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Bobby Habig, Angelinna Bradfield, Chris Nagy,
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Cover Photograph: As the Coyote (*Canis latrans*) expands its range throughout New York City and Long Island, Coyote pups are increasingly observed in urban greenspaces throughout the New York metropolitan area. Photograph © Chris Nagy

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Predictors of Coyote Occupancy and Detection Probability in the New York Metropolitan Area

Bobby Habig^{1,2,3,*}, Angelinna Bradfield², Chris Nagy⁴, Mark Weckel³, and David C. Lahti^{2,5}

Abstract - In recent decades, *Canis latrans* (Coyote) has become increasingly established in several urban greenspaces in the New York metropolitan area. However, there is limited information about their distribution patterns. To address this gap, we deployed motion-activated camera traps to survey Coyote occupancy and detection probability from 2015–2019 in 31 greenspaces throughout the New York metropolitan area, and we compared these findings to historical data. We also modeled anthropogenic and ecological covariates predicted to influence their distribution patterns. We found four key results. First, we documented Coyotes in 11 of the 31 urban greenspaces, 8 in the Bronx and 3 on Long Island, including 3 locations (1 in the Bronx and 2 on Long Island) not chronicled in previous surveys. Second, Coyote occupancy was higher on the mainland (Bronx) than on nearby islands (Long Island, Manhattan, Randall’s Island). Third, Coyote occupancy was higher in more heterogenous habitats during pup-rearing seasons and in human-altered greenspaces surrounded by neighborhoods with higher human population densities during non-pup-rearing seasons. Finally, Coyote detection was higher in greenspaces with smaller patch areas that were surrounded by neighborhoods with lower human population densities and more developed land cover. Our results indicate that Coyotes have become well-established in the Bronx, but that barriers separating the New York Islands continue to partially impede their dispersal, although they are predicted to continue their expansion into Long Island.

Introduction

Among mammals, large carnivores are especially sensitive to anthropogenic land use change (Ripple et al. 2014). The populations of most large carnivores in North America, such as *Canis lupus* L. (Wolf) (Benson et al. 2017, Berger and Gese 2007, Levi and Wilmers 2012), *Puma concolor* L. (Cougar) (Anderson et al. 2010, Ripple and Beschta 2006, Winkel et al. 2023), and *Ursus* spp. L. (Bear) (Collins et al. 2020, Laliberte and Ripple 2004, Mattson et al. 2005), have been decimated by anthropogenic change. However, one species has thrived: *Canis latrans* Say (Coyote) (Hody and Kays 2018, Ripple et al. 2013). Remarkably, Coyotes have expanded from their ancestral range in the western United States, filling the ecological niches of extirpated apex predators, and now have populations across all 48 contiguous states (Fener et al. 2005, Hody and Kays 2018, Toomey et al. 2012). In recent decades, Coyotes have colonized densely populated cities including Atlanta (Mowry and Wilson 2019), Chicago (Gehrt et al. 2009, 2011, 2013; Gese et al. 2012; Hennessy et al. 2012; Morey et al. 2007), Denver (Poessel et al. 2013, 2016), Los Angeles (Riley et al. 2003, Shargo 1988, Tigas et al. 2002), Toronto (Gelmi-Candusso 2023, 2024; Thompson et al. 2021), and most recently, the New York metropolitan area (Bradfield et al. 2022; Caragiulo et al. 2022; Henger et al. 2020, 2022; Nagy et al. 2016, 2017; Stark et al. 2020; Weckel et al. 2015).

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Associate Editor: Jeremy Pustilnik, University of Cambridge.

The expansion of Coyotes into the New York metropolitan area is of particular interest considering that over 23 million people inhabit the region, and the extensive development across this landscape (Nagy et al. 2016, Stark et al. 2020, United States Census Bureau 2021; Weckel et al. 2015). With a population density of over 43,000 humans per square kilometer, New York City itself is the most populous city in the United States (New York City Department of City Planning 2022). In addition to being highly urbanized, New York City presents an additional challenge to Coyote expansion because other than the Bronx, which is located on the mainland, all other boroughs are located on islands. Coyotes have become well-established in the larger tri-state area (New York, New Jersey, and Connecticut) surrounding New York City, and despite the geographic challenges, several individual Coyotes have now crossed from mainland New York into Manhattan and Long Island (Henger et al. 2020, Nagy et al. 2017). Coyotes are predicted to continue their range expansion further into Long Island, one of the few remaining large land masses in the United States in which there are apparently a limited number of documented breeding individuals (Nagy et al. 2016, 2017; Weckel et al. 2015).

Three habitat characteristics of urban greenspaces that might influence the probability that a Coyote is present at a given location (hereafter “occupancy”) and the probability of observing a Coyote if it occupies a given location (hereafter “detection probability”) are (1) greenspace type; (2) patch area; and (3) habitat heterogeneity (Bradfield et al. 2022). First, within a highly urbanized landscape, Coyotes can make use of two broad greenspace types: *human-altered greenspaces* and *urban natural greenspaces* (Bradfield et al. 2022). Human-altered greenspaces have been modified for use by humans; examples are manicured lawns, athletic fields, playgrounds, and golf courses. Urban natural greenspaces have been minimally modified by humans and have relatively lower levels of human activity; examples include secondary growth forest, wetlands, and grasslands (Gallo et al. 2017). In general, Coyotes select urban natural greenspaces and tend to avoid human-altered greenspaces (Franckowiak et al. 2019; Gehrt et al. 2009, 2013; Gese et al. 2012; Mueller et al. 2018; Poessel et al. 2016). However, Coyotes may also use human-altered greenspaces as secondary land cover types where they can search for prey and other resources (Gese et al. 2012, Morey et al. 2007). Indeed, urban Coyotes often shift their activities so that they are more active at night, when they are least likely to encounter humans within these spaces (Farmer and Allen 2019, Gese et al. 2012, Poessel et al. 2016, Thompson et al. 2021). In addition to greenspace type, a second factor that might influence the distribution of Coyotes is patch area. The greenspaces situated in large cities that Coyotes can potentially occupy vary considerably in patch size (Gehrt et al. 2009, Nagy et al. 2016, Riley et al. 2003). On average, suburban and urban Coyotes have been found to maintain a home range size of $\sim 10 \text{ km}^2$ and a density of $\sim 1.5\text{--}2.5$ individuals per km^2 (Šálek et al. 2014). Because Coyotes are territorial, this limits the number of individuals that can occupy a given greenspace (Chamberlain et al. 2021, Gese et al. 1988, Knowlton et al. 1999), although their home ranges might sometimes overlap (Farmer et al. 2024). This suggests that a certain amount of patch area is required for Coyotes to procure sufficient food resources and to produce viable offspring. Accordingly, studies have found that Coyote abundance (Crooks 2002, Crooks and Soulé 1999) and occupancy (Crooks 2002) positively correlate with patch area. Notably, Cove et al. (2023) found that Coyotes in Washington DC were detected almost exclusively in greenspaces with patch areas greater than 1 km^2 . In addition to greenspace type and patch area, a third factor that might influence the distribution of Coyotes is habitat heterogeneity. Coyotes can inhabit areas that vary in habitat heterogeneity, defined as the number of different habitat types within a greenspace (McCoy and Bell 1991). In general,

heterogenous habitats provide Coyotes with a greater variety of prey resources (Johnson and Karels 2016), sources of shelter (Hinton et al. 2015), and suitable denning sites (Althoff 1980, Raymond and St. Clair 2023) than homogenous habitats. Therefore, Coyotes are expected to select more heterogenous greenspaces, especially during the pup-rearing season (Chamberlain et al. 2021).

Two anthropogenic features surrounding urban greenspaces that might influence the distribution (occupancy and detection probability) of Coyotes are human population density and percentage of developed land. The relationship between Coyote distribution and these two features is complex, as Coyotes are thought to be both attracted to and apprehensive of urban environments (Gehrt et al. 2009, Poessel et al. 2016). Coyotes are sometimes attracted to highly urbanized areas because in these environments they can supplement their diets with anthropogenic food resources (Henger et al. 2022, Larson et al. 2020, Morey et al. 2007, Newsome et al. 2015, Sugden et al. 2021). For example, Newsome et al. (2015) found that up to 50% of Coyotes' diets in Chicago were comprised of human-derived food sources. However, Coyotes also tend to spatially or temporally avoid highly urbanized environments because of potential conflict with or persecution by humans (Dumond et al. 2001, Farmer and Allen 2019, George and Crooks 2006, Gese et al. 2012, Gibeau 1998, Reed and Merenlender 2011, Thompson et al. 2021, Tigas et al. 2002). For example, Parsons et al. (2018) found that Coyotes were absent from the most highly urbanized areas of Raleigh, NC and Washington, DC where human population densities were the greatest, despite having high rates of detection in the surrounding suburban and exurban areas. However, despite their apparent apprehension of humans, other studies report a positive association between Coyote distribution and measures of urbanization (Greenspan et al. 2018, Ordeñana et al. 2010, Poessel et al. 2017, Stark et al. 2020). For example, Poessel et al. (2017), based on data from 105 urban areas across the United States, found that the occurrence of Coyotes was 100% in high and medium human population size categories, but only 74% in the low human population size category. Moreover, Stark et al. (2020), in a study of four nature preserves, two in Westchester County (NY) and two in New Jersey, found a positive association between Coyote occurrence and percentage of developed land surrounding a greenspace, suggesting that greenspaces in urban and suburban areas provide refugia for these animals. Based on previous literature, we might expect that the anthropogenic factors proximate to urban greenspaces, including human population density and percentage of developed land, to positively correlate with Coyote occupancy and detection probability. However, how these factors influence the distribution of Coyotes in the New York metropolitan area is largely unknown.

The distribution (occupancy and detection probability) of Coyotes might fluctuate between the pup-rearing (PR) and non-pup-rearing (NPR) seasons, and the direction and intensity of anthropogenic and ecological drivers are predicted to differ between these two periods (Nagy et al. 2016). The pup-rearing season occurs from approximately April 1st to September 30th and is characterized by the establishment of a den and the nursing and weaning of pups, whereas the non-pup-rearing season extends from approximately October 1st to March 31st and is characterized by the dispersal of sexually mature Coyotes from their natal territories and the transient behavior of adults searching for food (Gehrt et al. 2009, Nagy et al. 2016, Way et al. 2001). The distribution of Coyotes has been found to fluctuate between pup-rearing and non-pup-rearing seasons (Nagy et al. 2016). For example, Nagy et al. (2016) documented higher rates of occupancy and detection probability for Coyotes during the non-pup-rearing season than the pup-rearing season. These differences can be attributed to seasonal fluctuations in the activity patterns of Coyotes (Harrison and Gilbert 1985, Person and Hirth 1991). During the non-pup-rearing season, dispersing Coyotes tend

to travel further distances and to utilize urban environments as they search for anthropogenic food resources (Chamberlain et al. 2021, Gese et al. 2012). Conversely, during the pup-rearing season, Coyotes tend to be less mobile (Gese et al. 2012, Harrison and Gilbert 1985, Parker and Maxwell 1989), and despite the higher metabolic demands for milk production, they maintain proximity to pups, selecting greenspaces with dense vegetation cover (Althoff 1980, Raymond and St. Clair 2023). Because of these seasonal differences in behavior, we might expect that the habitat characteristics (greenspace type, patch area, and habitat heterogeneity) and anthropogenic features (human population density, percentage of developed land) that drive patterns of Coyote distribution to differ in their intensity and direction between the pup-rearing and non-pup-rearing seasons.

Geographic barriers to dispersal might also influence occupancy patterns of Coyotes in the New York metropolitan area. On a landscape scale, the New York metropolitan area is comprised of both continental (e.g., Bronx, Westchester) and island (e.g., Manhattan, Long Island, Randall's Island) land masses. Previous studies in this region report higher occurrences of Coyotes in the Bronx than in island locations (Nagy et al. 2016, 2017). This is likely because the New York islands, which are bound by water on all sides, potentially function as a barrier to Coyote dispersal (Bradfield et al. 2022; Nagy et al. 2016, 2017). For Coyotes to disperse from the mainland to these islands, they must either swim across large bodies of water, such as the Long Island Sound, or cross over heavily human-trafficked bridges (Bradfield et al. 2022; Nagy et al. 2016, 2017). Nevertheless, an increasing number of Coyotes have become established in the greenspaces of Long Island and Manhattan (Caragiulo et al. 2022; DeCandia et al. 2019; Henger et al. 2020; Nagy et al. 2016, 2017).

The aim of this study was to quantify Coyote distribution (occupancy and detection probability) in greenspaces of the New York metropolitan area, and to determine what factors best explain these distribution patterns. We addressed three major questions: (1) What are the overall and seasonal (pup-rearing versus non-pup-rearing season) distribution patterns of Coyotes in the New York metropolitan area? (2) How has the distribution of Coyotes in the greenspaces of the New York metropolitan area changed over time? (3) What factors contribute to Coyote occupancy and detection probability? To address these questions, we set up motion-activated cameras in 31 greenspaces in the New York metropolitan area from 2015 to 2019 and compared our findings to a previous survey that occurred from 2011 to 2014 (Nagy et al. 2016). We hypothesized that Coyotes would continue their range expansion and therefore predicted that the number of greenspaces occupied by Coyotes would increase in comparison to previous surveys. We hypothesized that the distribution of Coyotes would be influenced by multiple factors, including different habitat characteristics of urban greenspaces, the anthropogenic features surrounding urban greenspaces, and observed seasonal differences in Coyote behavior. Specifically, we predicted that Coyote occupancy and detection probability during pup-rearing seasons would be higher in urban natural greenspaces with larger patch areas and more habitat heterogeneity. Moreover, we predicted that Coyote occupancy and detection probability during the pup-rearing seasons would be higher in greenspaces surrounded by neighborhoods with lower human population densities and less developed land cover. For each of these habitat characteristics and anthropogenic features, we predicted the opposite pattern during the non-pup-rearing seasons when Coyotes presumably range more widely. Considering that geographical barriers between the mainland and islands potentially impede Coyote dispersal (Bradfield et al. 2022; Nagy et al. 2016, 2017), we also predicted that Coyote occupancy would be higher on the mainland (Bronx) than on the islands (Long Island, Manhattan, and Randall's Island).

Methods

Study population and field sites

This research is the second in a series of analyses focused on examining the distribution patterns (occupancy and detection probability) of Coyotes in the New York metropolitan area (Fig. 1; see Supplemental File 1, available online at <https://eaglehill.us/urnaonline/suppl-files/urna-243-Habig-sl.pdf>). The first analysis was based on data collected between 2011–2014 (Nagy et al. 2016). For each of these four years, Coyotes were studied in 10 to 13 greenspaces in the New York boroughs of Bronx, Queens, Manhattan, and Brooklyn. The current study concentrates on data collected between 2015–2019. For each of these four years, Coyotes were studied in 31 greenspaces across the New York metropolitan area (Table 1). Sixteen of the 31 greenspaces were in Long Island: 12 in Queens County, 3 in Kings County (Brooklyn), and 1 in Nassau County. Nine greenspaces were in the Bronx, 5 in Manhattan, and 1 in Randall's Island. We compare our findings from the 2015–2019 dataset (current study) to the previous survey that occurred from 2011–2014 (Table 1).

Camera Surveys

We adopted field sampling protocols from Nagy et al. (2016). During the survey period (2015–2019), we deployed 138 camera traps across 31 greenspaces in the New York metropolitan area (Fig. 1; Supplemental File 1). We used 3 different types of heat-and motion-activated Reconyx cameras: RC55, PC800, and HC500 (Reconyx, Inc., Holmen, WI, United

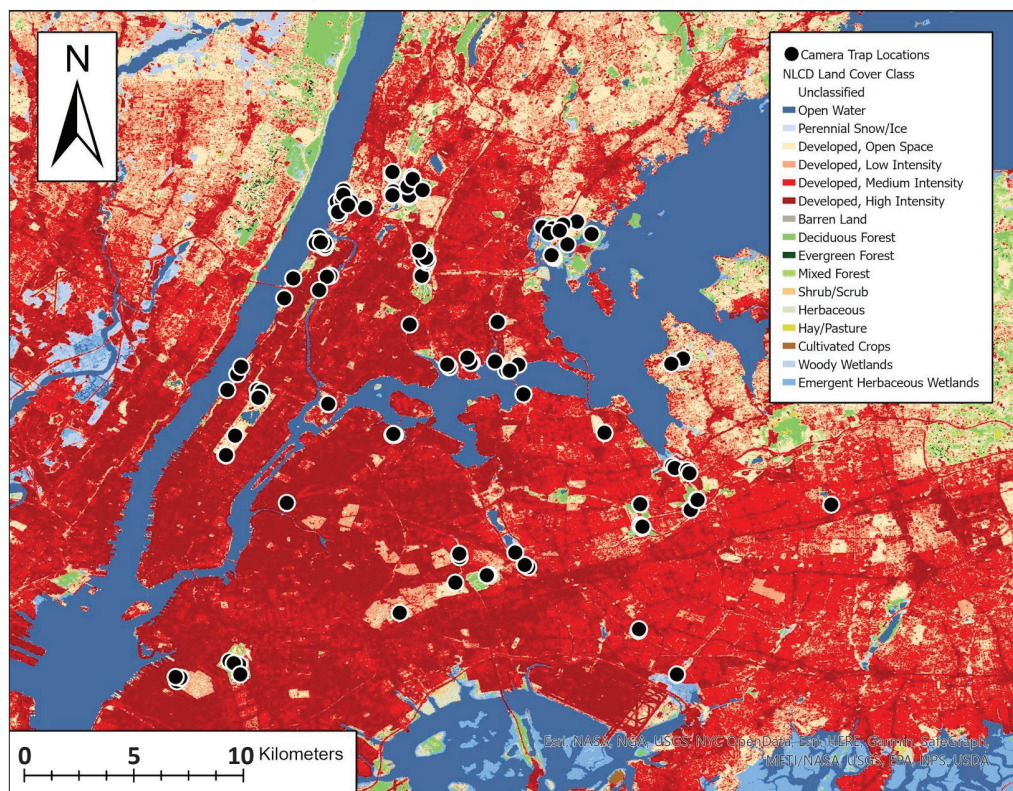


Figure 1. Map of camera trap locations where Coyotes were surveyed and land use characteristics across 31 greenspaces in the New York metropolitan area, 2015–2019.

Table 1. Detections of adult Coyotes or adult Coyotes and Coyote pups during the pup-rearing (PR) and non-pup-rearing (NPR) seasons from a historical survey conducted from 2011–2014 (Nagy et al. 2016) and from the current study, 2015–2019.

Study Site	County	Data collected from Nagy et al. (2016)						Data from the current study						
		PR (2011)	NPR (2012)	PR (2012)	NPR (2013)	PR (2013)	NPR (2014)	PR (2016)	NPR (2016)	PR (2017)	NPR (2017)	PR (2018)	NPR (2018)	PR (2019)
Bronx Park	BX	0	X	X	1	1	1	2	1	1	1	1	1	1
Ferry Point Park	BX	X	1	0	1	0	1	2	1	1	2	0	1	1
Hutchinson	BX	X	X	X	X	X	X	X	0	0	0	0	0	0
Pelham Bay Park	BX	2	1	2	1	1	1	2	1	1	1	1	1	1
Pugsley Creek Park	BX	1	1	0	1	0	1	0	1	2	1	0	0	0
Riverdale Park	BX	1	1	1	1	0	1	1	1	2	1	1	1	1
Soundview Park	BX	X	X	X	X	X	X	X	X	1	0	1	1	0
Starlight Park	BX	X	X	X	X	X	X	X	0	0	X	X	X	X
Van Cortlandt Park	BX	1	1	2	1	2	1	2	1	1	1	1	1	1
Green-wood Cemetery	K	X	X	X	X	X	X	X	0	0	0	0	0	0
Marine Park	K	0	X	X	X	X	X	X	X	X	X	X	X	X
Prospect Park	K	X	X	X	X	X	X	X	X	X	0	0	0	0
Ridgewood Highland	K	0	X	X	X	X	X	X	0	0	0	0	X	X
Kings Point Park	NAS	X	X	X	X	X	X	X	X	0	X	X	X	X
Central Park	NY	X	X	X	X	X	X	X	0	0	0	X	X	X
Fort Washington Park	NY	X	X	X	X	X	X	X	0	0	X	X	X	X
Highbridge Park	NY	X	X	X	X	X	X	X	X	X	0	X	X	X
Inwood Hill Park	NY	0	1	0	1	0	0	0	0	0	1	0	0	0
Randall's Island	NY	X	X	X	X	X	X	X	0	0	0	0	0	0
Riverside Park	NY	X	X	X	X	X	X	X	0	0	0	0	0	0

Table 1 continued. Detections of adult Coyotes or adult Coyotes and Coyote pups during the pup-rearing (PR) and non-pup-rearing (NPR) seasons from a historical survey conducted from 2011–2014 (Nagy et al. 2016) and from the current study, 2015–2019.

Study Site	County	Data collected from Nagy et al. (2016)						Data from the current study						
		PR (2011)	NPR (2012)	PR (2012)	NPR (2013)	PR (2014)	NPR (2014)	PR (2016)	NPR (2016)	PR (2017)	NPR (2017)	PR (2018)	NPR (2018)	PR (2019)
Alley Pond Park	Q	0	0	0	0	0	0	0	0	0	0	0	0	0
Clearview Golf Course	Q	X	X	X	X	X	X	0	0	0	0	0	0	0
Cunningham Park	Q	0	0	0	0	0	X	0	0	0	0	0	0	0
Elmjack Ingrams Field	Q	X	X	X	X	X	X	X	2	1	1	0	0	1
Forest Park	Q	X	X	X	X	X	X	X	0	0	0	0	0	0
Francis Lewis Park	Q	X	X	X	X	X	X	X	0	0	0	0	0	X
Idlewild Park	Q	0	X	X	X	X	X	0	0	0	0	0	0	X
Kissena Park	Q	0	X	X	X	X	X	X	X	X	X	X	X	X
Maple Grove Cemetery	Q	X	X	X	X	X	X	X	0	0	0	0	0	0
Queensline	Q	X	X	X	X	X	X	X	1	0	0	0	0	0
Railroad Park	Q	1	1	1	1	1	1	1	1	1	0	0	1	1
Smiling Hogshead Ranch	Q	X	X	X	X	X	X	X	X	X	0	0	0	X
Willow Lake	Q	X	X	X	X	X	X	X	0	0	0	X	X	X

BX = Bronx County; K = Kings County (Brooklyn); NAS = Nassau County; NY = New York County (Manhattan); Q = Queens County; NPR = non-pup-rearing season; PR = pup-rearing season; 0 = no detections; 1 = adult Coyote detections; 2 = adult Coyote and pup detections, "X" = site was not surveyed that season

BX = Bronx County; K = Kings County (Brooklyn); NAS = Nassau County; NY = New York County (Manhattan); Q = Queens County; NPR = non-pup-rearing season; PR = pup-rearing season; 0 = no detections; 1 = adult Coyote detections; 2 = adult Coyote and pup detections; "X" = site was not surveyed that season

States). All 3 cameras were programmed with the same trigger speed (0.2 s), trigger count (3 images in succession), and resolution (1080 p). The infrared flash ranges were similar among the 3 cameras (RC55 and HC500: 15 m, PC800: 21 m). The RC55 cameras included 2 models; an older version with 5.0 x 7.6 cm red/infrared flash for nighttime photography, and a newer version with a single LED bulb for “semi-covert” infrared flash.

Within the 31 greenspaces of the New York metropolitan area, camera trap locations were randomly selected using ArcGIS 9 and ArcGIS10 (ESRI, Redlands, CA, United States). Cameras were deployed either year-round, or more commonly, from January through April and again from June through August (Supplemental File 1). These two time-spans allowed for maximum detection of seasonally active Coyotes, including those dispersing during the winter months (Nagy et al. 2016). The number of cameras deployed at each greenspace ranged from 1 to 31 (Supplemental File 1) and was based on the patch area of each location. In most cases, there was at least one camera deployed every 0.5 km². At each camera trap location, we mounted a camera to a tree approximately 0.5 m above the ground. Some cameras were relocated within ~50 m due to legal complications, vandalism, theft, or for a more suitable placement. Following the survey period, we collected secure digital (SD) cards from each camera and used a Microsoft Access database originally designed for Colorado Parks and Wildlife (CPW Photo Warehouse; Ivan and Newkirk 2016) to record Coyote presence and the time and date of each detection.

Occupancy modeling

We used single season occupancy modeling to estimate Coyote occupancy and detection probability across camera trap locations. Occupancy was defined as the probability that a Coyote is present at a respective camera location, whereas detection probability was defined as the probability of observing a Coyote if it is known to occupy a camera location (Parsons et al. 2018). For each camera trap day, we coded the presence of a Coyote at a camera location with the number 1, the absence of a Coyote at a camera location with a 0, and missing data due to camera malfunction or absence of a camera as NA. The data were divided into pup-rearing seasons and non-pup-rearing seasons to account for seasonal fluctuations in Coyote activity. Pup-rearing seasons took place from 1 April–30 September of each year, while non-pup-rearing seasons occurred from 1 October–31 March (Gehrt et al. 2009, Nagy et al. 2016, Way et al. 2001). Occupancy models of non-pup-rearing seasons included four seasons of data (2015–2016; 2016–2017; 2017–2018; 2018–2019); occupancy models of pup-rearing seasons also included four seasons of data (2016; 2017; 2018; 2019). We compared our estimates of occupancy to data collected from 2011–2014 (Nagy et al. 2016), which allowed us to estimate how the overall distribution of Coyotes has changed over time.

Multiple parameter models

We used multiple parameter models to assess factors that might influence Coyote occupancy and detection probability. For these models, we included four possible response variables: occupancy during the (1) pup-rearing season (1 April–30 September) and (2) non-pup-rearing season (1 October–31 March), and detection probability during the (3) pup-rearing season (1 April–30 September) and (4) non-pup-rearing season (1 October–31 March).

For each of the 4 occupancy and detection probability response variables, we modeled three habitat characteristics of urban greenspaces (greenspace type, patch area, habitat heterogeneity) and two anthropogenic features surrounding urban greenspaces (human population density, percentage of developed land cover) as predictor variables. For the 2 occupancy response variables, we also modeled one geographic feature (landmass type) as

a predictor variable. Each of the predictor variables is described below:

Greenspace type: A greenspace was classified as either *human-altered* (> 50% of the area is comprised of human-modified spaces such as playgrounds, athletic fields, manicured lawns, and golf courses) or *urban natural* (> 50% of the area has been minimally modified by humans such as secondary growth forests, wetlands, and grasslands) (Bradfield et al. 2022, 2025; Gallo et al. 2017). The relative areas of greenspace were hand digitized using the “measure distance” tool over aerial photographs in Google maps (<https://www.google.com/maps>).

Patch area: The area of a greenspace calculated with the “measure distance” tool in Google maps (<https://www.google.com/maps>) by manually tracing the perimeter of the greenspace and converting this output to km².

Habitat heterogeneity: The number of different habitat types visually counted within a 500 m circular buffer at the center of each greenspace based on 4 broad habitat categories (greenspace, developed land, wetlands, barren land) as defined by the 2019 National Land Cover Database (DeWitz 2020), calculated in ArcGIS Pro 2.6. We converted the buffers to raster layers using the Polygon to Raster tool to maintain the same grid size (30 m resolution) as the NLCD layer.

Human population density: The number of humans per km², based on 2020 census data, in the zip code in which a greenspace is situated (<https://www.unitedstateszipcodes.org>) (Bradfield et al. 2022, 2025; Mahmud et al. 2024). If the greenspace extended across multiple zip codes, then the average human population density was calculated among these zip codes (Bradfield et al. 2022). We log-transformed human population to reduce outlier influence (Choi et al. 2022).

Percentage of developed land cover: The percentage of combined low intensity, medium intensity, and high intensity development within a 1 km circular buffer surrounding a greenspace (Bradfield et al. 2022, 2025; Goldstein et al. 2022; Stark et al. 2020) as defined by the 2019 National Land Cover Database (DeWitz 2020), calculated in ArcGIS Pro 2.6 using the Polygon to Raster tool (ESRI, Redlands, CA).

Landmass type: The type of landmass where a greenspace was located, coded as either *island* (Long Island, Manhattan, or Randall’s Island sites), or *mainland* (Bronx sites). Because landmass type is a regional-scale variable, this measurement was modeled as a predictor variable for occupancy, but not for detection probability.

Statistical analyses

We completed all statistical analyses using R version 4.4.1 (R Core Team 2024). We used the unmarked package (Fiske and Chandler 2011) to estimate occupancy and detection probability for four distinct non-pup-rearing seasons (2015–2016; 2016–2017; 2017–2018; 2018–2019) and four distinct pup-rearing seasons (2016; 2017; 2018; 2019). For multiple parameter analyses, we created one model that combined the four pup-rearing seasons and a second model that combined the four non-pup-rearing seasons. For these two models, we used a stacked design treating each camera location–season combination as a distinct site, which allowed us to evaluate predictor variables while including sampling season as a fixed effect to account for temporal non-independence (Crum et al. 2017; Fuller et al. 2016; Goldspiel et al. 2019; Twining et al. 2022, 2024). We first tested for multicollinearity using Pearson correlation tests; we detected no problematic multicollinearity as all combinations of covariates yielded correlation coefficients less than 0.4 (Parren et al. 2022). During multiple parameter analyses, we first modeled each response variable using a global model that included all covariates. Starting with the global model, we used the “dredge” function in

the muMin package (Bartoń 2024) to test all possible covariate combinations and to rank each model based on Akaike Information Criteria (AIC). We used AIC values to determine the most parsimonious combination of occupancy and detection covariates. When two or more parameter combinations yielded a difference less than two AIC units from the best model, we used the “model.avg” function to conduct model averaging for all parameter combinations that yielded an AICc difference <2 (Burnham and Anderson 2004). We used the summed weight method (Burnham and Anderson 2004) and conditional R^2 to calculate model-averaged coefficients (Nakagawa and Schielzeth 2013), which helped to reduce the bias and unpredictability associated with selecting one “best” model (Grueber et al. 2011). We used the “PlotEffects” function to calculate marginal effect sizes holding numerical covariates at their median value and categorical covariates at their reference level, which enabled us to produce figures.

Results

Distribution of Coyotes in the New York metropolitan area

Coyotes were detected by at least 1 camera in 11 of 31 greenspaces surveyed in the New York metropolitan area. Seven of these greenspaces were located on the mainland; four were located on islands. Coyote pups were detected at 4 greenspaces, 3 of which were located in the Bronx (Ferry Point Park; Pugsley Creek Park; and Riverdale Park) and 1 in Queens (Elmjack Ingrams Field) (Fig. 2; Table 1). At the camera-site level (138 total motion-activated cameras deployed across 31 greenspaces), Coyote occupancy and detection probability varied from year-to-year across the 4 non-pup-rearing and pup-rearing seasons (see Supplemental File 2, available online at <https://eaglehill.us/urna-online/suppl-files/urna-243-Habig-s2.pdf>). Across all 8 seasons, Coyote occupancy was 14.6% higher during the non-pup-rearing ($\Psi = 0.456$) than the pup-rearing ($\Psi = 0.394$) seasons, and Coyote detection probability was 19.4% higher during the non-pup-rearing ($p = 0.085$) than pup-rearing ($p = 0.070$) seasons. Therefore, across non-pup-rearing seasons, the likelihood that a Coyote was present at a given camera trap location was 45.6% and the probability of detecting a Coyote if it was present at a given camera trap location was 8.5%. During pup-rearing seasons, the likelihood that a Coyote was present at a given camera trap location was 39.4% and the probability of detecting a Coyote if it was present at a given camera trap location was 7.0%.

Expansion of Coyotes in the New York metropolitan area

We found that Coyotes are expanding their range into additional greenspaces in the New York metropolitan area. Coyote occupancy increased from 8 greenspaces in 2011–2014 (Nagy et al. 2016) to 11 greenspaces in 2015–2019 (Table 1). In the previous survey, Coyotes were detected in 6 greenspaces in the Bronx, 1 greenspace in Long Island, and 1 greenspace in Manhattan. In the current study, Coyotes were detected in all 6 Bronx greenspaces where they were discovered previously, as well as in 1 additional greenspace: Soundview Park. Coyotes were also found in 2 additional greenspaces on Long Island, an increase from 1 to 3 greenspaces. In Manhattan, Coyotes were identified in 1 greenspace (Inwood Hill Park) in both the current and previous survey. In the current study, we also sampled a nearby island (Randall’s Island), but no Coyotes were detected at this location.

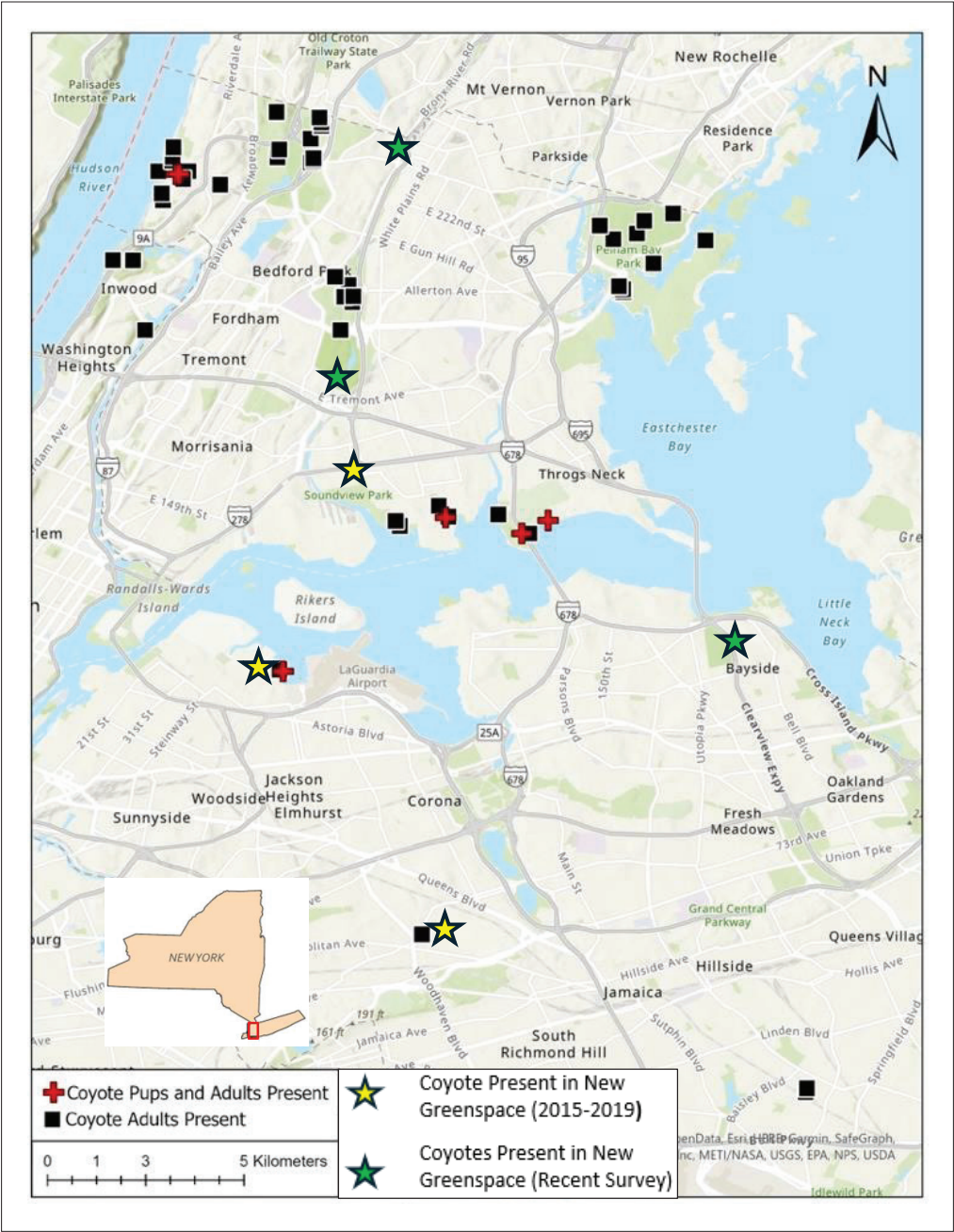


Figure 2. Camera trap locations where adult Coyotes and Coyote pups were detected across 31 greenspaces in the New York metropolitan area, 2015–2019. Black squares indicate camera locations in which adult Coyotes were present in the current study. Red plus marks indicate camera locations in which both adult Coyotes and pups were present in the current study. Yellow stars indicate three greenspaces (Elmjack Ingrams Field, Soundview Park, and Queensline) in which coyotes were present in the current study, but not in previous surveys. Green stars represent three additional greenspaces in which coyotes are now present based on recent research (Henger et al. 2020: Alley Pond Park, Nath et al. 2025: Muskrat Cover Park, Mitsubishi River Walk).

Predictors of Coyote occupancy in the New York metropolitan area

Two of the three habitat characteristics were statistically significant predictors of Coyote occupancy: (1) greenspace type (non-pup-rearing seasons only) and (2) habitat heterogeneity (pup-rearing seasons only) (Table 2; see Supplemental File 3, available online at <https://eaglehill.us/urnaonline/suppl-files/urna-243-Habig-s3.pdf>). Specifically, during the non-pup-rearing seasons, Coyote occupancy was higher in human-altered greenspaces than urban natural greenspaces ($\beta = -1.796$, CI: -3.217 to -0.301, $P = 0.018$; Fig. 3A; Table 2), and during the pup-rearing seasons, Coyote occupancy was higher in more heterogenous habitats than less heterogenous habitats ($\beta = 1.042$, CI: 0.375 to 1.801, $P = 0.003$; Fig. 3D; Table 2). The third modeled habitat characteristic, patch area, was not significantly associated with Coyote occupancy during either season.

Of the two anthropogenic features surrounding urban greenspaces that were assessed in this study (human population density and percentage of developed land cover), only human population density was significantly associated with Coyote occupancy, and only during non-pup-rearing seasons (Table 2; Supplemental File 3). Specifically, Coyote occupancy was higher in greenspaces surrounded by neighborhoods with higher

Table 2. Best supported model for each response variable based on model averaging. Model average coefficients, odds ratio [$\exp(\text{coefficient})$], standard error (SE), z-value, and P value are shown. Season is fixed on all models.

Response Variable	Predictor Variables	Estimate	Odds Ratio	SE	z-value	P value
Coyote occupancy (Ψ), non-pup-rearing season	Greenspace: urban natural	-1.796	0.166	0.758	2.368	0.018
	Human population density	3.705	40.650	1.823	2.032	0.042*
	Landmass: continent	3.416	30.447	0.700	4.882	<0.001***
	Percent developed land cover	-1.774	0.170	1.232	1.440	0.150
Coyote detection probability (p), non-pup-rearing season	Greenspace: urban natural	1.717	5.568	0.246	6.976	<0.001***
	Habitat heterogeneity	0.832	2.298	0.130	6.380	<0.001***
	Human population density	-5.689	0.003	0.645	8.826	<0.001***
	Patch area	-0.223	0.800	0.047	4.782	<0.001***
	Percent developed land cover	1.439	4.216	0.256	5.612	<0.001***
Coyote occupancy (Ψ), pup-rearing season	Habitat heterogeneity	1.042	2.835	0.350	2.975	0.003**
	Landmass: mainland	3.239	25.508	0.497	6.514	<0.001***
	Patch area	0.173	1.189	0.148	1.171	0.241
Coyote detection probability (p), pup-rearing season	Greenspace: urban natural	0.340	1.405	0.275	1.237	0.216
	Habitat heterogeneity	0.283	1.327	0.198	1.426	0.154
	Human population density	-1.909	0.148	0.660	2.891	0.004**
	Patch area	-0.239	0.787	0.057	4.222	<0.001***
	Percent developed land cover	0.010	1.010	0.003	2.960	0.003**

* Denotes significance $P < 0.05$; ** Denotes significance $P < 0.01$; *** Denotes significance $P < 0.001$

human population densities ($\beta = 3.705$, CI: 0.072 to 7.108, $P = 0.042$; Fig. 3B; Table 2). The percentage of developed land cover surrounding urban greenspaces was not significantly associated with Coyote occupancy during either season.

The one geographic feature that we modeled (landmass type) significantly predicted Coyote occupancy during both the non-pup-rearing and pup-rearing seasons. Specifically, Coyote occupancy was higher in greenspaces located on the mainland (Bronx) than on islands (Manhattan, Long Island, Randall's Island) (NPR: $\beta = 3.416$, CI: -4.604 to -1.954, $P < 0.001$, Fig. 3C, Table 2; PR: $\beta = 3.239$, CI: -4.127 to -2.170; $P < 0.001$; Fig. 3E; Table 2).

Predictors of Coyote detection probability in the New York metropolitan area

Three habitat characteristics were statistically significant predictors of Coyote occupancy: (1) patch area, (2) habitat heterogeneity (non-pup-rearing seasons only); and (3) greenspace type (non-pup-rearing seasons only) (Table 2; Supplemental File 3). Specifically, Coyote detection probability was higher in greenspaces with smaller patch areas during both seasons (NPR: $\beta = -0.223$, CI: -0.291 to -0.104, $P < 0.001$, Fig. 4A, Table 2; PR: $\beta = -0.239$; CI: -0.332 to -0.1229; $P < 0.001$, Fig. 5A, Table 2). During the non-pup-rearing seasons, Coyote detection probability was higher in more heterogeneous habitats than less heterogeneous habitats ($\beta = 0.832$, CI: 0.727 to 1.275, $P < 0.001$; Fig. 4B; Table 2), and in urban natural greenspaces than human-altered greenspaces ($\beta = 1.717$, CI: 1.327 to 2.315, $P < 0.001$; Fig. 4C; Table 2).

Both anthropogenic features surrounding urban greenspaces were significantly as-

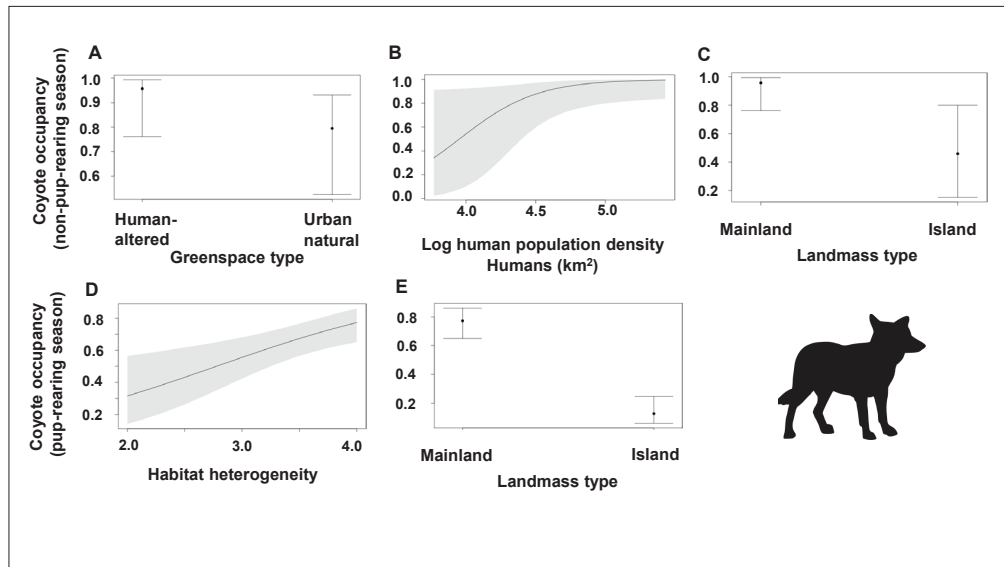


Figure 3. Predicted associations of Coyote occupancy with respect to (A) greenspace type, (B) log human population density, and (C) landmass type during the non-pup rearing seasons; predicted associations of Coyote occupancy with respect to (D) habitat heterogeneity and (E) landmass type during the pup-rearing seasons. Points and whiskers (A, C, E) represent the mean and SE. Shaded gray areas (B, D) indicate 95% confidence intervals. Data based on analysis of Coyote occupancy across 31 greenspaces in the New York metropolitan area, 2015–2019.

sociated with Coyote detection probability during both the non-pup-rearing and pup-rearing seasons: (1) human population density and (2) the percentage of developed land cover (Table 2; Supplemental File 3). Specifically, Coyote detection probability was higher in greenspaces surrounded by neighborhoods with lower human population densities (NPR: $\beta = -5.689$, CI: -7.272 to -4.643 , $P < 0.001$, Fig. 4D, Table 2; PR: $\beta = -1.909$, CI: -3.919 to -1.229 , $P = 0.004$, Fig. 5B, Table 2), and in greenspaces surrounded by more developed land cover (NPR: $\beta = 1.439$, CI: 0.010 to 0.021 , $P < 0.001$, Fig. 4E, Table 2; PR: $\beta = 0.010$, CI: 0.005 to 0.019 , $P = 0.003$, Fig. 5C, Table 2).

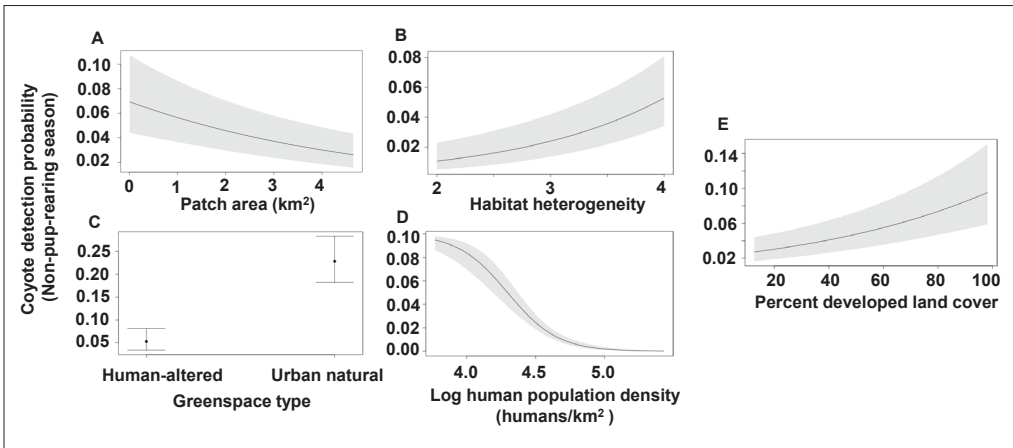


Figure 4. Predicted associations of Coyote detection probability with respect to (A) patch area, (B) habitat heterogeneity, (C) greenspace type, (D) log human population density, and (E) percent developed land cover during the non-pup-rearing seasons across 31 greenspaces in the New York metropolitan area, 2015–2019. Shaded gray areas (A, B, D, E) indicate 95% confidence intervals. Points and whiskers (C) represent the mean and SE.

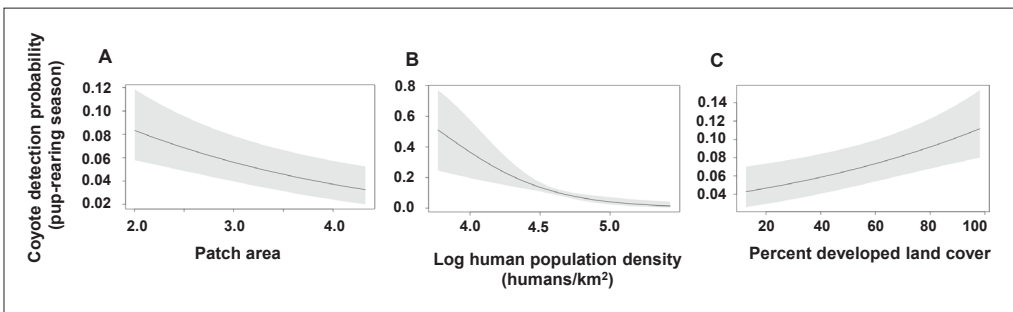


Figure 5. Predicted associations of Coyote detection probability with respect to (A) patch area, (B) log human population density, and (C) percent developed land cover during the pup-rearing seasons across 31 greenspaces in the New York metropolitan area, 2016–2019. Shaded gray areas indicate 95% confidence intervals.

Discussion

Our analyses revealed that Coyotes are expanding their range and now make use of at least 11 major greenspaces in the New York metropolitan area, and that several factors are associated with their distribution patterns. Both Coyote occupancy and detection probability were higher during non-pup-rearing seasons than pup-rearing seasons, which supports the hypothesis that Coyotes shift their behavior during reproductive months (Grinder and Krausman 2001, Harrison and Gilbert 1985, Nagy et al. 2016, Person and Hirth 1991). In accordance with our predictions, Coyote occupancy was higher in human-altered greenspaces during non-pup-rearing seasons, and in more heterogeneous greenspaces during pup-rearing seasons. Moreover, Coyote occupancy was greater on the mainland (Bronx County) than on nearby islands (Long Island, Manhattan, and Randall's Island) across both seasons. Additionally, there were several habitat characteristics and anthropogenic features that were significantly associated with Coyote detection probability, but not always in the direction predicted at the onset of the study. During both pup-rearing and non-pup-rearing seasons, Coyote detection probabilities were higher in greenspaces with smaller patch areas that were surrounded by neighborhoods with relatively lower human population densities and more developed land cover. Contrary to our predictions, during the non-pup-rearing seasons, Coyote detection probability was higher in more heterogeneous habitats, and in urban natural greenspaces rather than human-altered greenspaces. We elaborate on our key findings in the sections below.

Coyotes are expanding their range in the New York metropolitan area

Surveys dating back to 2011 indicate a long-term trend in which Coyotes have incrementally increased their total range in the New York metropolitan area. The first major survey of Coyote distribution patterns in New York City was conducted from 2011–2014 (Nagy et al. 2016), and in this study, Coyotes were present in 8 of 13 urban greenspaces: 6 greenspaces in the Bronx, 1 in Queens, and 1 in Manhattan. In the current study (2015–2019 dataset), we documented Coyotes in 11 of 31 urban greenspaces across the New York metropolitan area, including all 8 sites where they were documented during the previous survey (Nagy et al. 2016). While our documentation of the expansion of Coyotes into additional urban greenspaces is quite modest and possibly transitory, our long-term data suggest otherwise: Once Coyotes occupy a greenspace, they tend to remain there from year-to-year (Table 1). Moreover, an overall pattern of expansion is evident given the temporal pattern of documentation of Coyote occupancy in New York City (2011–present), and more recently, on Long Island (Nagy et al. 2016, 2017; Weckel et al. 2015).

Coyotes were present in 7 of the 9 greenspaces surveyed in the Bronx. An even more recent study of mammalian diversity along the Bronx River (Nath et al. 2025), documented Coyotes in 2 additional greenspaces in the Bronx not included in previous surveys: Muskrat Cove and Mitsubishi River Walk (Fig. 2). This brings the total number of urban greenspaces where Coyotes were documented in the Bronx to 9. In the current study, we detected Coyote pups at 3 of the Bronx greenspaces. In 2 of these greenspaces, Riverdale Park and Soundview Park, Coyote pups were detected for the first time (Table 1). However, there were three greenspaces (Bronx Park, Pelham Bay Park, and Van Cortland Park) where Coyote pups were detected in the 2011–2014 survey (Nagy et al. 2016), but not in the current study. Because pups largely remain in their den (Nagy et al. 2016), it is possible that pups were present at these sites, especially given the long-term persistence of Coyotes at these locations, but we cannot rule out the possibility that there were no pups present at these greenspaces between 2015–2019.

Coyotes were not detected on Randall's Island and were present in only 1 of the 5 greenspaces surveyed in Manhattan. These findings suggest that potential barriers to dispersal, including waterways and heavily trafficked roads, might be limiting their dispersal (Bradfield et al. 2022). However, Coyotes were present in Inwood Hill Park, which is located on the northern tip of Manhattan, both in the 2011–2014 survey (Nagy et al. 2016) and in the current study. Unlike the other Manhattan greenspaces, Inwood Hill Park is the only Manhattan site comprised of extensive old growth forest and naturally derived vegetation (Fitzgerald and Loeb 2008; Loeb 1986). The 4 Manhattan greenspaces where Coyotes were absent (Central Park, Fort Tryon Park, Highbridge Park, and Riverside Park) are highly modified landscapes created by the large-scale cultivation of both native and non-native trees and landscape plants; these greenspaces are also intersected by numerous pathways (Loeb 1986). Moreover, the urban greenspaces in Manhattan are situated in “super urban” areas, locations characterized by unusually immense infrastructure and exceedingly high human population density (DeCandia et al. 2019). These modified landscapes within a “super urban” matrix potentially pose challenges for Coyote dispersal and colonization (DeCandia et al. 2019). Despite these apparent barriers to dispersal and the challenges of traversing a “super-urban” matrix, a pair of Coyotes have recently colonized Central Park (C. Nagy, Mianus River Gorge, Bedford, NY, unpubl. data).

Our results also suggest that Coyotes are becoming increasingly established in their “final frontier”: Long Island, New York (Weckel et al. 2015). Long Island, which has a total area of about 3,645 km², consists of about 310 km of coastline that extends into the Atlantic Ocean (Pluhowski 1970). Two boroughs of New York City, Queens County and Kings County (Brooklyn) comprise the western portion of Long Island, whereas Nassau County and Suffolk County cover the eastern portion. In the current study, we did not conduct surveys in Suffolk County, and we only set up cameras in 1 greenspace in Nassau County (Kings Point Park); however, our surveys included 13 greenspaces in Queens and 4 greenspaces in Brooklyn, thus making it the largest survey of Coyotes on Long Island to date. Of these 18 Long Island locations, Coyotes were documented in 3 urban greenspaces, all located in Queens. Thus, the results of this study represent an increase in the presence of Coyotes in Long Island from 1 greenspace (Nagy et al. 2016) to 3 greenspaces (current study). Moreover, a recent scat analysis conducted by Henger et al. (2020) indicates that Coyotes are now present in 1 additional Long Island location: Alley Pond Park (Queens). Notably, Coyotes were not documented in Alley Pond Park in the previous (2011–2014) or current (2015–2019) surveys, which suggests that their presence is relatively recent. Lastly, surveys since 2020 have found Coyotes in Kings Point Park and have detected pups in Alley Pond Park (C. Nagy, Mianus River Gorge, Bedford, NY, unpubl. data). Thus, there is compelling evidence that Coyotes are expanding their range on Long Island. However, it should be noted that Coyotes were absent from most Long Island survey locations in the current study, a finding likely attributed to both anthropogenic development and physical barriers to dispersal (Bradfield et al. 2022, Curtis et al. 2007, Fener et al. 2005, Toomey et al. 2012, Weckel et al. 2015).

Coyote occupancy is influenced by greenspace type, habitat heterogeneity, and human population density

Coyote occupancy was influenced by different factors during non-pup-rearing seasons than during pup-rearing seasons. First, during non-pup-rearing seasons, Coyote occupancy was significantly higher in human-altered greenspaces than urban natural greenspaces and in greenspaces surrounded by neighborhoods with higher human population densities.

These results are consistent with our predictions and are aligned with previous research showing that dispersing Coyotes tend to utilize human-altered habitats to search for anthropogenic food sources during non-pup-rearing seasons (Chamberlain et al. 2021, Gese et al. 2012). Because the non-pup-rearing season also includes the breeding season, a period characterized by greater movement patterns by the dominant breeding pair than at any other time of the year (Lukasik and Alexander 2011, Way et al. 2004), this might also explain why Coyotes were more likely to be found in anthropogenic habitats during this period, especially given that humans tend to be less active during the winter months (Ferguson et al. 2021).

Second, during the pup-rearing seasons, Coyote occupancy was significantly higher in more heterogeneous habitats than less heterogeneous habitats. This finding is also consistent with our predictions and aligns with previous research showing that the presence of more habitat types allows Coyotes opportunities to find more suitable locations for Coyote dens, thus allowing parents to provide adequate shelter and cover for their pups (Althoff 1980, Raymond and St. Clair 2023, Way et al. 2001). Additionally, given that Coyotes move less during the pup-rearing season (Gese et al. 2012, Harrison and Gilbert 1985, Parker and Maxwell 1989), the exploitation of heterogeneous habitats helps them to improve their foraging efficiency and to acquire food and resources needed for their pups (Chamberlain et al. 2021, Gese et al. 2012, Hernández and Laundré 2003, Poessel et al. 2014).

Finally, two of the five covariates (patch size and percentage of developed land) were not significantly associated with Coyote occupancy in either the non-pup-rearing or pup-rearing seasons. Given the recency of Coyote arrival on Long Island, their occupancy patterns may not yet reflect their habitat preferences. Nonetheless, our overall findings indicate that Coyotes fluctuate their activity patterns and habitat choices between non-pup-rearing and pup-rearing seasons, selecting heterogeneous habitats when they're raising pups (Althoff 1980, Raymond and St. Clair 2023, Way et al. 2001) and apparently seeking out anthropogenic food resources in human-altered greenspaces following dispersal (Chamberlain et al. 2021, Gese et al. 2012).

Coyote occupancy is influenced by geography

Consistent with our initial prediction, Coyote occupancy was significantly higher on the mainland than on islands. Indeed, Coyotes were documented in 7 of 9 (77.8%) greenspaces located on the mainland (Bronx) but were recorded in only 4 of 22 (18.2%) greenspaces situated on islands (Manhattan: 1 of 5 [20.0%] greenspaces; Randall's Island: 0 of 1 [0.00%] greenspace; Long Island: 3 of 16 [18.8%] greenspaces). This finding suggests that biogeographical barriers, including the Long Island Sound and heavily human-trafficked bridges, continue to hinder the expansion of Coyotes (Bradfield et al. 2022; Nagy et al. 2016, 2017). However, the presence of Coyotes in 3 Long Island greenspaces, including the documentation of pups in 1 location (Nagy et al. 2017), suggests that at least some Coyotes are either swimming across waterways or crossing major bridges, making the difficult journey to new habitats (Henger et al. 2020, Nagy et al. 2016). Indeed, Coyotes have colonized numerous islands throughout North America (e.g., Cat and South Islands, SC: Etheredge et al. 2015; Aquidneck and Conanicut Islands, RI: Mitchell et al. 2015; Beaver Island, MI: Ozoga and Harger 1966). Coyotes have even been documented in Key Largo, Florida, apparently crossing over one of two bridges connecting the mainland to the island (Greene and Gore 2013). Long Island, New York, therefore, represents one of the last remaining large landmasses in the United States where Coyotes can expand their range (Weckel et al. 2015).

Habitat characteristics and anthropogenic features associated with Coyote detection probability

Three habitat characteristics and two anthropogenic features surrounding urban greenspaces were significantly associated with Coyote detection probability, but not always in the direction we predicted at the onset of the study. In terms of habitat characteristics, we found that Coyotes were more likely to be detected in greenspaces with smaller patch areas during both non-pup-rearing and pup-rearing seasons. Because greenspaces with smaller patches have less available area for Coyotes to roam, perhaps Coyotes were more easily detected by our cameras as their activity was concentrated within a smaller area. Additionally, smaller mammals tend to inhabit relatively smaller habitat patches (Crooks and Soulé 1999, Ekernas and Mertes 2006); therefore, the availability of prey might explain why Coyotes were more likely to be detected in greenspaces with smaller patch areas. Contrary to our predictions, we found that during the non-pup-rearing seasons, Coyotes were more likely to be detected in heterogenous than homogeneous habitats, and in urban natural greenspaces than in human-altered greenspaces. We expected dispersing Coyotes to be detected in anthropogenic habitats (homogenous habitats and human-altered greenspaces) during the non-pup-rearing season given that Coyotes tend to use these habitats more often following dispersal (Chamberlain et al. 2021, Gese et al. 2012). However, in large urban areas, dispersing Coyotes tend to avoid areas heavily populated by humans (Dumond et al. 2001, Farmer and Allen 2019, George and Crooks 2006, Gese et al. 2012, Gibeau 1998, Reed and Merenlender 2011, Thompson et al. 2021, Tigas et al. 2002). This suggests that Coyotes might avoid certain areas if it passes an absolute threshold of human disturbance, which could potentially explain why dispersing Coyotes were more likely to be detected in areas with relatively lower human activity: heterogeneous habitats and urban natural greenspaces (Gallo et al. 2017). Thus, in “super urban” areas with unusually high levels of human disturbance (DeCandia et al. 2019), dispersing Coyotes might select heterogenous habitats and urban natural greenspaces to potentially avoid conflict with humans.

In terms of the anthropogenic features surrounding urban greenspaces, we found that Coyote detection probability was negatively associated with human population density and positively associated with the percentage of developed land cover. This was the case for both non-pup-rearing and pup-rearing seasons. One hypothesis that might explain these contrasting findings is that increased human activity might deter Coyotes to a greater extent than landscape features or habitat conditions. In support of this idea, several studies have found that the activity patterns of Coyotes increase when there are fewer humans present (Farmer and Allen 2019, Gese et al. 2012, Poessel et al. 2016, Thompson et al. 2021). However, Coyotes might not be deterred from highly developed areas if there is relatively less human activity. In the current study, we found that certain greenspaces in the Bronx are surrounded by commercial and industrial structures, and therefore have high percentages of developed land cover, but they are also situated in neighborhoods with relatively lower human population densities compared to other study locations. An alternative hypothesis that might explain why Coyotes were more likely to be detected in areas surrounded by higher percentages of development is the urban refugia hypothesis (e.g., Bradfield et al. 2022, 2025; Goldstein et al. 2022, Stark et al. 2020), the idea that urban greenspaces serve as refuges from the surrounding built environment. In support of this hypothesis, Coyotes have been found to restrict the bulk of their activity within the greenspaces that they occupy and largely avoid the surrounding anthropogenic environments (Gehrt et al. 2009). Moreover, Stark et al. (2020) found that Coyotes and other carnivores were more likely to be detected in greenspaces surrounded by higher levels of development. Taken together, our results

suggest that Coyotes are probably more active in greenspaces where they are less likely to encounter humans and might restrict themselves within their greenspace if the surrounding neighborhoods have extreme levels of development.

Limitations

We recognize that there were some limitations to the current study. First, relationships between occupancy and covariates can be interpreted as habitat selection or habitat suitability. However, these model predictions do not distinguish between occupied greenspaces that harbored a single Coyote versus a pack, nor do they indicate successful reproduction. Second, because we did not tag individual animals, but instead relied on camera detections, we were unable to identify individual Coyotes. Therefore, our estimates of detection probability provide information on the likelihood of observing a Coyote if it occupies a camera trap location, but it does not provide any information on the relative abundance of Coyotes among occupied greenspaces. Third, because we used coarse measurements to estimate habitat heterogeneity and greenspace type, this limits our ability to compare fine scale differences, such as vegetation composition, between greenspaces. Finally, our sampling on Long Island was restricted to the westernmost locations (13 greenspaces in Queens County, four greenspaces in King County (Brooklyn), and one greenspace in Nassau County). Therefore, the central and eastern portions of Long Island (Nassau County and Suffolk County) were essentially unrepresented in our dataset.

Conclusions and future directions

At the onset of this study, we hypothesized that Coyotes would continue their expansion into urban greenspaces in Long Island and Manhattan and that their distribution would be influenced by multiple factors, including different habitat characteristics of urban greenspaces, the anthropogenic features surrounding urban greenspaces, landmass type (mainland versus island), and observed seasonal differences in Coyote behavior. Overall, our results are largely aligned with previous studies; however, some of our findings might change the way we think about Coyotes in a “super urban” setting.

In accordance with our predictions, Coyotes have become increasingly established in the most densely populated region in the United States: the New York metropolitan area. We found that Coyotes continue to occupy all the greenspaces where they were documented in previous surveys (Nagy et al. 2016), and that they are expanding into additional urban greenspaces. Although Coyotes appear to be incrementally increasing their range, barriers to dispersal, such as large bodies of water and heavily human-trafficked bridges, appear to be tempering their expansion as evidenced by significantly higher rates of occupancy on the mainland (Bronx) than on islands (Manhattan, Randall’s Island, Long Island). As Coyotes continue their expansion into Long Island and potentially establish new breeding territories, their increased presence is predicted to have direct and indirect trophic impacts on local wildlife (Bradfield et al. 2025) and may lead to increased conflicts with humans (Nagy et al. 2017, Weckel et al. 2015).

In support of our predictions, we found that Coyotes were more likely to occupy heterogeneous habitats during the pup-rearing seasons and human-altered greenspaces during the non-pup-rearing seasons. Additionally, Coyote detection probabilities were influenced by habitat characteristics of greenspaces and the surrounding anthropogenic environment. Notably, and in contrast with our original predictions, we found possible evidence that urban greenspaces in the most highly developed areas might serve as refuges for Coyotes (Stark et al. 2020). Indeed, Coyote detection probability was significantly higher in greenspaces surrounded

by more developed land cover. These results suggest that in “super urban” areas, Coyotes possibly spend most of their time within urban greenspaces and might only venture out into human-dominated areas to procure anthropogenic-derived food resources (Gehrt et al. 2009).

In future studies, we recommend the use of radio telemetry collars (e.g., Hennessy et al. 2012, Riley et al. 2003, Shargo 1988, Thompson et al. 2021) to monitor Coyote ranging behavior in the New York metropolitan area and for reconstructing their territories, and to test whether Coyotes in a “super urban” area confine their movements to avoid humans. We also recommend future studies that concentrate on temporal patterns of Coyote activity in the New York metropolitan area given that previous studies of urban Coyotes indicate a shift toward nocturnal activity (e.g., Gehrt et al. 2011, Grindler and Krausman 2001, Tigas et al. 2002). Finally, one logical next step is to survey the remainder of Long Island and to continue the long-term monitoring of Coyotes and other animals in current survey locations. The collection of baseline data in habitats unoccupied by Coyotes, such as the abundance and diversity of birds and other mammals, will allow for a natural experiment in which we can examine shifts in community composition before and after the expansion of Coyotes into new habitats (Weckel et al. 2015). With that in mind, the results of this study can be used by biologists to test ecological and evolutionary hypotheses using a pre- and post-colonization framework, and to also inform conservation practices.

Acknowledgements

We are grateful to Jeremy Pustilnik, Larissa Swedell, John Waldman, and three anonymous reviewers who provided feedback on previous drafts of this manuscript. We also thank Amanda Goldstein, who helped us to generate maps and land use data for analyses.

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