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Cover Photograph: Coyotes (*Canis latrans*) enjoying the parks and nightlife in the Bronx, New York City. Photograph © Gotham Coyote Project.

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Occupancy and Breeding Status of Coyotes in New York City Parks, 2011 to 2014

Christopher M. Nagy^{1,*}, Carolyn Koestner², Suzanne Clemente³, and Mark Weckel⁴

Abstract - Little is known about the distribution and spatial ecology of *Canis latrans* (Coyote) within New York City (NYC), one of the largest and most densely populated cities in the world. To determine the overall distribution, site-specific breeding status, and seasonal occupancy patterns of this species in New York City, we used camera traps to monitor several urban sites across the boroughs of the Bronx, Manhattan, Queens, and Brooklyn from 2011 to 2014. Data from 2012 to 2014 were divided into 3 pup-rearing (PR; 1 April–30 September) and 3 non-pup-rearing (NPR; 1 October–31 March) seasons. We performed three single-season, multi-state analyses and 3 single-season, single-state analyses on data from the PR and NPR seasons, respectively, to estimate occupancy (ψ), breeding proportion (R), and detection rates (p^1 , p^2 , and δ). We examined 3 measures of available habitat area and the total area of fresh water in each park as predictors of site occupancy and/or breeding status, but found no evidence for associations between the amount of habitat or water and site occupancy or site breeding status. Generally, site occupancy (i.e., the proportion of all parks being used by Coyotes) was higher during the 3 NPR seasons ($\psi_{\text{NPR}} = 0.778, 0.800, \text{ and } 0.716$) than the 3 PR seasons ($\psi_{\text{PR}} = 0.509, 0.439, \text{ and } 0.670$). By 2014, Coyotes were established in 6 sites and breeding in 4 sites, up from 2 in 2011, in the mainland borough of the Bronx, but only 1 resident Coyote was found in the island boroughs (Manhattan, Queens, or Brooklyn) from 2011 to 2014. Overall, Coyotes seem to be successfully colonizing suitable greenspaces in the Bronx, as evidenced by the increase in year-round occupancy and the increase in breeding sites over the 4 years of the study. While crossing from mainland Bronx to Queens on Long Island appeared to be a significant barrier during our 4 years of surveys, we expect that Coyotes will eventually establish themselves in the island boroughs of NYC as Coyotes more densely populate the Bronx and outward dispersal pressure increases.

Introduction

Canis latrans (Say) (Coyote) has expanded its range greatly since the early 20th century, and now occupies nearly all of North America. This species has colonized even highly urbanized places such as the Los Angeles area (Riley et al. 2003, Shargo 1988, Tigas et al. 2002), Chicago (Gehrt et al. 2009, 2011, 2013; Gese et al. 2012; Hennessy et al. 2012; Morey et al. 2007), Toronto (Adkins and Stott 1998), and others (Bogan 2012, Grinder and Krausman 2001, Poessel et al. 2013), although most studies have focused on the outlying or adjacent suburban areas rather

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than dense urban centers (but see Newsome et al. 2015, Randa and Yunger 2006). One of the urban centers to fall more recently within the Coyote's breeding range is New York City (NYC). While eastern Coyotes are well-established just north of NYC in the suburban and exurban Westchester County (Nagy et al. 2012, Weckel et al. 2010) and west across the Hudson River in inland New Jersey (New Jersey Upland Wildlife and Furbearer Research Project 2012), NYC's extreme level and area of urbanization combined with its complex and islanded geography have delayed the establishment of Coyotes there compared to other eastern US locales, even those farther east (Boston: Way 2007; Narragansett Bay, RI: Narragansett Bay Coyote Study 2014). Beginning in the 2000s, Coyote sightings have become more common in 2 of the larger parks in the Bronx as well as in the relatively less-urbanized neighborhood of Riverdale, and there were also sporadic unconfirmed reports throughout the rest of NYC (Toomey et al. 2012, Weckel et al. 2015). Ecologists now have a rare opportunity to directly observe the range expansion of a relatively large carnivore into one of the most-urbanized areas in the world. Studying this progression will generate information on how Coyotes respond to intense urbanization and how they affect the urban food web (Gehrt and Prange 2007, Gehrt et al. 2013, Gommper 2002, Harrison et al. 1989, Prange and Gehrt 2007), thus providing land managers with data needed to inform management and policy recommendations.

After a pilot camera trap survey of 14 parks across 4 boroughs in 2011, we more intensively surveyed 10 wooded parks in 3 boroughs from 2012 to 2014 to examine overall distribution, site occupancy changes, and breeding status. Beyond the baseline question of where Coyotes were presently occurring in NYC, we were particularly interested in the rate at which occupied sites became breeding sites, and whether sites changed occupancy or breeding status from season to season. We also hoped to identify predictive covariates that could be used to identify sites in NYC that will likely be occupied and/or will likely contain breeding pairs in the future.

Field Site Description

The complex geography, intense urbanization, and large human population of NYC are important factors affecting the spatial ecology of all species living there. The 5 boroughs of NYC encompass 783.7 km² of land and had an estimated human population of 8.4 million in 2013 (10,725.4 people/km²), with the greater New York Metropolitan Area covering an area of 34,490 km² with an estimated human population of over 23 million (US Census Bureau 2010). Within NYC itself, 19.9% of the area is devoted to municipal or federal parks (Harnik et al. 2014) of various use designations (e.g., undeveloped open space, recreational fields, playgrounds, parking lots, gardens, etc.). In 2011, our study sites were located in the Bronx (5 parks), Queens (6 parks), Manhattan (1 park), and Brooklyn (1 park) (Fig. 1). Given equipment and logistical restraints, we could not survey every park in NYC; parks in Brooklyn and Staten Island were not surveyed after 2011 due to their distance from mainland New York compared to other boroughs, and we assumed parks in Bronx, Queens, or Manhattan would likely be colonized by Coyotes before sites in Brooklyn or Staten Island. We were particularly interested in the colonization of the

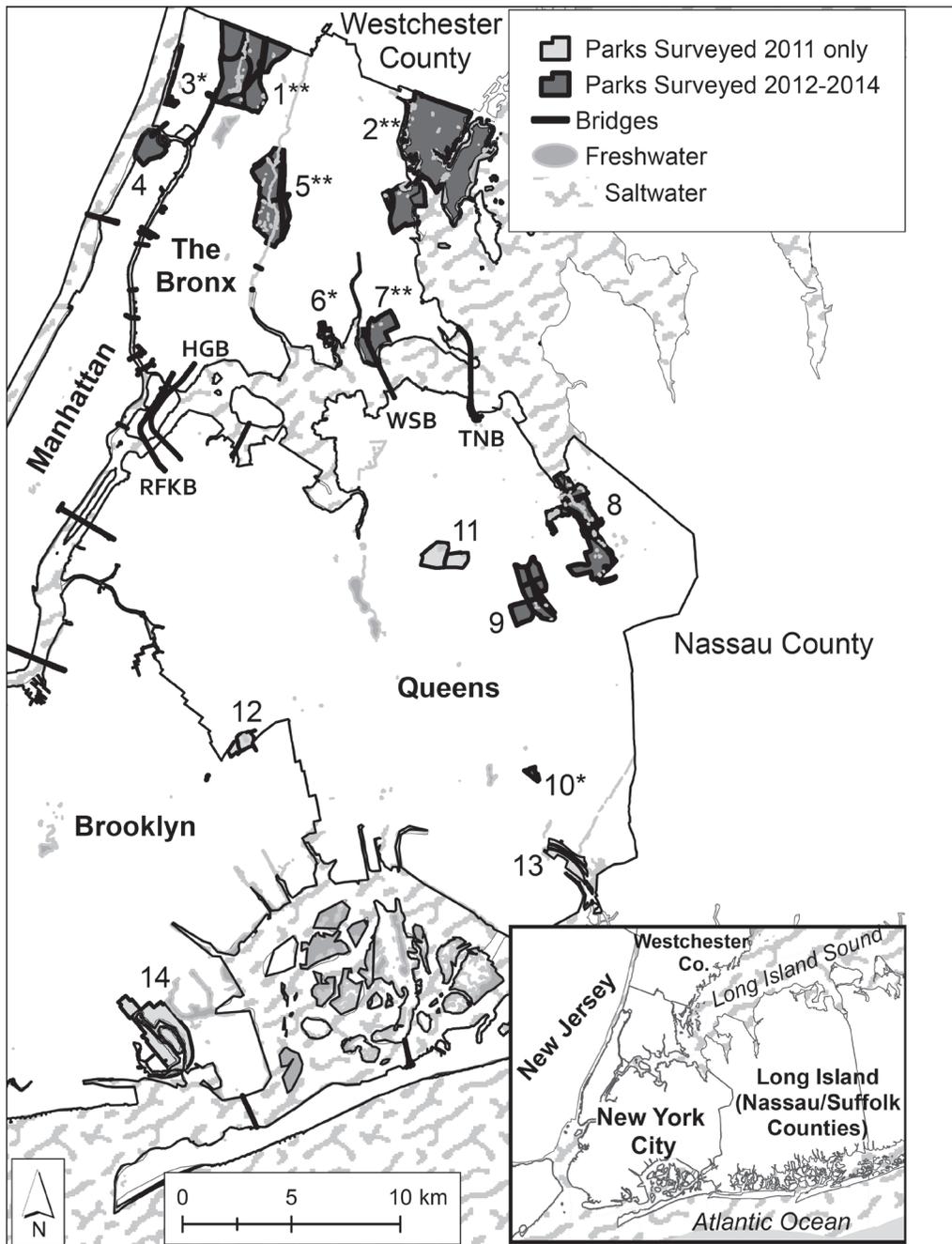


Figure 1. Parks (1 = Van Cortlandt, 2 = Pelham Bay, 3 = Riverdale, 4 = Inwood, 5 = Bronx, 6 = Pugsley Creek, 7 = Ferry Point, 8 = Alley Pond, 9 = Cunningham, 10 = Railroad, 11 = Kissena, 12 = Highland, 13 = Idle Wild, and 14 = Marine) surveyed for Coyotes in New York City, 2011–2014, and all bridge crossings (Bronx–Queens bridges are labeled as RFKB = Robert F. Kennedy Bridge, HGB = Hellgate Bridge, WSB = Whitestone Bridge, and TNB = Throgs Neck Bridge). Park labels with “*” were occupied, and parks marked with “**” were sites with successful dens in the pup-rearing season of 2014.

larger wooded parks in northern Queens by Coyotes, presumably dispersing from the Bronx, and focused our survey effort in these 2 boroughs. In 2012–2014, we surveyed 6 parks in the Bronx, 3 in Queens, and 1 in Manhattan (Fig. 1).

The Bronx (148.7 km², 12,704 people/km²; US Census Bureau 2010) is the southernmost tip of mainland New York, and is contiguous with the more suburban Westchester County, and thus has the highest dispersal pressure from the north where Coyotes are well established. It also has the largest and third-largest parks in NYC (Pelham Bay and Van Cortlandt Parks, respectively). Manhattan Island (87.5 km², 26,821 people/km²; US Census Bureau 2010) is the smallest yet most populous and urbanized borough in NYC. It is one of the most urbanized locations in the world, but the northernmost tip of the island is the 78-ha Inwood Park, which has 57 ha of mature hardwood forest separated from the Bronx by a water channel less than 250 m wide crossed by a ground-level commuter train bridge. Queens (460 km², 4848 people/km²; US Census Bureau 2010) lies across the Long Island Sound and is geographically the largest NYC borough. Urban development within Queens varies from dense areas of high-rise buildings in the west to less-developed residential areas in the east.

It is worth noting that the boroughs of Queens and Brooklyn make up the westernmost portion of a much larger island, Long Island, which extends approximately 200 km east and consists of Nassau and Suffolk counties (totaling 4463 km²). Brooklyn lies primarily on the southwestern tip of Long Island, with Queens making up the northwestern coast of Long Island as well as the eastern border of NYC (with Nassau County; Fig. 1). Thus, in addition to the ecological ramifications within NYC itself, the colonization of NYC by Coyotes poises this species to enter and spread throughout Long Island, the last large land mass in the continental US that is devoid of Coyotes (Weckel et al. 2015).

We selected parks for study based on the presence of undeveloped open space, location in the NYC landscape relative to likely sources of dispersing Coyotes, and/or previous confirmed or unconfirmed Coyote sightings. Park area consisted of developed parkland (e.g., lawns, ball fields, playgrounds) and undeveloped mixed forest, small meadows, or salt marsh. Van Cortlandt and Pelham Bay Parks also had golf courses on site. All had public trail systems and were surrounded by urbanized residential or commercial space and city roads. All were bisected by or within a few hundred meters of local roads, major interstates, and/or parkways.

Methods

In all 4 years of this study, we deployed Reconyx RC55, PC800, and HC500 motion- and heat-activated camera traps (Reconyx, Inc., Holmen, WI) in wooded parks across NYC. These camera models had identical trigger speeds (0.2 seconds), digital resolutions (1080p) and similar infrared flash ranges (PC800: 21m, RC55 and HC500: 15m). The older RC55 model had a 5.0 x 7.6 cm red/infrared flash for night pictures, whereas the newer models had a “semi-covert” infrared flash consisting of a single small LED bulb. We established camera locations in wooded sections of parks selected for study in a 2-step process. Prior to field deployment, we randomly chose planned camera locations within forest patches with a minimum

distance of 500 m from each other using ArcGIS 9 and 10. We often were forced to adjust these mapped locations in the field to minimize the risk of vandalism and theft (e.g., keeping cameras out of sight from human-used trails, away from illegal camping sites) and/or to find a suitable tree to attach the camera. Actual locations were within ~50 m of the predetermined locations. Camera density was at least 1 camera per 0.5 km² per park; thus the total number of cameras in each park varied according to park size. This standard density was occasionally reduced in Ferry Point and Inwood Parks because suitable locations were not always found due to a high amount of illegal activity and concerns for our field technicians' safety, restrictions on land access (for public safety near bridges or train tracks or privately leased land where we were not granted permission to access), or when cameras failed or were vandalized. Generally, the cameras were deployed in the same locations each year unless the cameras were tampered with or stolen or, in a few cases, the location proved unusable due to flooding or storm damage. After each deployment, photographic events of adult Coyotes, pups, and other wildlife of interest (e.g., *Odocoileus virginianus* Zimmerman [White-tailed Deer], *Vulpes vulpes* L. [Red Fox], *Meleagris gallopavo* L. [Wild Turkey]) were recorded.

In 2011, we conducted consecutive 4–8 week surveys at 13 parks across NYC to establish baseline data on where Coyotes had established themselves. These surveys were done consecutively, i.e., all cameras were deployed at 1–4 sites (depending on area and our supply of cameras) for 4–8 weeks and then moved to the next site(s) for the next 4–8 weeks. This allowed us to survey many sites in one year to quickly establish baseline knowledge regarding how far Coyotes had penetrated into NYC, but did not allow comparisons among parks in terms of seasonal patterns. We also were unable to ascertain breeding status for those sites not sampled in the summer when pups were observable. In 2012, we surveyed 9 parks continuously from January 2012 to February 2013, with a tenth park surveyed from October 2012 to February 2013, to examine seasonal occupancy and breeding patterns. Based on this 14-month continuous survey, we identified a potential seasonal fluctuation in park occupancy (see Results) and we moved to biannual 10–24 week surveys in the winters and summers of 2013 and 2014 to sample the denning through pup-rearing periods (1 April–30 September; hereafter, PR season) and non-denning and non-pup-rearing periods (1 October–31 March; hereafter, NPR season) of the year (Gerht et al. 2009, Harrison and Gilbert 1985, Way et al. 2001) in these 10 parks.

We analyzed data from January 2012 to August 2014, making up 3 PR and 3 NPR seasons, in multiple single-season occupancy analyses, with each 2-week segment representing a single survey within a seasonal deployment (see MacKenzie et al. 2006). Multi-state occupancy analyses were performed on PR season data, using the 2-state conditional parameterization of Nichols et al. (2007), while traditional single-state occupancy analyses were performed on NPR season data. We could not perform a single multi-state, multi-season analysis because it was not possible to observe breeding state (i.e., photograph pups) in the NPR seasons; this limitation confounded parameters in the multi-season, multi-state framework (MacKenzie et al. 2009) that are estimates of probabilities conditional on the breeding status

of the prior season (e.g., the probability of breeding in season t given breeding in season $t - 1$). We restricted data for PR season surveys to trap effort occurring from 1 June to 30 September; pups are born in late March through April and are not out of the den until the end of May (C.M. Nagy, pers. observ.; Way et al. 2001). With one exception, the earliest pup photographs we obtained were in late June and July after the pups became more mobile. The exception was from an additional camera opportunistically placed at a den site from which we were able to photograph pups on the first day they left the den (May 23); such early pup detections would not be obtained from typical random camera placements. These same pups were also detected later in July at our randomly placed cameras at this site.

Previous research showed that forest and grassland areas are the main habitat types used by Coyotes in adjacent Westchester County (Nagy et al. 2012, Weckel et al 2010) and that urban/suburban Coyotes tend to select natural areas for the majority of their home ranges and denning sites (Bogan 2012; Gehrt et al. 2009, 2012; Randa and Yungler 2006; Way et al. 2002). We hypothesized that these preferences would hold true for the species in NYC and that Coyotes could likely use nearly any park regardless of size, but probably would only breed in the larger parks. To test these 2 predictions, we examined the relationship between the amount of available “natural” area in each park and occupancy and/or breeding status. We measured available habitat area using 3 methods: 1) utilizing the 2011 National Land Cover Database (NLCD; Homer et al. 2015) land-use cover types, 2) hand-digitizing land-cover polygons based on ArcGIS Online aerial photographs and our personal knowledge of the parks and, and 3) using the total area of each park as a surrogate for available habitat. In the past, we have noted discrepancies between the characterizations of the NLCD versus what we see on the ground in small urban parks. For example, all of Railroad Park in Queens is characterized in the 2011 NLCD as “developed, open space” but is actually young-to-medium-aged hardwood forest and old field. These discrepancies could be very important in fragmented or urban places where small patches of habitat are important for certain species and thus must be classified correctly. The rationale then for testing these 3 methods of quantifying land cover was to find the best balance between the precision and specificity of the land-cover measurements versus the amount of mapping work needed to measure these values.

Other research has suggested that Coyotes may select areas or den sites near available fresh water (Arjo and Peltscher 2004, Gerht et al. 2009, Way et al. 2001). In a coastal city such as NYC, many of the waterways are estuarine and quite brackish. We hypothesized that fresh water might be a scarce resource for Coyotes and that the amount of freshwater streams, ponds, and wetlands in a site might be a predictor of Coyote occupancy and/or breeding. We extracted all water raster cells from the NYC 0.9-m Landcover Raster (University of Vermont Spatial Analysis Laboratory and NYC Urban Field Station 2012) and eliminated salt water areas from this resulting high-resolution “surface-water map” of NYC by overlaying the National Wetlands Inventory (US Fish and Wildlife Service 2014) map and removing patches of wetlands and river sections characterized as estuarine or marine. This procedure left only freshwater streams, ponds, wetlands, and non-estuarine river areas from the NYC Landcover Raster.

Areas (ha) of forest (deciduous, evergreen, mixed, and woody wetlands categories) and short vegetation cover (grassland, herbaceous wetlands, and shrub categories) estimated from the NLCD (For-NLCD, Grass-NLCD, and summed F&G-NLCD), hand digitized areas of natural habitat (NA-Hand), total park size (ParkSize), and fresh water area (WA) were measured using ArcGIS 10.2 and entered as covariates of site occupancy (ψ) and breeding proportion (R) into the occupancy models for each season, along with constant (“dot”) models. We modeled probabilities of detection given occupancy (p^1), detection given breeding (p^2), and of correctly identifying breeding given occupancy (δ) as constant terms in each season (see Nichols et al. 2007). We compared models using Akaike’s Information Criterion corrected for small samples sizes (AIC_c). We also examined Pearson’s r correlations among the 3 land-cover covariates. Occupancy modeling was performed using Presence 6.5 (Hines 2006), model estimates and descriptive statistics were examined using Microsoft Excel 2007, and graphics were produced by the XL Toolbox add-in v6.53 (Kraus 2014) and ArcGIS 10.2.

Results

By the time of our first NYC survey in 2011, Coyotes had already colonized 4 parks (out of 5 surveyed that year) in the Bronx, and were breeding in at least 1 (Pelham Bay Park; Table 1). By 2014, we identified a total of 4 parks where Coyotes were breeding, all in the Bronx. Two of these sites, Ferry Point and Bronx

Table 1. Park-specific results of seasonal (NPR = non-pup-rearing season; PR = pup-rearing season) camera-trap surveys in New York City Parks, 2011–2014. Occupancy states are unoccupied (0), occupied (1), or breeding (2); a record of “2” is not possible in NPR seasons. Values in parentheses indicate the estimated probability of a false negative or positive result; either a 0 really being a 1 (based on p^1) or a 1 really being a 2 (based on δ), the latter possible in PR seasons only. “X” indicates that park was not surveyed that season.

Park ^A	2011–2012		2012	2012–2013	2013	2013–2014	2014
	2011 ^B	NPR	PR	NPR	PR	NPR	PR
Bronx (BX; 270.7)	0	X	X	1	1 (?) ^C	1	2
Ferry Point (BX; 129.2)	X	1	0 (0.039)	1	0 (0.078)	1	2
Pelham Bay (BX; 895.4)	2	1	2	1	1 (?) ^C	1	2
Pugsley (BX; 25.4)	1	1	0 (<0.001)	1	0 (0.078)	1	0 (0.016)
Riverdale (BX; 18.6)	1	1	1 (0.162)	1	0 (0.014)	1	1 (<0.001)
Van Cortlandt (BX; 435.6)	1	1	2	1	2	1	2
Alley Pond (Q; 248.8)	0	0 (0.001)	0 (<0.001)	0 (0.002)	0 (0.078)	0 (0.033)	0 (0.002)
Cunningham (Q; 152.3)	0	0 (0.005)	0 (<0.001)	0 (0.002)	0 (0.014)	0 (0.008)	X
Highland (Q; 42.0)	0	X	X	X	X	X	X
Idle Wild (Q; 70.1)	0	X	X	X	X	X	X
Kissena (Q; 97.9)	0	X	X	X	X	X	X
Railroad (Q; 9.0)	1	1	1 (0.004)	1	1 (?) ^C	1	1 (0.016)
Inwood (M; 78.6)	0	1	0 (0.116)	1	0 (0.014)	0 (0.124)	0 (0.016)
Marine (BK; 265.7)	0	X	X	X	X	X	X

^APark name, borough (Q: Queens; BX: Bronx; BK: Brooklyn; M: Manhattan), and size (ha).

^BFor 2011, only naive occupancy is presented: 0 = no detections; 1 = Coyote photographed.

^C δ , error rates not estimatable this season.

Park, had been surveyed seasonally since 2012 and 2010, respectively, and thus are likely genuine observed transitions from a non-breeding to a breeding site during our study period. In Bronx Park, we observed a full transition from unoccupied to breeding: it was unoccupied in 2010 (Nagy et al. 2012) and 2011, was colonized sometime between autumn 2011 and autumn 2012, remained consistently occupied through 2013, and transitioned to a breeding site in 2014.

The extent of natural area in each park had no detectable effect on ψ or R (Table 2). The total area covered by fresh water in each park seemed to have a small negative relationship with occupancy in the NPR seasons ($w_i = 0.12$ – 0.17), but this finding was likely an artifact of the arrangement and sizes of parks (see Discussion, below). Occupancy in NPR seasons remained relatively stable during 2012–2014 and was higher than in PR seasons. Occupancy rate in PR seasons increased over time (Table 3) as more sites became permanently occupied in contrast to the temporary occupation characteristic of NPR seasons. R also increased from 0.395 ± 0.219 (mean \pm SE) in 2012 to 0.749 ± 0.238 in 2014 (Fig. 2). These increasing

Table 2. Truncated model selection results (top 3 or cumulative $w_i \geq 0.8$) for single- and multi-state occupancy models of seasonal (NPR = non-pup-rearing season; PR = pup-rearing season) Coyote distribution in New York City Parks, 2012–2014. Detection parameters (p^1 , p^2 , and δ) modeled as constants in all models.

Season	Model ^a	ΔAIC_c	w_i	k	-2LogLik
2011–2012 NPR	$\psi(\cdot)$	0	0.55	2	48.82
	$\psi(\text{WA})$	2.23	0.18	3	46.76
	$\psi(\text{NA-Hand})$	3.76	0.10	3	48.29
2012 PR	$\psi(\cdot), R(\cdot)$	0.00	0.92	5	78.62
	$\psi(\cdot), R(\text{NA-Hand})$	8.17	0.02	6	71.79
	$\psi(\cdot), R(\text{ParkSize})$	8.17	0.02	6	71.79
2012–2013 NPR	$\psi(\cdot)$	0	0.51	2	97.16
	$\psi(\text{WA})$	2.28	0.16	3	95.15
	$\psi(\text{NA-Hand})$	3.81	0.08	3	96.68
	$\psi(\text{ParkSize})$	4.26	0.06	3	97.13
2013 PR	$\psi(\cdot), R(\cdot)$	0.00	0.97	5	33.70
	$\psi(\cdot), R(\text{NA-Hand})$	10.64	<0.01	6	29.34
	$\psi(\cdot), R(\text{WA})$	10.64	<0.01	6	29.34
2013–2014 NPR	$\psi(\cdot)$	0	0.86	2	49.52
	$\psi(\text{WA})$	3.89	0.12	3	49.12
	$\psi(\text{Gr-NLCD})$	8.99	0.01	3	54.22
2014 PR	$\psi(\cdot), R(\cdot)$	0.00	0.96	5	47.38
	$\psi(\cdot), R(\text{WA})$	8.07	0.02	6	40.45
	$\psi(\cdot), R(\text{Gr-NLCD})$	8.14	0.02	6	40.52

^aCovariate abbreviations: WA = hectares of fresh surface water derived from the NYC Landcover Raster and the National Wetlands Inventory; NA-Hand = hectares of natural/undeveloped area delineated via digitizing by hand; ParkSize = size of park in hectares based on municipal boundaries; Gr-NLCD = areas of grassland (combined grass, shrub, and herbaceous wetland) from the 2011 National Landcover Database; and For-NLCD = combined areas of forest (mixed, deciduous, and coniferous, and woody wetlands) from the 2011 National Landcover Database.

trends, however, occurred only in the Bronx—the single Manhattan Park surveyed in all seasons was only occasionally occupied, and the 3 Queens parks surveyed for all seasons did not change status (Table 1). Rates of detection were adequately high (Table 3) to make us confident that parks were sufficiently sampled so that instances where no Coyotes were photographed were most likely truly unoccupied.

While extent of natural area did not prove useful in predicting ψ or R , we could compare the different measurements to each other. NLCD-based measurements of total natural area tended to be smaller than our own determinations via digitizing manually; the average difference between total NLCD-For plus NLCD-Grass areas and our digitized areas was 60.8 ha \pm 83.9 (mean \pm SD). Nearly all habitat

Table 3. Parameter estimates for single- and multi-state occupancy models of seasonal (NPR: non-pup-rearing season; PR: pup-rearing season) Coyote distribution in New York City Parks, 2012–2014. Ψ = probability of occupancy, R = probability of breeding, given occupancy, p^1 = probability of detecting Coyotes, if the site is occupied, p^2 = probability of detecting Coyotes, if breeding is occurring, Δ = probability of detecting breeding, if breeding is occurring.

Season	Ψ (SE)	R (SE)	p^1 (SE)	p^2 (SE)	Δ (SE)
2011–2012 NPR	0.778 (0.139)		0.735 (0.076)		
2012 PR	0.509 (0.161)	0.394 (0.219)	0.660 (0.099)	0.938 (0.061)	0.598 (0.130)
2012–2013 NPR	0.800 (0.127)		0.578 (0.062)		
2013 PR	0.439 (0.198)	0.284 (0.286)	0.573 (0.173)	0.346 (0.587)	N/A ^A
2013–2014 NPR	0.716 (0.149)		0.763 (0.075)		
2014 PR	0.670 (0.158)	0.749 (0.238)	0.876 (0.174)	0.906 (0.087)	0.527(0.171)

^AParameter not estimatable, 1 park with 1 detection of breeding that season.

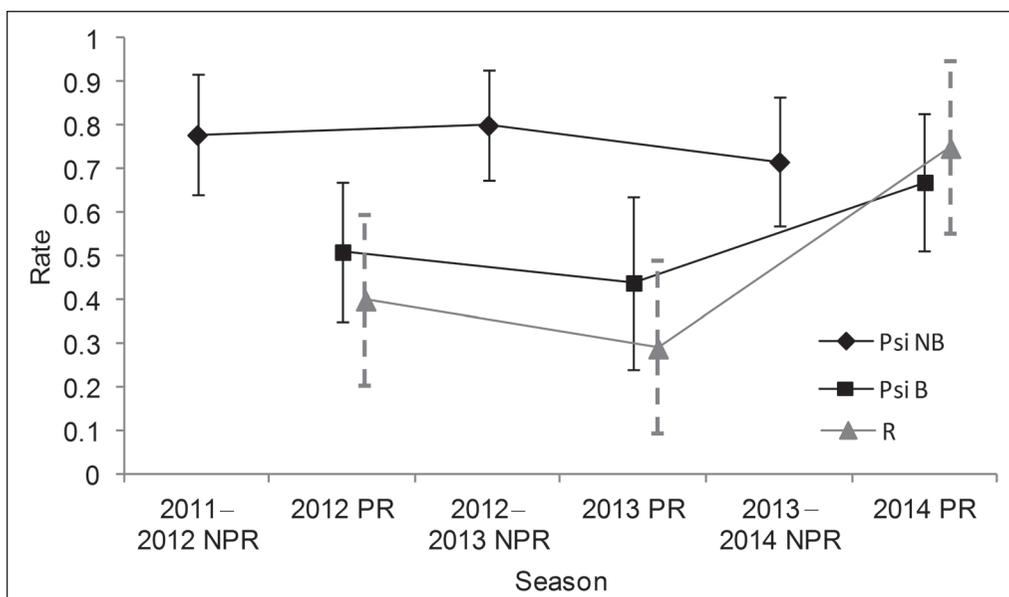


Figure 2. Seasonal occupancy (ψ) in pup-rearing (PR; April through September) and non-pup-rearing (NPR: October through March) seasons and proportion of occupied sites with successful breeding (R) of Coyotes in 10 New York City Parks (mean \pm SE), 2012–2014.

measurements were highly correlated (Pearson's r ranged from 0.78 to 0.99) with the exception of NLCD-Grass and NLCD-For, which were moderately correlated ($r = 0.60$). There were a few notable mismatches between the satellite-derived NLCD and our direct observations of land cover on the ground; specifically, Railroad Park was characterized as "developed, open space" in the NLCD but actually resembles undeveloped hardwood forest with no existing trails, paved paths, mowed lawns, or buildings of any kind. Portions of other parks, such as Pugsley Creek, Riverdale, and Ferry Point were also mischaracterized.

Discussion

The most obvious pattern in Coyote distribution over the 4 years of this study was the stark difference between the steady progression of colonization in the Bronx versus the unchanging occupancy status of sites in Queens and Brooklyn on Long Island. In 2011, we surveyed 5 parks in the Bronx and 7 parks in Queens and Brooklyn (and 1 park in Manhattan), and found Coyotes in 4 Bronx Parks but only in 1 in Queens or Brooklyn. By 2014, Coyotes were found at least some of the year in the 7 Bronx sites we had surveyed from 2012 onward, but still were only found in the single Queens Park out of the 3 in which we maintained survey effort for 3+ years (Table 1). It appears that Coyotes can move into and within the Bronx, but the East River/Long Island Sound still poses a substantial dispersal barrier from the mainland to Long Island, in addition to the challenge of navigating the urban matrix and extensive highway system once there. For a Coyote to reach Queens/Long Island, it must either swim across the Long Island Sound, which at its narrowest gap is 395 m, or cross one of the City's vehicle or train bridges that span the Sound. The narrowest gap, known as Hell's Gate, is between the Bronx and Queens on the western end of the Long Island Sound as it merges with the East River. This gap is difficult but likely not impossible for a Coyote to swim (Way 2002), but is exceedingly rough and experiences high boat traffic. The next narrowest gaps are farther east and ≥ 900 m in length. The 3 car and 1 train bridges across the Long Island Sound that connect the Bronx to Queens are highly trafficked and 40–43 m above the water. Only the westernmost crossing, the Robert F. Kennedy Bridge across Hell's Gate (Fig. 1), has a pedestrian walkway separated from the vehicle lanes. Harrison (1992) found that rivers and lakes >150 m in width deflected the movement of dispersing Coyotes. In contrast, Sacks et al. (2004) found that presumed dispersal barriers such as highways and waterways did not appear to lead to genetic structure in Coyotes in California; however, the San Francisco Estuary—similar in size to the Long Island Sound—was an exception that did appear to be a barrier as evidenced by distinct genetic structure on either side. Instances of Coyotes crossing the Long Island Sound have been rare but seem to be on the rise. The park in Queens that was occupied, Railroad Park, appears to contain only a single Coyote that has lived there since approximately 2009, according to sightings reported by residents, and was photographed reliably in all of our surveys. We collected 1 road-kill Coyote near Alley Pond in 2014 (M. Weckel, unpubl. data) and a single Coyote was photographed in Suffolk County in 2013 (R. Wesnofske, resident, and J. Stiller,

New York State Department of Environmental Conservation, Stony Brook, NY, USA, 2014 pers. comm.). In early 2015, 3 Coyote sightings were made in Queens and widely publicized by local media.

Regarding seasonal distribution patterns, NPR season occupancy remained around 0.7 to 0.8, with all or nearly all Bronx parks being occupied at some point during the year. In comparison, PR season occupancy rates were consistently lower than those of NPR seasons but increased over time (Fig. 2). Until 2014, there appeared to be 2 possible hypotheses for this seasonal difference: either adult Coyotes concentrate their activity near their dens in the north Bronx during the PR season and roam farther in the NPR season (Person and Hirth 1991), implying that we were observing the same individuals using different seasonal ranges; or the detections of Coyotes in the smaller parks in the south Bronx and Manhattan (Pugsley Creek, Ferry Point, and Inwood) were of dispersing juveniles that left or died by the subsequent PR season. Ferry Point Park and Bronx Park both transitioned to breeding sites in 2014, while existing dens were maintained in the north Bronx; these findings suggest these parks had been occupied by dispersing juveniles in NPR seasons who were able to survive and breed in the next PR season.

Regardless, Coyotes are clearly expanding their range throughout the Bronx. We identified 3 “levels” of site occupancy from our observations: 1) parks used only during NPR seasons (e.g., Inwood, Pugsley Creek), 2) parks consistently occupied year-round that were also breeding sites (e.g., Van Cortlandt, Pelham Bay), and 3) parks occupied seasonally that then transitioned to breeding sites (Bronx and Ferry Point Parks). Railroad Park, a small park in the far south of Queens, was an anomaly in that it was occupied in all 6 seasons but never became a breeding site; as best could be determined from photographs, a single Coyote had managed to cross onto Long Island, travel south >20 km, and establish a territory there. Overall, the number of breeding sites doubled from 2 to 4, and there were no occurrences of a breeding park reverting to unoccupied or non-breeding in subsequent years. Year-round occupancy (i.e., occupied for both PR and NPR seasons) was also highest in 2014, going from 4 to 6 parks from 2012 to 2014. These rates of increase may not hold long-term as empty sites fill up in the Bronx, but they can be used as a measure of what to expect when Coyotes reach Queens and make their way into Nassau and Suffolk counties.

The dynamic nature of this system likely confounded some of our efforts to make conclusions regarding habitat selection and site quality. If an unoccupied park in 2011 or 2012 could become occupied and breeding within a few seasons (as occurred in Bronx and Ferry Point Parks), ψ and R patterns become reversed as parks formerly classified as “absence” sites become breeding habitat. Indeed, given the history of the Coyote in the last 100 years as the ultimate generalist and superb urban adapter, conclusions about site-specific features or characteristics as determinations of future presence and/or breeding may be less important than making general predictions regarding timing of initial arrival, the rate of subsequent permanent occupation, and later breeding status. Our results indicate that Coyotes can find suitable habitat patches even in the most urban landscapes, and once occupied,

these patches can become breeding sites within a few years. However, this transition from occupied to breeding did not occur at all sites. There may be a more complex relationship where area, habitat (Bogan 2004, Gehrt et al. 2009, Kamler and Gibson 2000, Kays et al. 2008, Sacks et al. 2005, Way et al. 2001), prey base (Kamler and Gibson 2000), and/or human activity (Gerht et al. 2009, 2012; Gese et al. 1996; Kays et al. 2008; Way et al. 2001) play roles in determining the breeding suitability of a site.

Our covariate modeling was also hindered by low sample size—while we surveyed nearly all sizable, wooded parks in the Bronx and Queens where cameras could be safely deployed, this amounted to a mere 10 parks. This limited sample size then favored the simplest model when using AIC_c . Additionally, only a few individual Coyotes have ever been recorded on Long Island, and therefore Queens Parks likely are not realistically available to Coyotes. While the single Coyote in Railroad Park shows that it is at least possible for Coyotes to disperse and survive in Queens, there simply has not been enough dispersal events across the Long Island Sound to deem land in that borough as available habitat. We re-ran the 2014 PR season models without Alley Pond and Cunningham Parks (the two unoccupied Queens Parks in our study in 2012–2014) and still found no pattern between area and ψ or R .

Our model-selection results (Table 2) yielded some support for a slight negative relationship between the area of fresh water in each park and occupancy in NPR seasons. On closer inspection it was apparent that, again, we were hindered by low sample size and the lack of sufficient time or propagule pressure to define Queens parks as available habitat—Alley Pond and Cunningham parks have the second and third most surface water area, respectively, and were devoid of Coyotes. Van Cortlandt and Pelham Bay parks, which have the first and fourth most surface water area, respectively, were occupied in all 6 seasons and have had breeding Coyotes in 2012, 2013, and 2014.

The suitability of Manhattan, the other island to which Bronx Coyotes can disperse, for supporting a viable Coyote population is hard to predict. Our 1 Manhattan site, Inwood Park, was only sporadically occupied by Coyotes. Manhattan is the most densely populated county in the USA (26,821 people per km²; US Census Bureau 2010), and there may not be any habitat patches on the island not heavily trafficked by people. While Coyotes are able to acclimate to proximity to people by adjusting their activity temporally and staying hidden (Gehrt et al. 2009, 2011; Grindler and Krausman 2001; Way et al. 2004), Coyote sightings in Manhattan typically have led to a large police chase and capture (see Toomey et al. 2012). It seems unlikely that a pair or family group of Coyotes could remain hidden in Manhattan, and thus Coyotes' future there likely depends on stakeholders' acceptance capacity (Decker and Purdy 1988) as much as habitat or other ecological factors. For example, Central Park is a 315-ha park in the center of Manhattan which contains 3 forested sections, gardens, and seemingly abundant prey. However, visitation is estimated at over 100,000 people a day (Central Park Conservancy 2011). Whether Coyotes ultimately establish themselves anywhere in Manhattan

is still unpredictable and remains a key question for urban wildlife research in the near future. Alternatively, Queens represents an area similar in overall landscape to the Bronx, with a number of sizable parks that are less heavily used by residents and contain substantial natural space as well as less-urbanized residential neighborhoods in its eastern portions. The progression of Coyotes from mainland New York State to Queens and the rest of Long Island offers a tremendous opportunity to observe and study the colonization of a dense urban area and subsequent transition back to a more rural habitat.

Future research on Coyotes in the Bronx would benefit from genetic sampling, obtainable from scat samples and roadkill with the help of city agencies. Such data would shed light on important questions regarding the region of origin of NYC populations, how Coyotes are related across NYC, and give rough estimates of abundance and how far individual Coyotes roam. There are also research needs and opportunities regarding Staten Island, which is the least urbanized borough of NYC and likely has ample habitat for Coyotes. To strengthen our and other researchers' ability to model habitat use, we will also soon combine our NYC camera-trap data with datasets from other urban areas where Coyotes have established themselves. Finally, in this analysis we were interested in patterns at the whole-park level, but other habitat associations may exist at the within-park scale. We are currently evaluating the use of spatial occupancy models that allow for modeling at the scale of individual survey points while accounting for correlations among nested "sites" within larger sites, i.e., cameras in parks (Broms et al. 2014, Chelgren et al. 2011, Johnson et al. 2013).

From 2012 to 2014, PR season occupancy and breeding activity of Coyotes increased in the Bronx as more parks were used year-round and more parks became breeding sites. This pattern will likely continue until all suitable sites in the Bronx are saturated, at which point we expect greater dispersal pressure into Queens and Manhattan. Both of these areas offer interesting opportunities to examine the flexibility of Coyote behavior and ecology as well as important human dimensions of conservation in regards to people's attitudes—and their potential for change—towards Coyotes, predators, and urban wildlife.

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