban habitat heterogeneity and leads to a loss of biodiversity as native animal populations respond to the lack of vegetative complexity (McKinney, 2008).

Still, the extent to which urbanization impacts native species of flora and fauna varies greatly. In some cases, specifically regarding plants, urbanization increases biodiversity as nonnative species move in to occupy available ecological niches more quickly than native species disperse (McKinney 2002, 2006a). One example of the increasing establishment of nonnative plant species in urban areas occurred in Adelaide, Australia from 1836 to 2002. In Adelaide, plant species richness increased by 46% over the course of six years, as the rate of the introduction of plant species exceeded the rate of species extinction (Tait et al., 2005).

The positive correlation of urbanization and biodiversity is not often observable in animal species, as increased landscape fragmentation divides animal territories and many animal species are not able to rapidly adapt to changing food sources. A comprehensive accumulation of research collected by McKinney (at different spatial scales) from 185 nations (including island nations), 50 US states, and 23 protected areas demonstrated that nonnative animal species are less likely to inhabit urban environments as rapidly and extensively as nonnative plants. The results of McKinney's study found that the percentage of nonnative plant species constituted a higher proportion of total species overall than amphibians, reptiles, birds, and mammals (McKinney, 2006b).

Resilient Species

Some species actually thrive with increasing urbanization. For example, the raccoon and the Eurasian badger have higher population densities in urban environments than they do in natural territories (Bateman and Fleming, 2012). Even wild carnivores have historically derived some benefits from association with human settlements, and we can observe the impacts of this close contact today. Grey wolves, for example, first began associating closely with humans around 100,000 years ago, and the domestic dog is the product of this close association (Bateman and Fleming, 2012). Wild cats likely began to feed on rodents lingering around human settlements approximately 9500 years ago, and the domestic cat bears this history of association (Bateman and Fleming, 2012). Striped hyaenas are another persisting carnivorous species that has been found to benefit from urbanization. A study in Israel found that striped hyaenas with access to anthropogenic food sources (such as livestock carcasses and garbage waste) exhibited accelerated growth and an increased residual body size (Yom-Tov, 2003). Black bears are also a carnivorous species that feeds on anthropogenic sources near urban areas, and a recent study in

Nevada found that urban black bears have tripled in population numbers from the recorded historical baseline (Beckmann and Lackey, 2008). As settlements have become increasingly more developed, and urban sprawl dominates more natural landscapes than ever before, intrepid animal species continue to learn to adapt to rapid anthropogenic changes.

For species who are opportunistic feeders and make beneficial use of artificial shelters, urbanization provides viable new territories for expansion. Coyotes, or *Canis latrans*, are one such species. Coyotes appear not to be negatively affected by the ecological impacts of increased landscape fragmentation in North America, and the coyote's adaptability is demonstrated both by the species' expanding territorial ranges mapped in Figure 1 (Hody and Kays, 2018), and by the coyote's recent colonization of urban areas such as New York City. The human population size of the United States continues to increase rapidly (Passel and Cohn, 2008), as does the territory of the coyote.

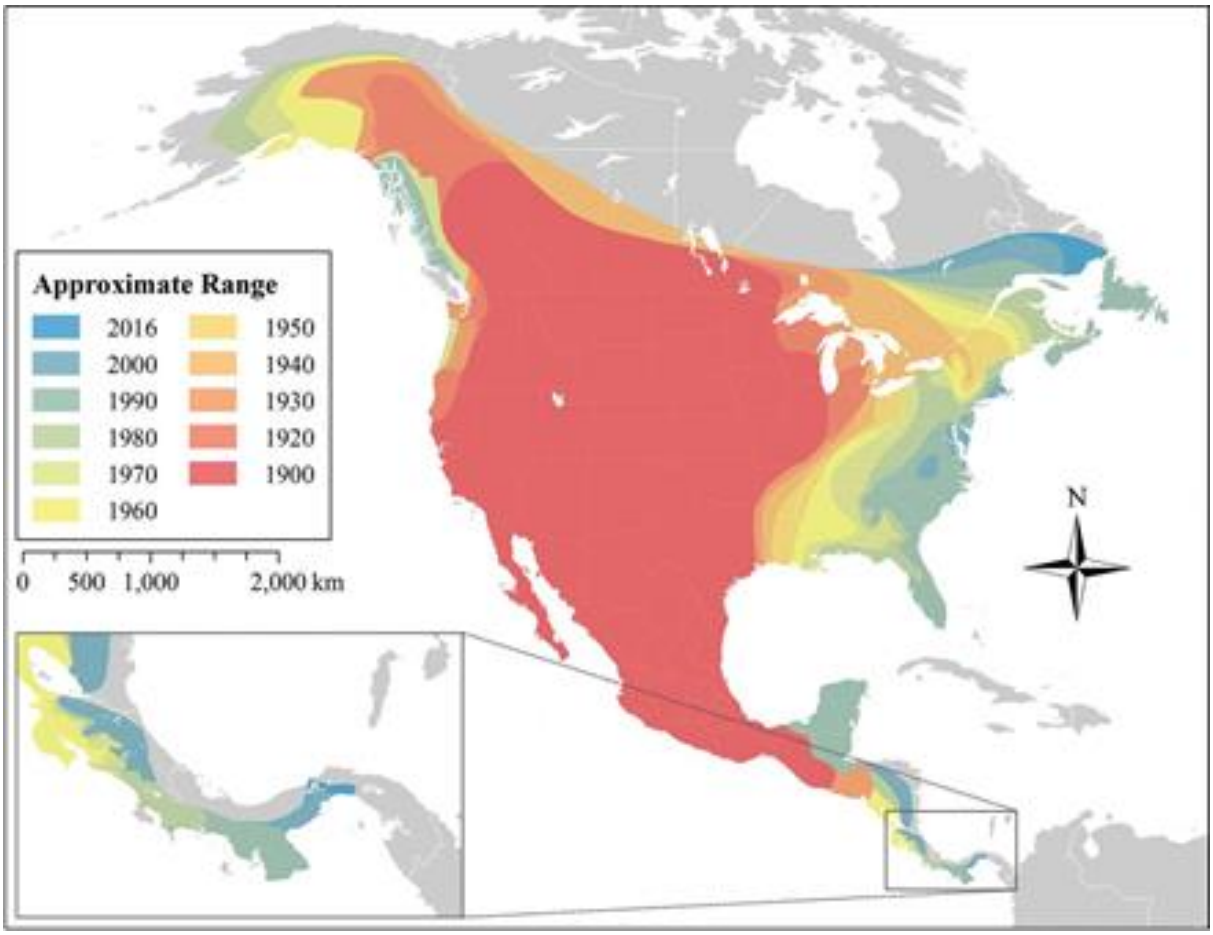


Figure 1: A map of *Canis latrans*' territorial expansion over the last century in North America. Red indicates territories measured in 1900 and dark blue indicates territories measured in 2016 (Hody and Kays, 2018).

A Historical Understanding of Coyote-Human Interactions

The coyote's movement into human settlements is not a new phenomenon. It is important to note that historical interactions between coyotes and humans inform how modern people live alongside this species today. In the face of the coyote's rapid territorial expansion into increasingly urban spaces, accounts of past coyote-human associations should augment our scientific understanding of the species' behavior so that we can better understand how coyotes and humans can best coexist.

The earliest coyote storytellers were the Paleolithic people, who depicted the animals as trickster archetypes (Flores et al., 2016). Coyote, a derivative of the Aztec name *kie-ote*, is

viewed in some Native American stories as a totemic creature exposing human flaws, often with humor and intelligence (Flores et al., 2016). Chinook texts describe Coyote learning to catch salmon by consulting his feces, while Anishinaabe tribal member Gerald Vizenor refers to the coyote figure *Naanabozho* as "the tribal trickster" (Elliott, 2003).

Human perceptions of coyotes in North America began to take a more negative turn as agricultural practices expanded in the western United States. Coyotes began to prey on the readily available food sources of sheep and goat populations. Farmers and ranchers retaliated, and in 1931 the Bureau of Biological Survey received federal funding to eradicate the species. From 1947 to 1956, 6.5 million coyotes were killed in the United States alone (Flores et al., 2016).

In the 1960's and 1970's, popular culture began to take notice of the species and champion the coyote case. For example, Walt Disney produced pro-coyote films such as *Chico, the Misunderstood Coyote*, while Warner Brothers Studios created the cartoon character of Wylie E. Coyote to add positive coyote narratives to the negative discourses surrounding the species at the time. The social movement to protect coyotes gained enough traction to motivate the issue of a ban to prohibit the use of poison on coyotes. Even so, approximately 500,000 coyotes continue to be killed annually in the United States (Flores et al., 2016). This eradication is legal and enacted through aerial hunting and other forms of management on private, state, and federal property.

Coyotes: A Scientific Understanding of Adaptability

Despite this history of persecution, the population density and territory size of coyotes continues to increase in North America. We can look to the evolutionary history of the coyote

and proposed mechanisms of behavioral change to better understand how the coyote has managed to exhibit such resiliency.

Coyotes evolved from the canid family in North America into an individual species during the Pleistocene, approximately 40–11 Ka where coyotes existed within a carnivorous guild that positioned them as meso-predators (Meachen and Samuels, 2012). The survival of coyotes necessitated that they develop the ability to both hunt and avoid predators. As a result, coyotes evolved a fission-fusion social structure that describes the coyotes' adaptive ability to roam both as singles or pairs and as pack predators (Worrall and Flores, 2016). We see a similar fission-fusion social adaptation within hyena clans, and the constraints posed by limited resources (food/water) and persecution by larger predators affect the social structure of this species as well. Fission-fusion is demonstrated when animals advantageously band together to protect resources and then disperse when environmental conditions dictate. For example, mothers with small cubs separate from packs to avoid the possibility of infection (Smith et al., 2008). Social and ecological conditions dictate whether it is more advantageous for animals to move alone or in groups (Smith et al., 2008). For example, when coyotes survive eradication efforts, they often split up and scatter across landscapes for survival.

The coyotes' evolutionary adaptability was highlighted through their successful expansion east (Figure 1), but other displays of versatility came to light during the coyotes' movement east as well. Coyotes selectively mated with wolves when beneficial for their survival. As Heppenhimer et al. summarize in their report, coyotes expanded east by traveling through two geographically separate paths (2018). First, coyotes traversed through the southern edge of Canada that bridges the Northern Great Lakes Region to arrive in their current eastern territorial ranges (Figure 2). This movement through new northern territories led to the mating

and hybridization of wolves and coyotes. It is this hybridization that resulted in the physically larger Northeastern coyotes we see in New York State today. The second path of the coyote's territorial expansion occurred 40 years later through the midwestern United States (Figure 2). No hybridization of wolves and coyotes occurred along this path of movement because wolves had been extirpated from this region of the United States (Heppenheimer et al., 2018).

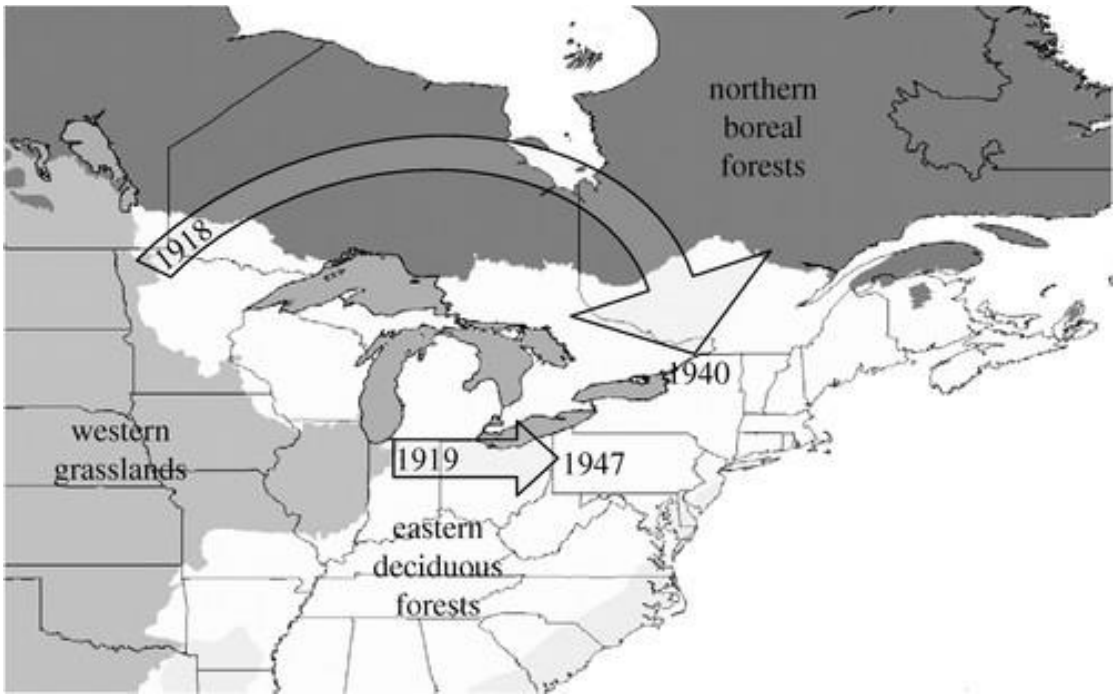


Figure 2: A map of coyotes' directional paths as the species expanded territories into the Eastern United States (Kays et al., 2009).

Reports of coyotes in northern New York began in the 1900s and increased until the coyote became firmly established around 1980 (Fener et al., 2005). Today, coyotes have been observed in Manhattan, Queens, and the Bronx (Nagy et al., 2012). Long Island remains one of North America's last remaining large land masses that does not sustain a breeding population of coyotes (Gotham, 2020). There are some physiological differences between Northeastern coyotes and Western coyotes that are worth noting. For example, the larger body of the Northeastern coyote (a possible result of wolf-coyote hybridization) allows for more efficient deer hunting.

This adaptation could be the result of phenotypic plasticity, which describes the ability of genetic makeups (genomes) to change and respond to environmental conditions (Pigliucci, 2001). However, this adaptation is likely the result of genetic variation introduced by hybridization with wolves (Kays et al., 2009).

The Northeastern coyote's evolutionary adaptability may be the result of learning and selection (Breck et al., 2019). Behavioral plasticity, which occurs when animal behavior changes rapidly and involves learning (Sol, et al., 2013), could contribute to the phenomena of the coyote's resiliency. The coyote's resiliency could also be the result of natural selection, or of the species' genetic selection of beneficial behavioral traits as they evolved (Breck et al., 2019). The third mechanism that could contribute to the Northeastern coyote's adaptability (in addition to learning and selection) is sorting. Sorting describes a phenomenon in which only fit individuals with adaptive behavioral traits colonize new environments (Breck et al., 2019). Individuals are sorted through dispersal, establishment, and habitat selection (Sol et al., 2013). Mechanisms of behavioral change do not operate in a vacuum, and likely influence each other by acting in tandem (Breck et al., 2019). Adaptive behaviors can be influenced by past environments, evolutionary history, present environments, and individual fitness. The integrative influences of these variables on both individuals and entire populations can be more easily understood and visualized in Figure 3 (Sih et al., 2011).

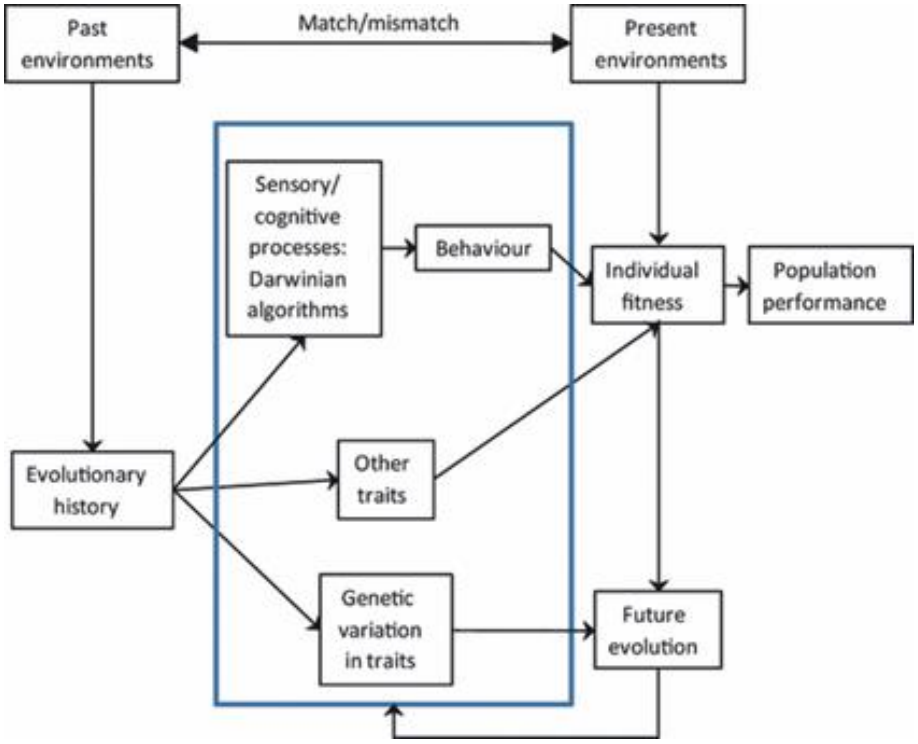


Figure 3: A diagram of behavioral influences across species that describes the effect of past and present environments on population performance. In this figure, the blue box highlights the influence of evolutionary history on sensory/cognitive processes, genetic trait variation, and other traits. These in turn influence individual fitness and future evolution, and loop back to again drive the genetic variation in traits (Sih et al., 2011).

Coyote Boldness and Trepidation

As coyotes have moved into urban spaces within the United States, citizens have reported accounts of coyote boldness and aggression observable through coyote-human interactions. In 2019, a surveillance camera captured a video of a coyote chasing a young girl in Villa Park, Illinois (McCarthy, 2019). Reports have been documented of coyotes attacking and killing domestic pets (Hall, 2018), and of coyotes becoming less hesitant and fearful of human activity (Nagy et al., 2012). A recent scientific finding supports these accounts by suggesting that animals generally are more aggressive, exploratory, and bold in urban environments than in rural environments (Miranda et al., 2013). Evidence suggests that coyote behavioral changes in urban areas are the result of learned behaviors that are beneficial to the coyote's survival in new

environments (Breck et al., 2019). However, the data for coyote boldness in cities must be scientifically quantified and identified as a behavioral population trend rather than individual variation before the mechanisms of this behavioral change can be fully understood.

A recent Nature publication highlighting Western coyotes in Utah (rural) and Colorado (urban) provided the groundwork evidence for the observation of urban boldness (Breck et al., 2019). By deploying a Flight Initial Distance test with radio collars (wherein the spatial and behavioral responses of coyotes fleeing approaching humans was recorded for analysis) and a Novel Object Test (wherein novel objects were set up at rural and urban sites to represent human landscape modifications and the spatial and behavioral responses of coyotes were analyzed), Breck and his colleagues found that coyotes in urban areas behave more boldly than coyotes in rural areas. The Novel Object Test utilized motion-activated video cameras to measure the duration (in seconds) of coyotes' spatial and behavioral responses to the site treatments (novel object or baseline). Camera traps are becoming a widespread methodology for use in scientific conservation studies as they present a relatively non-invasive opportunity to record observations of animal populations and behaviors (Wearn and Glover-Kapfer, 2017). Roland Kays and his colleagues launched a more expansive research project that draws upon Stuart Breck's Novel Object Test methodology to measure coyote behaviors across the United States using data collected with motion-activated cameras. This experiment was designed to build on collective understanding of the coyote's adaptability in the face of increased landscape fragmentation and urbanization in North America. The *Novel Object Test for Coyotes* aims to quantify coyote boldness across the rural/urban gradient within many territories of the United States by collaborating with a network of ecologists and citizen scientists. This methodology is standardized for all collaborators, and has already been implemented in North Carolina,

California, and Wyoming. My study utilizes the same methodology as this nationwide project, and the data I collected in my study will contribute to a future analysis of coyote behavior that will be grounded in a much more comprehensive nationwide body of data.

For the purposes of my study, I aim to determine if the behaviors of urban coyotes in New York City are bolder than the behaviors of rural coyotes in upstate New York. Although Roland Kays' study will focus on identifying bold and aggressive behaviors, I selected bold and trepid behaviors for analysis, and further categorized boldness and trepidation into four behavioral states (investigative, vigilant, comfortable, and shy) that are consistent with the behavioral classifications of the larger study, but modified (through adjustments of respective definitions) for my purposes. These definitions are further explained in Methods.

While Breck et al. found urban coyotes behave more boldly than rural coyotes, their study was conducted in Colorado (urban) and Utah (rural) where Western coyotes have experienced efforts of eradication in rural territories for centuries (2019). This history of persecution has likely selectively pressured Western coyotes to learn and adopt adaptive behaviors for survival in rural territories. My study is designed to build on the findings of Breck et al. and to contribute to the scientific body of knowledge on coyote behavioral adaptability and resiliency in the United States by studying the spatial and behavioral responses of Northeastern coyotes. I am interested to find whether the same pattern of coyote boldness variability (rural vs. urban) discovered in the west is occurring in the east. This study is especially timely as New York exists at the eastern edge of the coyote's territorial expansion. Coyotes are new colonizers of New York and have not had sufficient time to develop differentiation between behavioral traits in urban and rural territories. Considering variation in the evolutionary histories of Western and Northeastern coyotes, I predict that I will not be able to find a statistically significant

difference between the bold-trepid behaviors of New York coyotes in rural versus urban environments.

METHODS

Site Description

I deployed twenty camera traps in rural areas of Rockland and Orange County, west of the Hudson River. My cameras were placed in Black Rock Forest, Harriman State Park, Bear Mountain State Park, Storm King State Park, Gonzaga Park, property of the Open Space Institute, and on property of several private landowners with connections to Black Rock Forest. My rural coyote data was augmented by urban coyote data from Chris Nagy, a wildlife biologist and co-founder of The Gotham Coyote Project (2020). Nagy and his colleagues deployed eighteen cameras at urban sites east of the Hudson River from New York City northward to Westchester County. The camera sites are shown below in Figure 4.

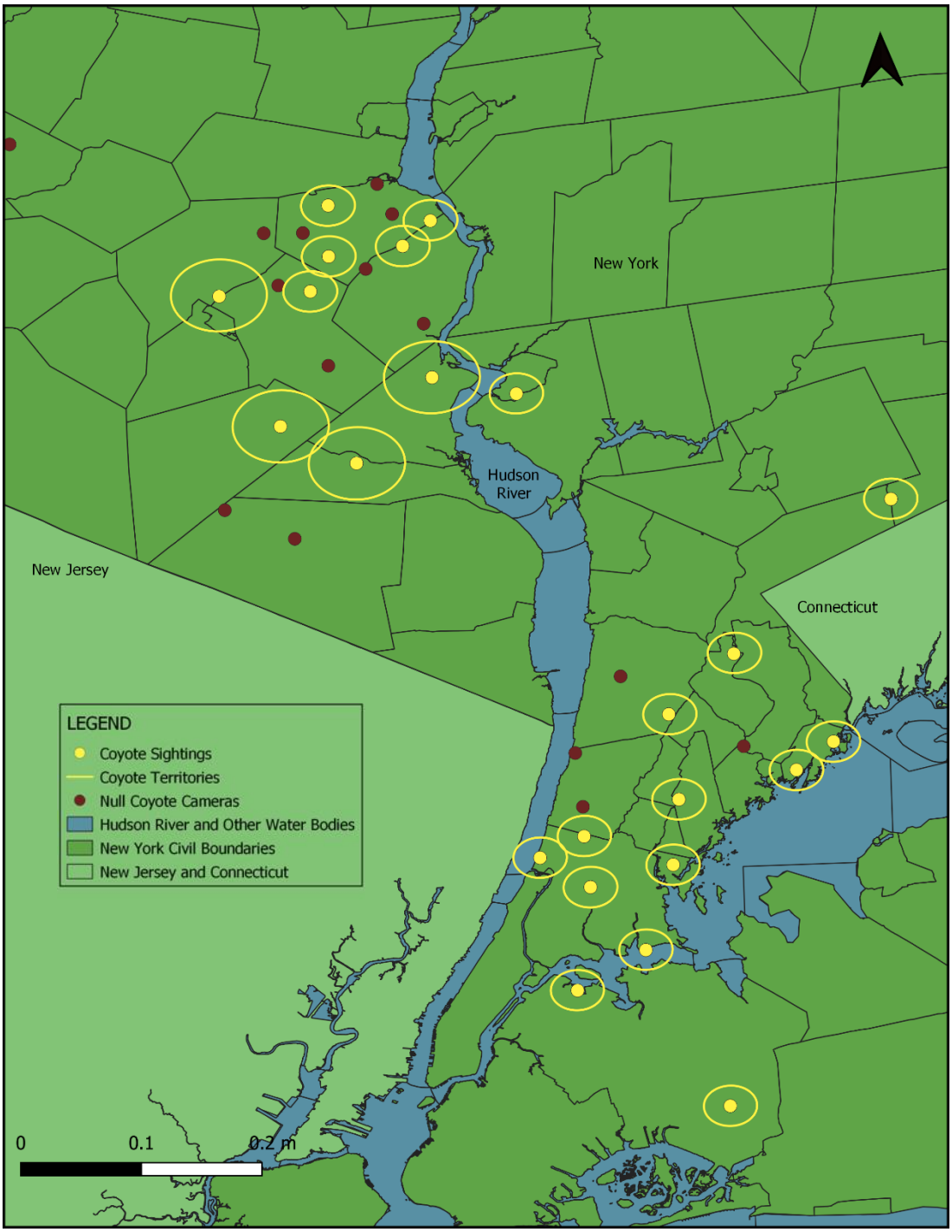


Figure 4: Map of camera locations in Orange County, Rockland County, the Queens, the Bronx, and Westchester County. Sites that captured footage of coyotes are indicated by yellow site placements. Estimated territories (see text for details) are shown as yellow circles around each site with captured coyote footage. Sites that were not successful in capturing coyote presence are indicated by maroon site placements. My sites are located west of the Hudson River, while Chris Nagy's sites are located east of the Hudson River (NOAA 2006, NOAA 2002, Paskevich 2002, USCB 2016, QGIS 2020).

To determine the region classification of urban and rural for my sites, I consulted population density data by county from the United States Census Bureau (2018). I made an operational decision to classify sites closest to New York City in the counties of the Bronx, Queens, and Westchester as urban because these counties have higher population densities, and all contain more than 5,500 people per square mile (Table 1). For the purposes of this study, I classified sites farthest from New York City in Rockland and Orange County as rural because these counties have lower population densities of less than 800 people per square mile. My determination was also influenced by a consideration for the major geographic boundary of the Hudson River. This body of water is likely a barrier to the free movement of coyotes from New York City northward along the urban to rural gradient. For the purposes of this study, all sites east of the Hudson River were designated as urban, and all sites west of the Hudson River were designated as rural.

Table 1: Population density and total population numbers for the counties included in this study. Numbers are drawn from the US Census Bureau (2018) and then classified by region (urban/rural).

County	**Total Population**	**Area (mi^2)**	**Population Density**	**Region**
Rockland	323,686	430.4	752.1	Rural
Orange	378.227	812.1	465.7	Rural
Westchester	968,815	173.4	5,587.2	Urban
Queens	2,298,513	108.7	21,145.5	Urban
Bronx	1,437,872	42	34,235.0	Urban

Coyote territories vary greatly and are influenced by geographic barriers, available food sources, and habitat fragmentation (Šálek et al., 2015). To determine the placement of camera sites within the landscape and to reduce the possibility of recording the same coyote on multiple

cameras, I referenced parameters used by Šálek et al. to determine a local home range size of 35 km² for coyotes in rural "natural" environments. These natural environments are "dominated by" agricultural and forested areas with sparse human development (Salek et al., 2015). The diameter of spacing between cameras was determined to be 6.68 km. This territory designation was only used in sites (n = 8) in large natural forested areas that are largely undeveloped (Highland State Park, Gonzaga Park, and Harriman State Park). I used two different approaches to set cameras at rural sites; the method described above for sites with largely continuous habitat, and the method I will describe below for rural environments with more fragmented habitat. Because habitat fragmentation from increasing urbanization reduces the territorial ranges of coyotes residing in less continuous areas (Salek et al., 2015), I referenced parameters used by Šálek et al. to determine a local home range size of 11 km² for coyotes in more developed natural environments. Therefore, cameras (n = 12) were placed at least 3.74 km apart at the remaining locations. Chris Nagy and his colleagues also placed urban cameras at least 3.74 km apart. This spacing is a guideline that follows the protocol established in the methods for the Nationwide Coyote Behavioral Test (Novel Object Test for Coyotes, 2019), but placement was variable considering other barriers to accessibility such as geography and land permits. As a result of these variables, some selected sites overlapped. However, overlap areas were minimal.

To further ensure that I was not double counting individual coyotes appearing at multiple sites, I looked for identifiable characteristics to verify my camera placements. The two sites with the most overlapping territory (that captured footage of coyotes) were the site at Storm King State Park and the neighboring site at Black Rock Forest. However, the coyote individual at Storm King State Park is distinguishable from other individuals due to the presence of its

stubbed tail and is, therefore, easily differentiated from the individual that appeared at the Black Rock Forest site.

It is important to note that the locations of my sites were also largely determined by the influence of local landowners, as I needed to request and obtain the permission for each site before accessing land for the purposes of this study. I also consulted wildlife ecologist Scott LaPoint to determine my camera sites, as LaPoint had collected camera trap data recently for another wildlife study in the area. Similarly, The Gotham Coyote Project has been collecting data on coyotes in New York City and Westchester County for various scientific studies and for the purposes of maintaining a general record of documentation of the coyote's territorial expansion into new boroughs (2020). As a result, Nagy and his colleagues at the Gotham Coyote Project had an extensive knowledge of coyote locations in New York City before selected sites for this project. For the urban camera sites, Nagy received a permit to deploy cameras in county parks and then selected the most urban of those sites (2019).

Both Chris Nagy and I designated locations for each camera trap on Google Maps. We used a hand-held GPS to locate the predetermined coordinates and then installed cameras, attractants, and respective treatment at each site. For each urban location, Nagy maintained enough green space to safely hide his cameras. For my rural sites, I hiked away from roads, trails, and evidence of settlement for approximately 0.80 kilometers before deploying each camera.

Novel Object Test

The Novel Object Test is designed to collect data on whether human influence on the environment impacts animal behavior. Methodology for the Novel Object Test was developed by Stuart Breck et al. in part from observation and conclusions referenced from studies conducted

by Real et al. (2007), and Smith and Blumstein (2008), who studied the effects of animal temperament/personality on adaptability and fitness (2019). In both the Western coyote study conducted by Breck et al. and in my study, “novel object” is the term used to describe four wooden stakes visible 1 meter above the surface arranged in a 1m x 1m square area and tied together with white paracord (Figure 5).



Figure 5: A camera trap photograph capturing a coyote approaching a novel object treatment site at the Open Space Institute’s property of Legacy Ridge. This fence-like treatment (novel object) surrounds a fatty acid tab and “sweet meat” attractant placed in the center of the 1m x 1m area.

Of the 20 camera traps that I deployed at rural territories west of the Hudson River, 10 were randomly selected as control sites and 10 were designated to be treated with novel objects. Of the 18 camera traps deployed by Chris Nagy and the Gotham Coyote Project, 9 were randomly selected as control sites and 9 were designated to be treated with novel objects. At all sites, a motion-activated video camera was mounted 0.5 to 1.5 m from the ground, as determined by surrounding vegetation. The camera was then turned on and locked to a nearby tree. A metal

t-post was secured to each tree (Figure 6), as suggested by Roland Kays' protocol to maintain consistency in camera mounting methodology through forested areas and grasslands, where a t-post is often necessary to secure the camera (Novel Object Test, 2019). It is important to acknowledge that the deployed cameras are themselves novel objects, but this was unavoidable because of the time constraints of this study. There was not sufficient time to first deploy the cameras, wait for the coyotes to habituate, and then commence the testing period.



Figure 6: A Reconyx Hyperfire camera is secured and locked on a tree pointed at a novel object treatment site in Harriman State Park. The standardized t-post is shown to the right of the tree.

Baseline (control) sites included a mounted camera and a buried attractant consisting of one fatty acid tablet and approximately one tablespoon of "sweet meat" lure covered in leaves. "Sweet meat" predator bait is manufactured by Russ Carman and consists of animal glands and

ground meat. “Sweet meat” and fatty acid tabs are the standard attractant protocol for every wildlife ecologist participating in the collaborative national study proposed by Roland Kays. The attractant was placed 3.5 meters from the base of each respective mounted camera. A small hole was dug in the ground, and approximately one tablespoon of “sweet meat” bait was dropped into the cavity. The bait was then covered slightly with leaves, and one fatty acid tab was placed on top of the leaf covering. Treatment sites included the above attractant stipulations with additional treatment of the novel objects. The posts of this fence-like novel object structure were pounded into the rocky topsoil with a large metal fence post driver.

Video Sequences

Each camera trap was initially in operation for a minimum of three weeks before the sites were checked for video footage of coyote approaches. If a coyote appeared on the video footage, the cameras (along with novel objects for treatment sites) were taken down from sites. If a coyote did not appear at the site during the first three weeks, the site was baited with new “sweet meat” and a fresh fatty acid tablet. Data from the initial three-week deployment was then downloaded, and the cameras were remounted to be left in operation for an additional four weeks before the completion of the experiment. After these four weeks, all cameras and novel objects were taken down from all sites.

From the camera trap data, I recorded cumulative data (number of sites visited by coyotes and total coyote observations), spatial responses, and behavioral responses at both rural and urban sites. Each camera recorded sequences of movement for 30 seconds. For sequences with coyotes present that contained more than 30 seconds of data, I considered consecutive sequences that were less than 1 hour apart as videos recording the same individual. For cumulative data, all sequences that occurred more than 1 hour apart were recorded as separate coyote observations.

There were no cases in which more than one coyote appeared on camera during the first sequence. In subsequent sequences where more than one coyote appeared on camera at the same time, I coded the appearance as one observation to account for the occurrence rather than the number of individuals. I made this determination because I was more interested in measuring the number of time coyotes detected and approached the sites than the number of individual coyotes approaching the sites. Spatial data was recorded for each coyote video as the duration of time (in seconds) spent in three spatial states: far, close, or on the attractant. (1) Far denotes time spent greater than $1m^2$ from the attractant, (2) close indicates time spent within $1m^2$ of the attractant, and (3) on indicates time spent sniffing, pawing, standing, or chewing on top of the attractant. Behavioral data was recorded as the duration (in seconds) spent by individuals in each of the four behavioral states described in Table 2. I scored the spatial and behavior responses for only the first coyote individual to appear on camera to avoid double counting responses of the same individual.

Behavioral State Definitions

For my study, I defined boldness as behavior that displayed an ability for risk-taking (i.e. explorative, confident). I defined trepidation as coyote behavior that indicated fearful alarm, apprehension, or agitation. To further break down these behavioral states into definitions that can be coded in coyote camera trap videos, I referenced Roland Kays' definitions and modified them slightly for the purposes of my study. Boldness was broken down into investigative and comfortable behavior. Trepidation was broken down into vigilant and shy behavior. These behavioral states are defined in Table 2.

Table 2: Definitions of coyote behavioral states referenced and adapted from the Novel Object Test for Coyotes (2019).

Behavioral State	Definition
Vigilant	Characterized by a tucked tail or hesitant walk toward the object. Vigilant activities indicate caution and include pacing, flinching, and crouching.
Investigating	Characterized by directed movement without hesitation. Investigating behavior typically includes an erect tail and a tall posture.
Comfortable	Characterized by time spent shaking, rolling, digging, scratching, defecating, etc.
Shy	Jumping/Running away.

Statistics

I considered the amount of time (in seconds) a coyote spent at each of the three distance classes for the spatial analysis, and in each of the four behavioral classes for the behavioral analysis. For all analyses, I explored the influence of the total observation length of the coyote sequence (in seconds), region (a categorical variable with two levels: 'rural' and 'urban'), trial (a categorical variable with two levels: 'control' and 'treatment'), and the interaction of region and trial. I added the behavior category (four levels) and the distance category (three levels) to the model for their respective response variables. I tested whether my response variables were normally distributed, first with histograms and then with a Shapiro Wilkes test. Both the behavior duration data and the distance duration data are non-normally distributed (Shapiro Wilkes, $p < 0.001$) and are zero-inflated since I recorded '0' if a coyote did not exhibit a behavior or enter a distance category during any sequence (i.e., a 30 second video, or series of videos). To quantify the effects of my explanatory variables on the coyote's behaviors and

proximity to our cameras, I ran a generalized linear model using the glmmadmb function available within the glmmADMB package for program R (Fournier et al., 2012; Skaug et al., 2016; R Core Team, 2019). I chose this model because it handles a zero-inflated, count (i.e., Poisson family distribution) response variable (Skaug et al., 2016). The full model considered behavior category or distance category, observation total, region, trial, and region-trial interaction as independent variables that influence the response variable of duration (in seconds) spent by coyotes at our sites. I included the region*trial interaction term to measure whether coyotes in different regions (urban or rural) react differently to the novel object treatment. The decision to include observation total as an explanatory variable directly accounts for the effect of total observation time on the duration of time coyotes spent in each behavioral state as an alternative to converting the data to proportions of time spent in behavioral states. I decided not to use proportional data (wherein Duration is the proportion of time spent in a particular behavioral state) for my analysis because individual instances in which coyotes appear on camera and spend an extended duration of time responding to the attractant/treatment at various region/trial sites is important to take into account when considering the full body of data. Similarly, individual instances in which coyotes appear on camera and respond only briefly to the attractant/treatment at various region/trial sites is important to consider when analyzing the full body of data. Using proportions would compare these instances directly as if individual response times were equal, and this may reduce and subvert important information. I then performed a model selection process using the dredge function of the MuMIn package for program R (Barton, 2020; R Core Team, 2019). Through this exercise, I identified the best performing model guided by each model's AICc, loglikelihood, and model weight.

RESULTS

Cumulative Data

Coyotes were documented at urban sites (n=14) more frequently than at rural sites (n=9) (Table 3). Also, the proportion (number of sites visited by coyotes divided by total number of sites) was 0.45 for rural sites and 0.78 for urban sites, indicating that the frequency of coyote observations was higher at urban sites than at rural sites.

Table 3: Report of cumulative data. Region/treatment classifications, coyote visits, and total coyote observations for each respective category.

Region	**Treatment**	**Number of Sites**	**Number of Sites Visited by Coyotes**	**Total Coyote Observations**
Rural	Treatment	10	4	16
Rural	Baseline	10	5	13
Urban	Treatment	9	9	47
Urban	Baseline	9	5	45

Coyotes were documented at 13 treatment sites but only at 10 baseline sites when urban and rural sightings were combined (Table 3). The respective proportions of coyote observations (number of sites visited by coyotes/total number of sites) are 0.53 for baseline sites and 0.68 for treatment sites, indicating that the frequency of coyote observations was higher at sites with the novel object treatment than at control sites.

Behavioral Data

I ran a zero-inflated negative binomial mixed model in R (Fournier et al., 2012; Skaug et al., 2016; R Core Team, 2019). The full model considered behavior, observation total, region, trial, and region-trial interaction as explanatory variables for the response variable of duration (in seconds) spent by coyotes in various behavioral state. Subsequent iterations of the model

included various combinations of these explanatory (i.e., independent) variables. The results of the 20 competing models with various combinations of independent variables are reported in Table 4.

Table 4: Report of behavior duration data model selection results. Modeling results describe the effects of behavioral response (in seconds), observation total (in seconds), region, trial, and region-trial interaction on total duration. In the Model Components column, each row names the explanatory variables included in that model and rows are ordered from best to least best performing. Behavior is defined as either vigilant, investigative, comfortable, or shy; region is either rural or urban; trial is either baseline or treatment; null is the model with no explanatory variables; additive variables are indicated by a +; and interactive variables are indicated as a *. AICc is Akaike's Information Criterion value of the model adjusted for small sample sizes, and ΔAICc is a comparative measure between the listed Model Components and the model with the lowest AICc value. Weight describes the Akaike weight of each model and can be used to quantify the relative strength. LL is the log likelihood value of the model.

Model Components	**AICc**	**ΔAICc**	**Weight**	**LL**
Behavior + Obs. Total + Trial	591.8	0.00	0.703	-288.271
Behavior + Obs. Total + Region + Trial	594.1	2.29	0.224	-288.223
Behavior + Obs. Total + Region + Trial + Region*Trial	596.4	4.58	0.071	-288.152
Obs. Total + Trial	605.2	13.34	0.001	-298.358
Obs. Total + Region + Trial	607.4	15.57	0.000	-298.357
Obs. Total + Region + Trial + Region*Trial	615.7	23.90	0.000	-301.385
Behavior + Obs. Total	615.9	24.10	0.000	-301.486
Behavior + Obs. Total + Region	617.4	25.58	0.000	-301.060
Obs. Total + Region	634.6	42.77	0.000	-313.072
Obs. Total	635.2	43.34	0.000	-314.445
Behavior + Trial	720.4	128.57	0.000	-353.719
Behavior + Region + Trial	722.2	130.41	0.000	-353.474
Behavior + Region + Trial + Region*Trial	722.4	130.57	0.000	-352.363
Behavior	743.1	151.27	0.000	-366.209
Behavior + Region	745.3	153.49	0.000	-366.178
Trial	754.4	162.55	0.000	-374.051
Region + Trial	755.8	163.98	0.000	-373.678
Region + Trial + Region*Trial	758.0	166.21	0.000	-373.677
Null	786.1	194.24	0.000	-390.961
Region	787.9	196.09	0.000	-390.822

For the behavioral response data, the Akaike weight of the best fit model is 0.703, indicating that this model has 70.3% of the explanatory support for this analysis. This model shows that behavioral response (vigilant, investigative, comfortable, or shy), total observation time, and trial (treatment or baseline) had significant effects on the duration of time coyotes spent in behavioral states. Region (urban or rural) did not have a significant effect on coyote responses in the best fit model. The results of the best fit Poisson regression model are reported in Table 5.

Table 5: Results (p-values, estimates, and standard errors) of explanatory variables for the best fit generalized linear mixed model.

Explanatory Variable	**P-Value**	**Estimate**	**Standard Error**
Observation Total	2e-16	0.011007	0.000553
Investigative Behavior	0.09256	-0.170290	0.101240
Shy Behavior	0.00029	-0.682510	0.188270
Vigilant Behavior	0.00101	-0.355968	0.108260
Novel Object Treatment	3.2e-07	-0.546046	0.106800
Intercept	2e-16	2.647159	0.109250

Total observation time (p = 2e-16) and novel object treatment (p = 3.2e-07) have statistically significant effects on coyote responses. Cumulative behavioral responses (duration spent in camera view) are highest at novel object treatment sites (Figure 7). Similarly, shy behavior (p = 0.00029) and vigilant behavior (p = 0.00101) appear to affect coyote responses. Comfortable behavior and baseline sites also appear to affect coyote responses, as indicated by the intercept (p = 2e-16).

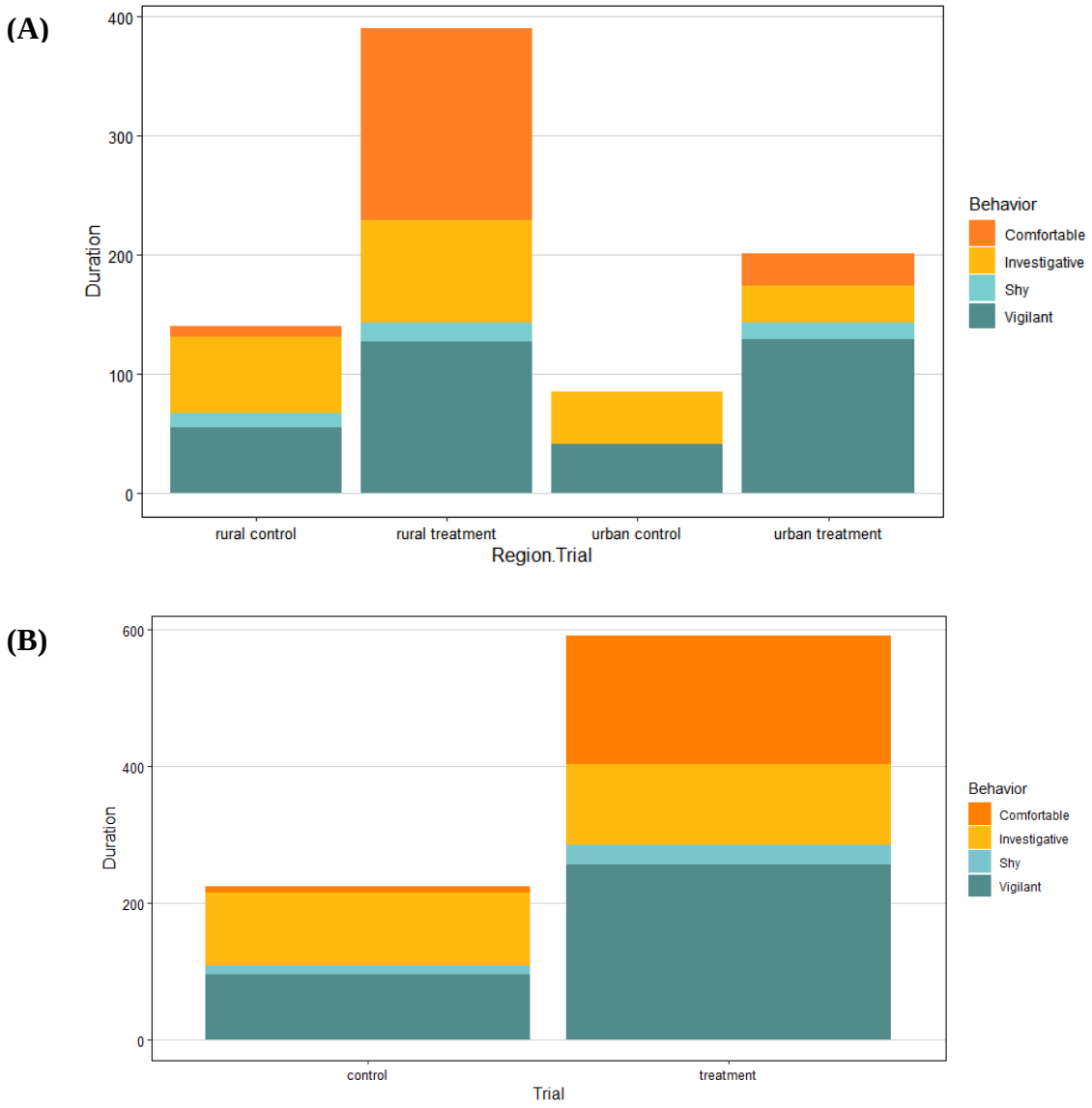
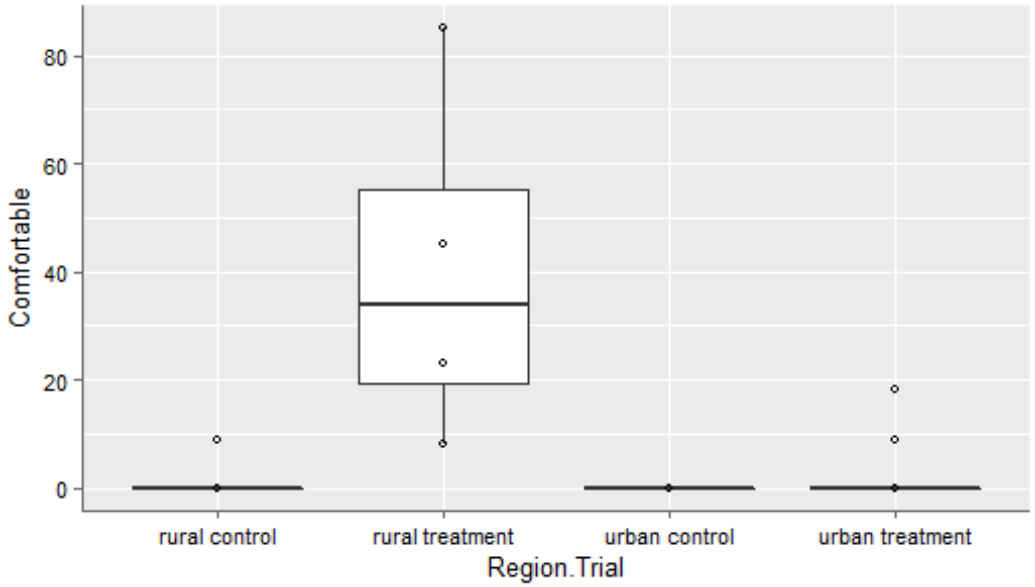


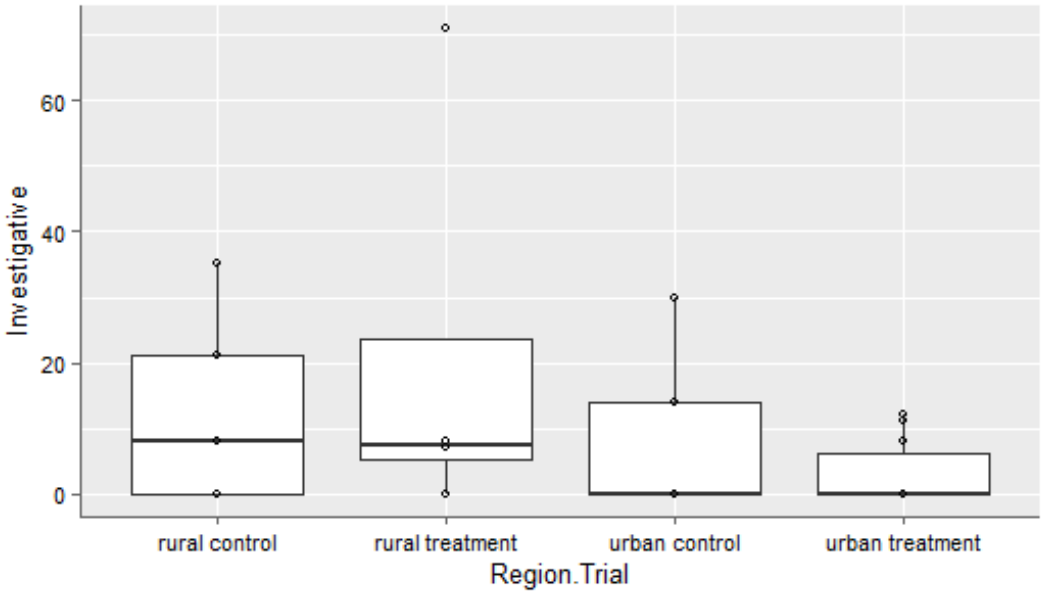
Figure 7: Stacked bar graphs depicting cumulative comfortable, investigative, shy, and vigilant behavioral responses (in seconds). Bold behaviors (investigative/comfortable) are indicated by yellow and orange, respectively. Trepid behaviors (shy/vigilant) are indicated by light blue and dark blue, respectively. Panel **(A)**: Trial/region combinations are distinguished on the x- axis. Behavioral response categories are reported by the colors described in the key and respective cumulative behavioral response durations (in seconds) are indicated on the y-axis. We see that cumulative behavioral responses are higher at novel object treatment sites than at baseline sites in both urban and rural regions, and that rural sites treated with the novel object show the highest total duration of coyote behavioral responses. Panel **(B)**: Trial distinctions of control and treatment are distinguished on the x-axis. Behavioral response categories and respective cumulative durations are plotted as in Panel (A). We see that cumulative behavioral responses are higher at novel object treatment sites than at baseline sites. This figure was generated through the computer program R (R Core Team, 2019).

For my behavioral data visualizations, I separated treatment affect by region, even though region and the interaction of region and trial was not considered an important explanatory variable in the best model (Figure 8). Although the models did not show region to be significant, visualization of the interaction of region and trial was done to consider these variables in respect to each behavioral category (comfortable, investigative, vigilant, and shy, respectively) and to report a comprehensive distribution of data.

(A)



(B)



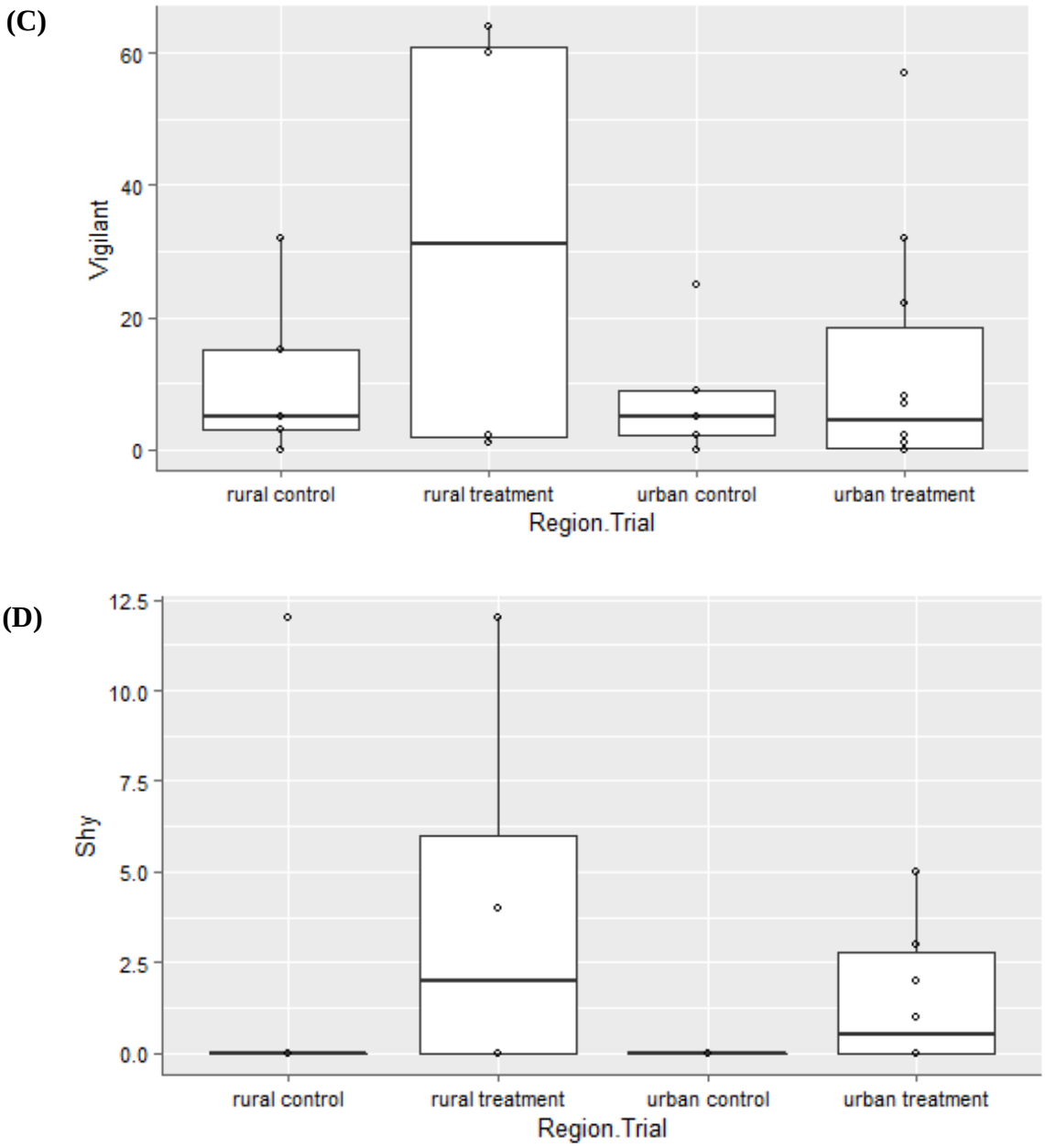


Figure 8: Box plots depicting cumulative comfortable, investigative, shy, and vigilant behavioral responses (in seconds), respectively, at each region/trial combination. Panel **(A)***:* Comfortable behavioral responses are on the y-axis as duration in seconds. Trial/region combinations are on the x- axis. The middle quadrants of comfortable, vigilant, and shy behavioral responses are highest at rural novel object treatment sites. Panel **(B)**: Investigative behavioral responses are on the y-axis as duration in seconds. Trial/region combinations are on the x- axis. Panel **(C)**: Vigilant behavioral responses are on the y-axis as duration in seconds. Trial/region combinations are on the x- axis. Panel **(D)**: Shy behavioral responses are on the y-axis as duration in seconds. Trial/region combinations are on the x- axis. This figure was generated through the computer program R (R Core Team, 2019).

At the novel object treatment sites, rural coyotes spent more time in the comfortable behavioral state, on average, than urban coyotes (Figure 8, Panel A). Without the presence of the novel object, no coyotes exhibited comfortable behavior at urban sites, and only one coyote individual exhibited comfortable behavior at rural sites. Coyotes at rural sites appeared to spend slightly more time exhibiting investigative behavior than coyotes at urban sites (Figure 8, Panel B). Novel object treatment did not appear to affect investigative behavior appreciably. Coyotes at rural sites appeared to be spending more time exhibiting vigilant behavior than coyotes at urban sites (Figure 8, Panel C). This was especially evident with the presence of the novel object, as coyotes exhibited the most vigilant behavioral responses at rural sites treated with novel objects. Rural and urban designations appeared to have little effect on shy behavior, but novel object treatment considerably affected shy coyote behavior (Figure 8, Panel D). Coyotes at sites treated with novel objects responded with shy behavior more often than coyotes at baseline sites, and coyotes at rural treatment sites exhibited more shy behavior that coyotes at urban treatment sites.

Spatial Data

To analyze spatial data, I ran a zero-inflated negative binomial mixed model in R (Fournier et al., 2012; Skaug et al., 2016; R Core Team, 2019). The full model considered distance, observation total, region, trial, and region-trial interaction as explanatory variables for the response variable of duration (in seconds) spent by coyotes at various distances (far, close, and on). The results of the 20 competing models with various combinations of independent variables are reported below in Table 6.

Table 6: Report of spatial response duration data model selection results. Modeling results describe the effects of spatial response (in seconds), observation total (in seconds), region, trial, and region-trial interaction on total duration. In the Model Components column, each row names the explanatory variables included in that model and rows are ordered from best to least best performing. Distance is described as either far, close, or on; region is either rural or urban; trial is either baseline or treatment; null is the model with no fixed effects; additive variables are indicated by a +; and interactive variables are indicated as a *. AICc is Akaike's Information Criterion value of the model adjusted for small sample sizes, and ΔAICc is a comparative measure between the listed Model Components and the model with the lowest AICc value. Weight describes the Akaike weight of each model and can be used to quantify the relative strength. LL is the log likelihood value of the model.

Model Components	**AICc**	**ΔAICc**	**Weight**	**LL**
Distance + Obs. Total + Trial	547.6	0.00	0.958	-267.146
Distance + Obs. Total + Region	553.8	6.24	0.042	-270.264
Distance + Obs. Total + Region + Trial	569.5	21.91	0.000	-276.874
Distance + Obs. Total + Region + Trial + Region*Trial	569.9	22.31	0.000	-275.804
Obs. Total + Trial	572.6	25.06	0.000	-282.026
Obs. Total + Region + Trial	577.9	30.31	0.000	-283.495
Obs. Total + Region + Trial + Region*Trial	578.9	31.27	0.000	-282.782
Obs. Total	587.8	40.21	0.000	-290.720
Obs. Total + Region	589.1	41.49	0.000	-290.238
Distance + Region + Trial + Region*Trial	642.1	94.55	0.000	-313.190
Region + Trial + Region*Trial	642.3	94.69	0.000	-315.682
Distance + Region + Trial	644.9	97.31	0.000	-315.801
Region + Trial	646.2	98.62	0.000	-318.806
Distance + Region	652.8	105.19	0.000	-320.933
Region	654.7	107.08	0.000	-324.155
Distance + Trial	664.8	117.21	0.000	-326.941
Trial	669.2	121.57	0.000	-331.399
Null	685.7	138.13	0.000	-340.771
Distance + Obs. Total	707.1	159.51	0.000	-348.091
Distance	788.6	241.04	0.000	-390.014

For the spatial response, the model that considered distance, observation total, and trial was the best iteration. The weight of the best fit model is 0.958, indicating that this model had 95.8% of the explanatory support for this analysis. This model shows that both distance and trial

(treatment vs. baseline) had significant effects on the model. I reran the best fit Poisson regression model to output the results in Table 7.

Table 7: Results (p-values, estimates, and standard errors) of explanatory variables for the best fit generalized linear mixed model.

Explanatory Variable	**P-Value**	**Estimate**	**Standard Error**
Observation Total	2e-16	0.012081	0.000573
Far Distance	0.44	0.088324	0.113340
On Distance	8.6e-07	0.567288	0.115270
Novel Object Treatment	2.8e-05	-0.411361	0.098252
Intercept	2e-16	2.032676	0.096318

Total observation time (p = 2e-16), “on” distance (p = 8.6e-07), and novel object treatment (2.8e-05) had statistically significant effects on coyote responses. “Close” distance and baseline sites also appeared to affect coyote responses, as indicated by the intercept (p = 2e-16).

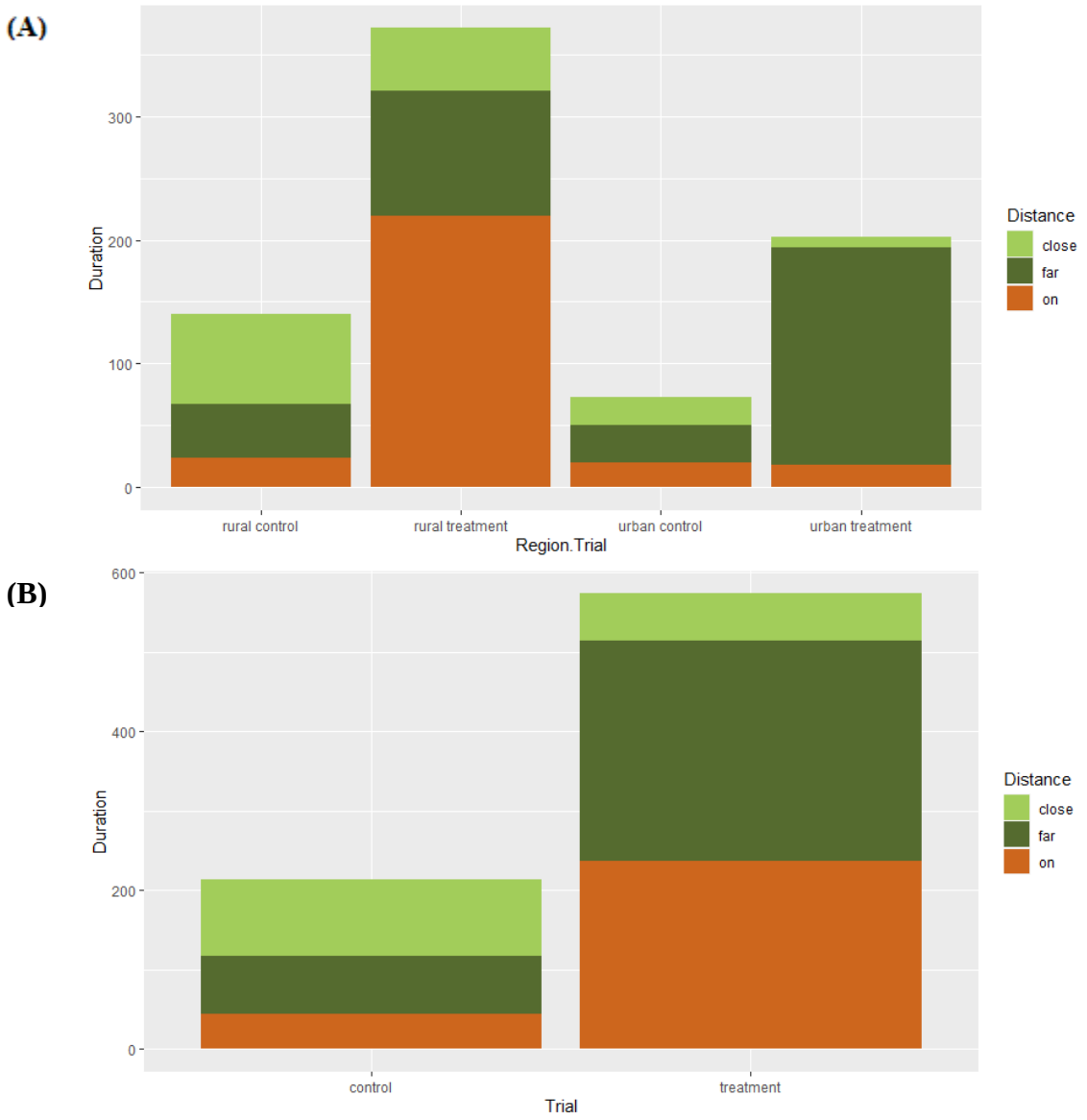
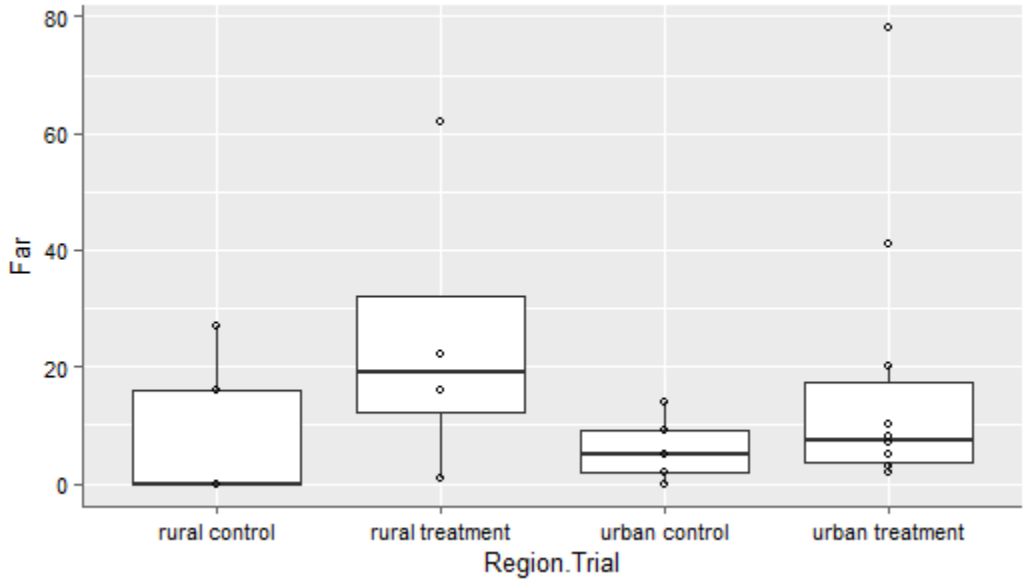


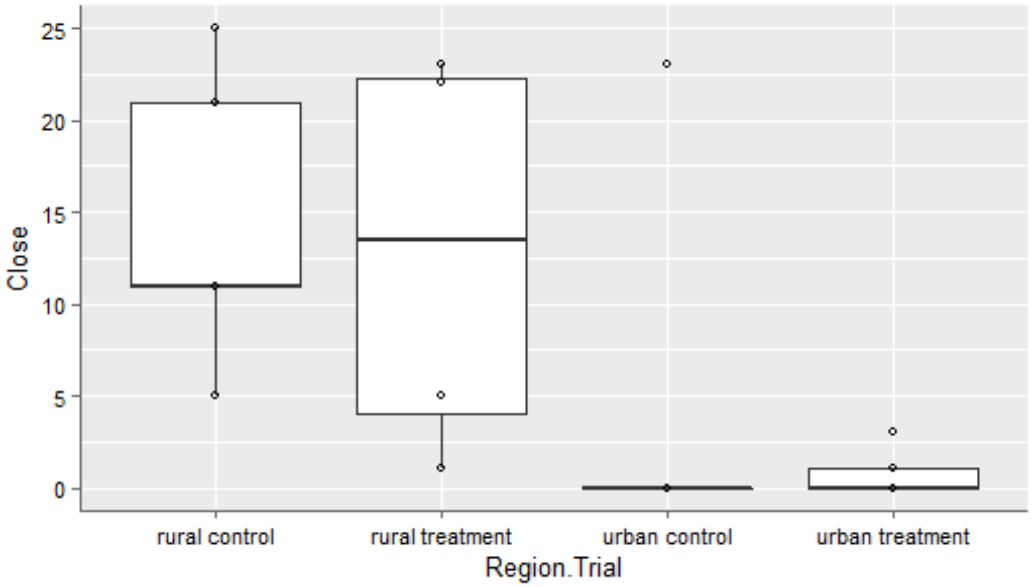
Figure 9: Stacked bar graphs depicting cumulative close, far, and on spatial responses (in seconds). Panel **(A)**: Trial/region combinations are distinguished on the x-axis. Spatial response categories are reported by the colors described in the key and respective cumulative spatial response durations (in seconds) are indicated on the y-axis. We see that cumulative spatial responses are higher at novel object treatment sites than at baseline sites in both urban and rural regions, and that rural sites treated with the novel object show the highest total duration of coyote spatial responses. Panel **(B)**: Trial distinctions of control and treatment are distinguished on the x-axis. Spatial response categories and respective cumulative durations are plotted as in Panel (A). We see that cumulative spatial responses are higher at novel object treatment sites than at baseline sites. Figure 9 was generated through the computer program R (R Core Team, 2019).

For my spatial data visualizations, I separated treatment affect by region, even though region and the interaction of region and trial was not considered an important explanatory variable in the best model (Figure 10). Although the models did not show region to be significant, visualization of the interaction of region and trial was done to consider these variables in respect to each spatial category (far, close, and on, respectively) and to report a detailed distribution of data.

(A)



(B)



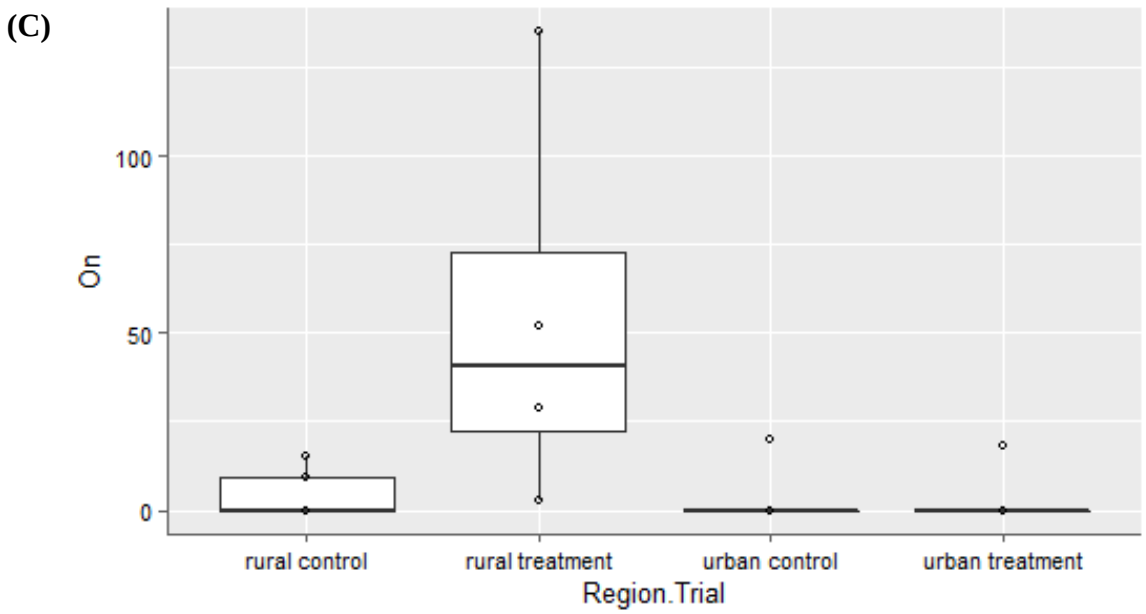


Figure 10: Box plots depicting cumulative far, close, and on spatial responses (in seconds), respectively, at each region/trial combination. Panel **(A)**: Far spatial responses are on the y-axis as duration in seconds. Trial/region combinations are on the x-axis. Panel **(B)**: Close spatial responses are on the y-axis as duration in seconds. Trial/region combinations are on the x-axis. Panel **(C)**: On spatial responses are on the y-axis as duration in seconds. Trial/region combinations are on the x-axis.

Supporting the results of the model, we can see in Figure 10 (Panel A) that region (rural vs. urban) did not appear to affect the duration of time coyotes spent "far" from the attractant, but that treatment (novel object vs. control) did. Coyotes spent more time "far" from the attractant at sites that were treated with the novel object than at sites that were not. Although regional differences (rural vs. urban) were not significant according to the above model, Figure 10 (Panel B) suggests that region (rural vs. urban) did affect the duration of time coyotes spent "close" to the attractant, and that "close" spatial responses were longer at rural sites than at urban sites. Treatment (novel object vs. control) appeared to negligibly affect "close" responses although coyotes at rural sites treated with novel objects remained "close" to the attractant for the longest duration of time. Despite the fact that regional differences (rural vs. urban) were not significant according to the above statistical model, Figure 10 (Panel C) depicts speculative

evidence that region did affect the duration of time coyotes spent "on" the attractant, as rural coyotes spent more time "on" the attractant than urban coyotes. Treatment (novel object vs. control) only noticeably influenced the "on" spatial response at rural sites, where coyotes appeared to remain "on" the attractant for longer durations of time than coyotes at urban sites.

DISCUSSION

I found strong evidence that region (rural or urban) does not have a statistically significant effect on the responses of Northeastern coyotes in this study. Although the second best fit models for both spatial and behavioral data did include region as independent variables, these models were appreciably less supported than the best fit models selected (Table 4, Table 6). This result, describing the nominal effects of region on coyote responses, contradicts results found by Breck et al. (using similar protocol and statistical analysis on coyotes in the West) that statistically, region does significantly affect coyote responses (2019). This discrepency may be the result of the long history of persecution in the West and of the coyote's recent territorial expansion and establishment in New York State (Flores et al., 2016; Hody and Kays, 2018). Coyotes in the rural Northeast have not been removed by human hunting with the same force as coyotes in the rural West. This selective pressure may have influenced rural Western coyotes to behave with more trepidation in "natural" areas than in new urban territories that do not carry the history of coyote eradication. Coyotes in the Northeast have had less of a cause to change their behaviors as they have not been persecuted in rural areas with the same force as their Western counterparts. Also, coyotes in the Northeast likely have not had sufficient time to adapt and change their behaviors to suit new urban environments, as even rural environments in the Northeast are relatively "new" territories as compared to the west (Hody and Kays, 2018).

Although region does not substantially affect Northeastern coyote responses, my linear regression model results show that the novel object treatment had a statistically significant affect on both the spatial and behavioral responses of coyotes. Coyotes at sites treated with novel objects spent a longer duration of time in front of the camera than coyotes at baseline sites. This willingness to respond to the attractant and novel object treatment may indicate a preoccupation with anthropogenic objects and a willingness to explore novelty which could indicate explorative tendencies. This explorative inclination in the presence of novel objects suggested by these results is also indicated by the cumulative data as the proportion of coyote observations (number of sites visited by coyotes/total number of sites) was higher at sites treated with the novel object (0.68) than at baseline sites (0.53). Of the sites treated with novel objects, coyotes appeared to spend the longest time responding to the treatment at rural sites (Figure 7, Figure 12). Although region was not a statistically significant explanatory variable for either the spatial or behavioral best fit models, this observation is of interest and may be because rural coyotes residing in more natural areas are markedly more interested in responding to human landscape modification than urban coyotes who often interact with human objects.

Although region and the interaction of region and trial were not considered significant variables to determine the duration of time coyotes spent in view of the camera, when the data is further parsed by region, one notable observation was that the duration of time spent in comfortable and investigative behavioral states is highest at rural sites treated with novel objects. Both comfortable and investigative responses indicated boldness, so this result suggested that boldness may be highest at rural treatment sites, which contradicts the results found by Breck et al. in their study of Western coyotes (2019). However, the behavioral data also indicated that shy and vigilant behavioral responses increased at sites treated with novel objects. This is visually

evident (Figure 7) at both urban treatment sites and rural treatment sites. Because both shyness and vigilance describe trepidation, these results indicated that coyotes appeared to be exhibiting more trepidation with the presence of novel object treatments. Although region appeared to have no effect on behavioral responses, it may be true that coyotes in their respective regions of urban and rural do change their responses when the presence of novel human objects interrupts their otherwise familiar territories. It may be that Northeastern coyotes moved into urban and rural territories at a similar time and experienced similar selective pressures, resulting in little differentiation between regional responses to the attractant deployed in this study. Nonetheless, as coyotes have now become established in both urban and rural territories, the sudden introduction of novel objects in this study in both regions increased trepid coyote responses.

Despite the fact that regional differences (rural vs. urban) are not significant according to the best fit statistical model, one notable spatial influence on coyote responses was that the duration of time spent "on" the attractant was highest at rural sites treated with novel objects, which could indicate increased boldness (Breck et al., 2019). However, "far" responses were higher at both urban and rural sites treated with the novel object than at baseline sites in both regions. This finding could indicate that coyotes spend more time surveying areas with new human modifications before approaching the sites, which appeared to be evidence pointing towards increased trepidation. Coyotes at rural sites spent more time "close" to the attractant than coyotes at urban sites, which could have indicated slight trepidation as coyotes at this distance neither avoided ("far") nor boldly sniffed, pawed, or chewed ("on"). Coyotes at both rural and urban baseline sites spent more time "close" to the attractant than coyotes at treatment sites, which could have indicated familiarity with a relatively undisrupted site as the coyote in neither avoiding "far" or boldly remaining "on" the attractant.

Also noteworthy, the frequency of coyote observations was much higher at urban sites than at rural sites. This could have indicated boldness and explorative behaviors in urban territories as more coyotes are approaching urban trial sites, but it could also simply be the result of Chris Nagy's comprehensive understanding of urban coyote presence resulting from previous research with the Gotham Coyote Project on coyote populations in New York City.

CONCLUSION

Statistical analysis clearly indicates that novel object treatment significantly influences the spatial and behavioral responses of Northeastern coyotes at my study sites. Region (urban vs. rural) does not have an appreciable effect on coyote responses. Behavioral responses do statistically influence coyote responses (Table 5), but bold behavioral responses of investigation and comfort and trepid behavioral responses of shyness and vigilance vary greatly between sites with various region/treatment interactions. A discernible trend of increasing boldness with the presence of increased urbanization or novel object treatment is not represented clearly by my data. Similarly, a significant trend of increasing or decreasing trepidation is not clearly shown. It is important to consider the variation of behavioral state observations in this study in their entirety, but it is not possible to state soundly a distinct trend across responses. Likewise, spatial responses do statistically influence coyote responses (Table 7) but vary greatly between sites with various region/treatment interactions.

RECOMMENDATIONS

For this study, I assumed that every camera had the same ability to detect motion. However, it is possible that individual motion-activated video cameras vary in their ability to detect motion. Chris Nagy selected the Browning Recon Force Advantage, the Bushnell 119437, and the Moultrie M880 camera models to use at his urban sites, and I selected a Reconyx

Hyperfire to use at my rural sites. This determination was made based on available resources, but in future studies it would likely be beneficial to standardize the camera model across study sites.

Also, I decided to use the binary regional classifications of rural and urban for my sites as a result of the relatively small sample size. I would recommend that future studies, specifically the nationwide coyote behavioral study, elect to study coyote responses along a regional landscape gradient from urban to rural that is meticulously defined and standardized across study sites. Using a landscape gradient from urban to rural would more effectively measure the potential subtle differences between regions that were not possible to detect within the parameters of this study. Regional classifications could be determined based on population density, land coverage, land use, proximity to major cities, and other variables, and could more effectively quantify their impact on coyote responses.

Also, I would recommend that future studies deploy the camera for several weeks before assembling the novel object and attractant. This time period would allow resident coyotes to become habituated to the presence of the camera before the attractant and novel object treatment were deployed, and would, therefore, reduce the chance that the camera is itself interfering with the results of the study by acting as a "novel" object.

For the purposes of my study, I considered observation total as an explanatory variable in my linear models to account for the influence of total observed time on the duration of behavioral and spatial responses. However, behavioral and spatial response data are dependent on individual coyotes. For each sequence of recorded video of an individual coyote, data was collected for shy, investigative, vigilant, and comfortable behavior as well as far, close, and on spatial responses. In effect, this data is dependent on the individual coyote for which the data was collected and should, therefore, not be considered as an independent explanatory variable. In

future studies, if there is a larger body of data collected, it may be more effective to consider the spatial and behavioral response data as "nested" within the total observation to account for this interaction. Also, it would be interesting to look at a linear model that considers observation total, region, trial, and region-trial interaction as explanatory variables for the response variable of duration (in seconds) spent by coyotes in each individual behavioral response and at each individual distance (far, close, and on).

Continuing to study the spatial and behavioral responses of coyotes is crucial because this research has the potential to lead to more sustainable decisions that address how humans and coyotes can best coexist peacefully within overlapping territories. If we can confidently quantify how coyotes react to novel objects and how this response varies in different territories, we will be able to further study the mechanisms of coyotes' behavioral changes. Further work in this area could possibly determine whether human interactions with current coyote populations can alter the behavior of human interactions with future coyote populations. For example, if we learn that coyote responses are the result of behavioral plasticity (which occurs when animal behavior changes rapidly and involves learning) it may be possible to interact with coyotes in a way that teaches them to avoid humans. This learned avoidant behavior could, in turn, prevent future violence and misunderstanding between coyotes and humans (Sol, et al., 2013). If behavioral plasticity is at play and humans encourage coyotes to inhabit densely populated human spaces by feeding them, coyotes will likely learn that boldly approaching humans is beneficial to their survival, and this boldness could quickly become aggressive. Certainly, researching the behavioral responses of coyotes can have applicable influences on sustainable policy decisions that will translate to peaceful human-coyote interactions.

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