

Transient persistence of bobcat (*Lynx rufus*) occurrence throughout a human-dominated landscape

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Abstract

Human developments have detrimental effects on wildlife populations globally with carnivores being particularly sensitive. The bobcat (*Lynx rufus*) is often considered an adaptable mesocarnivore that occurs throughout varied land-cover types within its wide distribution and may be less susceptible to the negative effects of development. Our objectives were to investigate the landscape occupancy dynamics of bobcats in a highly developed and densely populated region of the northeastern United States to evaluate the sensitivity of bobcat occurrence to natural and anthropogenic landscape features. We established a large-scale camera trapping survey throughout Rhode Island, USA, sampling from 2018 to 2020. Using dynamic occupancy models, we found initial site occupancy was positively influenced by the amount of forested wetland habitat, while increasing road density and shrub cover negatively influenced the probability of site colonization. Surprisingly, we found no hypothesized variables to influence site-level extirpation probability, or any seasonal effects on dynamic parameters. Lastly, we found that forest cover and road density negatively influenced the probability of detection. The probability of occupancy was high, >0.8, throughout much of the study area (49%), but we also found relatively high site transients, with the probability a site would change occurrence status from season to season at ≈ 0.27 in the majority of the study area (70%). Our results show that although bobcats can persist in human-dominated landscapes, they require contiguous natural areas to do so. Future expansion of road infrastructure may reduce habitat connectivity and increase road mortalities, thus jeopardizing the population.

KEYWORDS

bobcat, camera traps, dynamic occupancy models, *Lynx rufus*, urbanization

1 | INTRODUCTION

Landcover change associated with human development is a driver of global biodiversity loss and wildlife population declines (Newbold et al., 2015). The increase of road infrastructure globally has specifically been linked to

negative effects on natural ecosystems and wildlife populations (Benítez-López et al., 2010; Trombulak & Frissell, 2000). These effects include increased wildlife road-mortality (Bennett, 2017) and population declines (Fahrig & Rytwinski, 2009), the creation of edge and barrier effects that reduce habitat suitability and animal

movement (Benítez-López et al., 2010; Riley et al., 2006; Shepard et al., 2008), and increased human access to natural areas (Benítez-López et al., 2010; Červinka et al., 2015; Forman & Alexander, 1998). While road surfaces and their maintained roadsides alone do not cover a large percentage of land (e.g., 1% of the landcover in the United States; Forman & Alexander, 1998), the density of roads in an area can be an indicator of the extent of the anthropogenic footprint (Forman, 2000; Forman et al., 2003; Frair et al., 2008).

The United States has been in a period of landscape change and loss of natural areas due to urbanization since the mid-1900s (Brown et al., 2005; Theobald, 2010). More recently, there has been an expansion of exurban areas (Brown et al., 2005; Hansen et al., 2005), which necessitates road infrastructure. The loss of natural areas and the continued expansion of roads is projected to continue for many more decades (Bennett, 2017; Theobald, 2010), necessitating an acute understanding of how wildlife populations will respond. While many wildlife species can be negatively affected by increased road infrastructure and urbanization, carnivores are especially sensitive due to their large space-use requirements, slower population growth rates, and low densities (Crooks, 2002; Moss et al., 2016; Wait et al., 2018). Large carnivore species, such as mountain lions (*Puma concolor*), are typically the most sensitive to urbanization and fragmentation, and often avoid areas with higher road densities and human-developed areas (Crooks, 2002). In contrast, mesocarnivores, including coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and striped-skunks (*Mephitis mephitis*), may adapt and can even thrive in areas with higher levels of human development (Bateman & Fleming, 2012; Prange & Gehrt, 2004; Wang et al., 2015). However, the extent of any species' ability to adapt to these landscapes can vary by the structure and extent of human development (Parsons et al., 2019).

Bobcats (*Lynx rufus*) are generally considered an adaptable mesocarnivore that range throughout Central and North America, occupying diverse landcover types (e.g., desert, boreal coniferous and mixed forests, and coastal swamps; Kelly et al., 2016). However, their response to anthropogenic development and specifically to road infrastructure has been highly variable. Many studies have found negative associations, such as the avoidance of paved roads (Lovallo & Anderson, 1996; Riley, 2006) and areas with high human activity (Goad et al., 2014), decreased survival rates (Blackburn et al., 2021), lower population densities (Lewis et al., 2015), and lower detection rates (Goad et al., 2014). Yet, due to their associations with heterogeneous forest structure and forest edges (Donovan et al., 2011; Tucker

et al., 2008), bobcats also have been found to be insensitive to urban landcover given the urban area is surrounded by sufficient forested areas (Wait et al., 2018). They also are known to move through developed areas when natural corridors are unavailable (Tigas et al., 2002).

With exurban development and road densities predicted to increase in the United States (Bennett, 2017; Hansen et al., 2005), understanding the impacts these have on sensitive species is critical for regional conservation planning. For bobcats, reconciling the combination of factors that lead them to thrive despite this development is needed. In the northeastern United States, most natural areas are in close proximity to developed landscapes with high human densities. Despite continued increases in human development, bobcats, a previously uncommon species in many areas, are expanding their populations (Roberts & Crimmins, 2010). Prior studies on bobcat distribution in the northeastern United States have focused on areas where road densities are relatively low and have small anthropogenic footprints (Litvaitis et al., 2015; Reed et al., 2017). As such, less is known about how bobcat populations respond to anthropogenic disturbances in areas with higher human and road densities.

Our objectives were to (1) establish a large-scale, non-invasive trail camera survey to detect bobcats in natural areas surrounded by varying levels of anthropogenic development (e.g., road density); (2) estimate how natural and anthropogenic landscape features affect seasonal changes (winter, summer) in site-level occurrence, colonization, and extirpation; and (3) predict bobcat occurrence throughout the landscape for regional conservation planning. We hypothesized that bobcat occurrence would be driven by both landcover and anthropogenic factors. Specifically, we predicted high bobcat occurrence throughout highly forested regions and that road density would negatively affect bobcats by making their use of sites transient across the seasons with low site-level colonization and high extirpation probability.

2 | METHODS

2.1 | Study area

Our study took place in Washington, Kent, and Providence counties of Rhode Island, USA covering a total land area of 242,745 ha (Figure 1). Rhode Island is located in southern New England and borders the Atlantic Ocean between 71°70 W and 71°530 W, and 41°80 N and 42°10 N. Forests cover over 55.6% of the land area of Rhode Island, with deciduous forests covering 32% of the

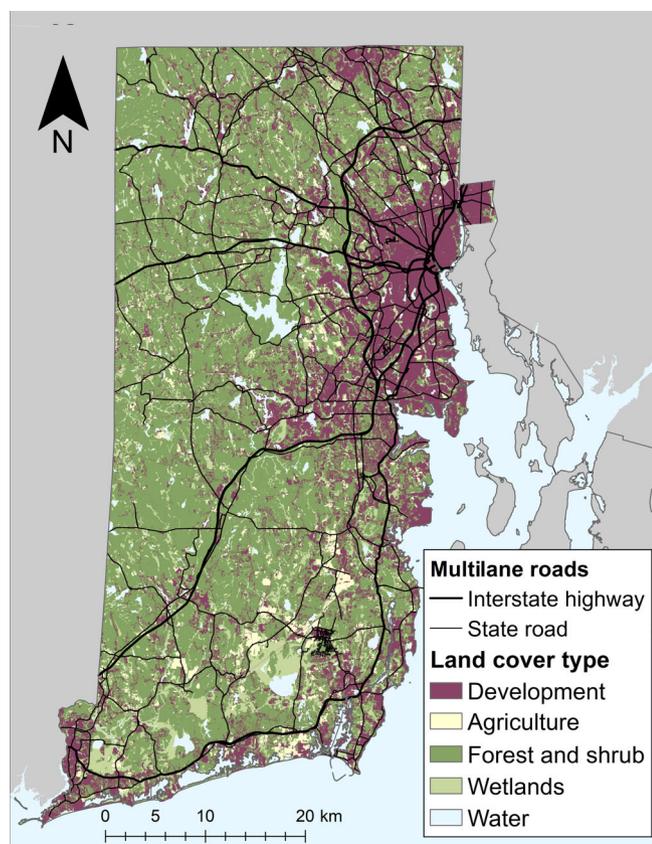


FIGURE 1 Map of the survey area in Rhode Island in the northeastern United States. The survey area is dominated by forested land cover; however, it is densely populated region and there are areas of high development along the coastlines with high road densities. Only major roads, including interstate highways and state-managed roads are depicted in this map [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

study area. The most common tree species in Rhode Island forests are red maple (*Acer rubrum*) and eastern white pine (*Pinus strobus*); (Butler, 2018). Forested wetlands are relatively common, covering 8% of the land area in the study area. This ecological community is more prevalent in Rhode Island, relative to the size of the state, than other states in New England (Anderson et al., 2013).

Rhode Island is the second most densely populated state in the United States (U.S. Census Bureau, 2021). In the study area, 27.5% is classified as developed land with 3.8% of developed land classified as high density residential (lots <1/8 acre), 33.5% classified as medium density residential (lots 1/8 to 2 acres), and 3.5% classified as low density residential (lots >2 acres). The average road density in our study area is 3.62 km/km² ($SD = 4.40$) ranging from 0 to 36.6 km/km². Excluding urban areas that were not surveyed (i.e., where road densities are >11.4 km/km²) the average road density is 2.69 km/km² ($SD = 2.76$); (URI Environmental Data Center & Rhode Island Geographic Information System, 2016).

2.2 | Camera surveys

We deployed camera traps throughout Rhode Island over three winters (November–March) and three summers (June–October; Table 1) from 2018 to 2020. Survey locations were selected by randomly placing points within accessible conserved land at a spacing of at least 4 km apart. In the field, we selected the survey site within 1 km of the original random point, so that the final spacing between survey sites was at least 2 km, which allowed us to reduce any spatial autocorrelation between sites while still allowing a scale that was fine enough to capture variation in microsites across the landscape. We attempted to select camera locations that would maximize detections of bobcats by targeting game trails, rock walls, and habitat edges.

During the first field season (winter 2018), we selected 40 sites in Washington County in southern Rhode Island to deploy one motion-triggered trail camera (Bushnell Trophy Cam, Bushnell Outdoor Products, Overland Park, KS, USA, or Browning Strike Force Pro XD, Browning, Morgan, UT, USA) for a 12-week period. Cameras were set to take three photos when triggered, with a 10-s delay between triggers. We applied a scent-based lure (Caven's Gusto, Minnesota Trapline Products, Pennock, MN, USA) to a tree in front of the camera at a height of approximately 1 m, and the lure was refreshed during the biweekly camera checks for the duration of the season. For the first summer field season (2018), we expanded the survey statewide for a total of 100 survey sites. Cameras were deployed for 6 weeks at each survey site, with one camera per site. Due to low detection rates during the first two field seasons, we added additional cameras to a subset of survey sites during winter 2019 to evaluate if increasing cameras at a site increased detection rates. We selected a subset of 20 previously surveyed sites in Washington County and added an additional one ($n = 10$ sites) or two ($n = 10$ sites) cameras within a 1-ha buffer around the original camera location (O'Connor et al., 2017), for a total of 20 sites and 50 cameras. Additionally, cameras were deployed for 20 weeks during this season to evaluate whether increasing the number of cameras at a site increased observations. We found the number of overall detections increased during this season, with all detections taking place at only a single camera at a site. Based on the results of the winter 2019 season, we added one additional camera, for a total of two cameras per site, to each survey site statewide ($n = 100$) for the remaining field seasons (summer 2019, winter 2020, summer 2020) and deployed cameras for 6 weeks during each season.

We used the photo database program Camelot (Hendry & Mann, 2018) to organize and identify species

TABLE 1 Survey effort by year and survey season, and bobcat detected each survey season in Rhode Island winter 2018 through summer 2020

Year	Season	Survey effort			Bobcat detections		
		Sites surveyed	Total cameras	Total effort (trap nights)	Total detections	Number of sites with detections	Number of sites with detections in the previous season
2018	Winter	40	40	3076	42	4	-
2018	Summer	100	100	4482	16	10	2
2019	Winter	20	50	6634	89	11	3
2019	Summer	100	200	7966	43	22	5
2020	Winter	100	200	8833	71	21	11
2020	Summer	100	200	8913	29	18	7

Note: Only one camera per site was deployed in 2018, and two cameras were deployed at each site from 2019 to 2020. A detection is counted as independent if the timestamp on the photos is ≥ 20 min apart. Bobcats were not always detected at the same sites each season, so we calculated the number of sites each season where a bobcat was detected in both the current and the previous season.

in each photo. We treated multiple photos of the same species as independent detections if the time between photos was >20 min. The data from multiple cameras within a single site were combined by concatenating the detection histories. A survey occasion was set to 7 days for subsequent occupancy analyses.

2.3 | Occupancy modeling

We used the detection/non-detection data from the camera survey to fit dynamic occupancy models to estimate site-level initial occurrence (ψ_1), colonization (γ), extirpation (ϵ), and detection probabilities (p ; MacKenzie et al., 2003). Based on habitat selection findings of bobcats in Rhode Island (Mayer et al., 2021), we selected a suite of landscape covariates that we hypothesized would affect each model parameter (Table 2). Covariates fell within two general categories: natural and anthropogenic features. Natural features included landcover types and site-specific characteristics, while anthropogenic features included the amount of development and road density at a site. Site-specific characteristics (e.g., trail, rock wall, or wetland edge) and distance to wetland (m) were recorded at each survey site. Landcover types were calculated as the percentage of total area, and road density was calculated as km/km², and each were calculated at 0.25 and 1.00 km² areas around each survey site, representing local and broader landscape scale conditions, respectively. By considering these two scales in separate analyses, we can better understand the drivers of bobcat occurrence within local areas of Rhode Island and at a broader scale.

For all considered models, ψ_1 was hypothesized to be influenced by percent forested wetlands within the survey grid (0.25 or 1.00 km² cell scale). Detection

probability is an estimate of relative activity (a joint product of abundance and individual movement rates) at occupied sites. As such, we hypothesized p would be influenced by percent upland and wetland forest cover, distance to wetland, road density within the survey cell, and site feature (Table 2). We hypothesized that γ would be influenced by combinations of natural and anthropogenic features and seasonal effects, and ϵ would be influenced by combinations of anthropogenic features and seasonal effects (Table 2). In a preliminary analysis, we separated the forest landcover variable by forest type (coniferous or deciduous) and modeled occupancy with these variables. There was no difference in overall effect of the model when compared to the simpler version where coniferous and deciduous forests were combined as percent total forests as a single covariate, so we chose the simpler covariate. We evaluated the correlation among covariates in the same submodel using the Pearson correlation coefficient (r). We found $|r| < 0.4$, except for road density and development ($r = 0.64$), which were used to model site-level extinction probability. However, the inclusion of these variables together did not change the estimated effects compared to when used separately. In total, we evaluated 33 models each for both survey scales (Table S1).

We fit dynamic occupancy models in a Bayesian framework using the R package “ubms” (Kellner, 2021) in R version 4.04 (R Core Team, 2021). We considered models at the two scales, 0.25 and 1.00 km² survey grid cell sizes, using separate model sets. All continuous covariates were centered at zero and scaled to unit variances. Thus, estimated coefficients are directly comparable as 1 unit change in SD of the covariate value. We evaluated model fit within a model set using the conditional predictive ordinate (CPO; Hooten & Hobbs, 2015)

TABLE 2 Description and justification of covariates used for occupancy (ψ_1), colonization (γ), extirpation (ϵ), and/or detection (p) in building dynamic occupancy models for bobcats in Rhode Island

Variable	Model use	Description	Justification
Forest	p	Percentage of all forested habitat (upland and wetland) within 250 or 500 m of survey location	Bobcats are often associated with forested areas (Donovan et al., 2011; Tucker et al., 2008). This landcover type provides shelter from developed areas. Large contiguous forested areas may limit detection.
Forest-wet	ψ_1, γ	Percentage of forested wetlands within 250 or 500 m of survey location	Previous studies have shown that bobcats prefer forested wetland areas (Mayer et al., 2021).
Distance to wetland	p	Distance (m) from survey site to nearest wetland edge	Bobcats are often found near wetland areas (Clare et al., 2015) and may be more likely to be detected in areas close to wetlands.
Road density	γ, ϵ, p	km of roads per km ²	Roads can be sources of mortality and may be avoided (Broman et al., 2014). Areas with high road density may increase detection due to limiting movements to other land classes.
Site feature	p	Hiking trail, game trail, wetland edge, or rock wall located at camera site	Cameras placed in an area with a noticeable feature may have higher detection of bobcats.
Developed	ϵ	Percentage of developed land within 250 or 500 m of survey location	Bobcats avoid developed areas and may leave an area that has high percentages of human development (Goad et al., 2014; Lovallo & Anderson, 1996; Riley, 2006).
Shrub	γ	Percentage of shrub habitats within 250 or 500 m of survey location	Shrublands provide shelter and hunting opportunities for bobcats (Fuller & DeStefano, 2003; Litvaitis, 2001).
Season	γ, ϵ	Survey conducted in winter (November–March) or summer (June–October)	The change between winter and summer may affect persistence of a bobcat in an area.
Season-year	γ, ϵ	Survey session (1–6)	There may be a change in occupancy rates over the course of the study period.

where smaller values indicate more support. We made inferences from the most supported models by investigating the size of estimated coefficients, whether the 95% credible intervals include zero, and the probability a coefficient was different than zero (derived as the number of posterior samples >0 or <0 , indicating positive or negative support, respectively). Further, we used these models to predict and map detection, occurrence, extirpation, and colonization throughout the study area. Occupancy was predicted at the equilibrium of colonization and extirpation for each site i where ($\psi_i^{eq} = \gamma_i / (\gamma_i + \epsilon_i)$); (MacKenzie et al., 2017). The equilibrium occurrence probability is helpful to capture a long-term perspective on site occurrence in a dynamic system. We did not predict values outside of the variation observed in covariate values, which eliminated the most urban areas of Rhode Island, leaving 92.89% of our initial study area remaining for predictive mapping. Lastly, we evaluated the amount of the landscape that is predicted to be used only transiently.

We quantified this by deriving site-turnover (τ), as the probability that sample site i changes occupancy state from one season to the next (i.e., occupied \rightarrow unoccupied or unoccupied \rightarrow occupied) as, $\tau_i = \psi_i \epsilon_i + (1 - \psi_i) \gamma_i$, where higher values of turnover (τ) indicate site transients.

3 | RESULTS

3.1 | Camera surveys

We surveyed 116 sites across six field seasons—three winters and three summers—for a total trap effort of 39,904 trap nights and collected over 335,000 images (Table 2). During the first two winter seasons, we did not complete a statewide survey of sites; however, during every summer season we had 100 survey locations statewide (Figure S1). We surveyed 19 sites for all six seasons,

19 sites for five seasons, 48 sites for four seasons, 14 sites for three seasons, one site for two seasons only, and 15 sites for only one season. Bobcats were detected at 48 sites during the study (27 sites in winter and 39 sites in summer), and there were 290 total independent detections (202 winter detections and 88 summer detections) with a minimum time between detections of 46 min. Bobcats were detected during a single field season only at 26 sites, and during all six field seasons at just one site.

During the first two field seasons when a single camera was deployed per site, 10% of sites on average had bobcat detections. In winter 2019, when multiple cameras were deployed at each site, average percentage of sites with a bobcat detection increased to 55%, with all independent detections occurring at a single camera at a site. The number of bobcat detections at sites with two cameras (76 detections at five sites) was greater than sites with three cameras (17 detections at six sites). Overall, the average time to first bobcat detection was 7.36 weeks

($SE = 1.44$), and the average detection rate was 0.72 detections/100 trap nights.

3.2 | Occupancy modeling

We found the same model was most supported (measured via CPO) at both spatial scales with the same overall inference from the estimated parameters (Table 3; Table S2). Notably, we found that the percentage of forested wetland habitat in the surrounding area positively influenced site colonization probability, and the percentage of road density and shrub habitats negatively influenced this probability (Figure 2). While there was uncertainty in all parameters at both scales, the probability of support for a negative effect was high for both road density (0.97 at the 0.25 km² scale; 0.96 at the 1.00 km² scale) and shrub habitat (>0.99 at the 0.25 km² scale; 0.98 at the 1.00 km² scale); (Table 3; Figure 2).

TABLE 3 Estimated mean coefficients, *SE*, 95% credible intervals, and the probability of a positive effect for the most supported models of dynamic bobcat occupancy in Rhode Island at two spatial scales

	0.25 km ² grid cell					1 km ² grid cell				
	Coefficient	<i>SE</i>	2.5%	97.5%	Prob. effect >0	Coefficient	<i>SE</i>	2.5%	97.5%	Prob. effect >0
Occupancy (ψ_1)										
Intercept	-7.66	3.98	-16.91	-1.91	5.00×10^{-4}	-4.72	3.05	-11.76	0.68	0.34
% Forested wetland	8.42	5.14	1.73	20.54	1.00	8.19	5.61	1.47	22.41	1.00
Colonization (γ)										
Intercept	0.58	1.13	-1.38	3.05	0.67	0.84	1.10	-1.03	3.24	0.78
% Forested wetland	1.95	1.32	-0.47	4.78	0.95	2.32	1.23	-0.06	4.83	0.97
% Shrub	-2.63	1.14	-5.22	0.87	2.5×10^{-4}	-0.77	0.49	-1.90	1.5×10^{-3}	0.02
Road density	-1.57	1.06	-3.94	0.10	0.03	-1.01	0.65	-2.48	0.07	0.04
Extirpation (ϵ)										
Intercept	-1.87	0.94	-4.20	-0.58	0.00	-1.77	0.79	-3.66	-0.58	0.00
Detection (p)										
Intercept (site feature: yes)	-3.34	0.19	-3.73	-2.99	0.00	-3.60	0.18	-3.95	-3.24	0.00
% Forest	-1.75	0.15	-2.03	-1.46	0.00	-2.04	0.17	-2.38	-1.73	0.00
Distance to wetland	-0.43	0.08	-0.58	-0.28	0.00	-0.41	0.08	-0.57	-0.25	0.00
Road density	-0.65	0.18	-1.00	-0.32	0.00	-0.94	0.16	-1.25	-0.64	0.00
Site feature: none	-8.75	5.92	-23.23	-0.98	2.5×10^{-3}	-9.02	5.95	-23.26	-0.98	2.2×10^{-3}

Note: Light gray cells indicate support for a positive or negative effect in that the probability of an effect >0 was either >0.95 or <0.05, indicating positive or negative support, respectively.

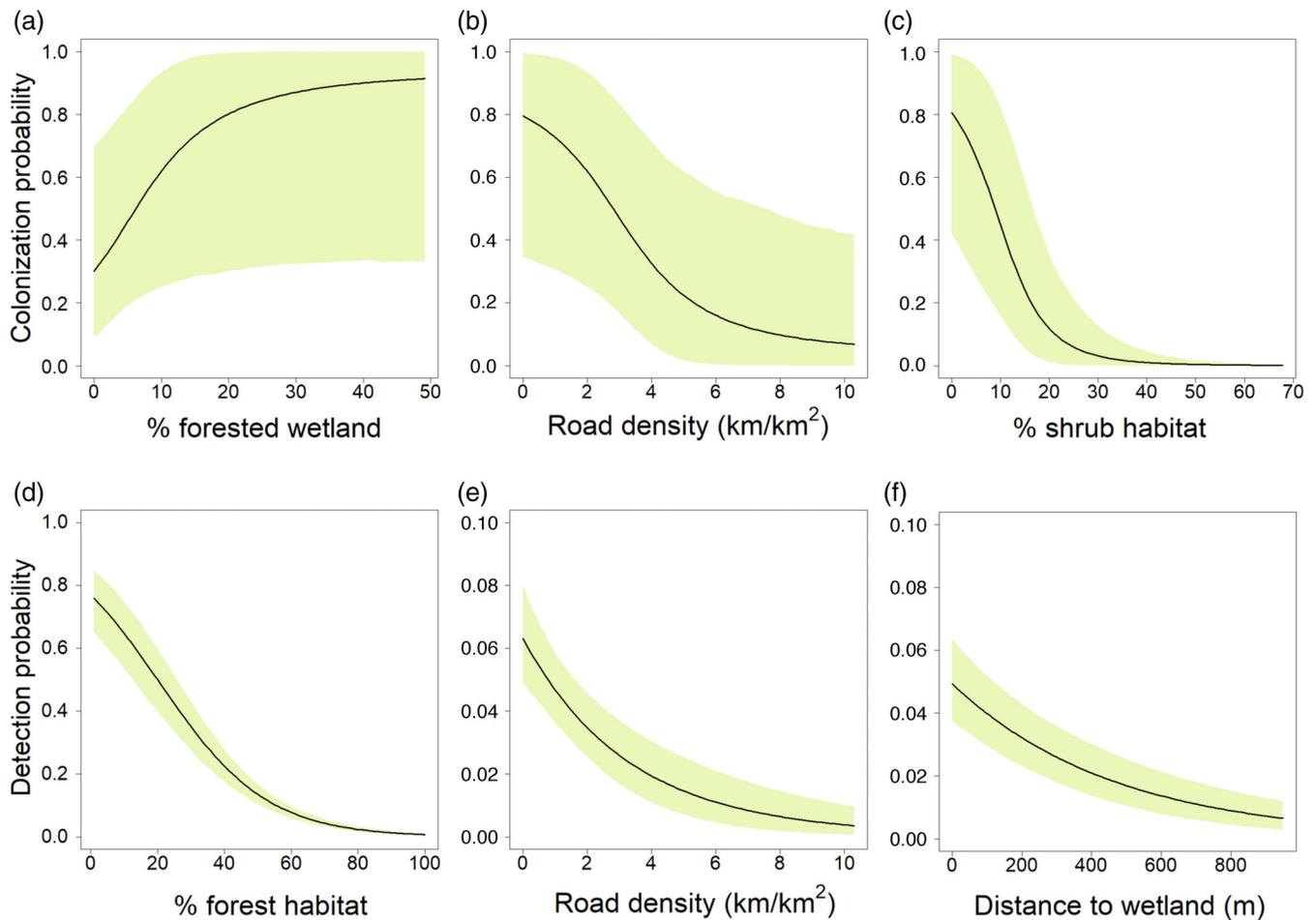


FIGURE 2 Marginal effect plots of the probabilities of (a–c) colonization (γ) and (d–f) detection probability (p) by covariate. Covariates are estimated from the most supported model (via conditional predictive ordinate) at a scale of 0.25 km^2 survey grids. The solid lines indicate the estimated mean and the shaded region indicates the 95% credible intervals. Covariates in the model that were not plotted for each subplot were held at their mean value [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/1438-390X.12123)]

Interestingly, we found no support for a seasonal (winter or summer) or seasonal by annual change (survey 1–6) in site-level colonization or extirpation. We found no hypothesized factor influenced the probability of extirpation ($\epsilon = 0.15$, $SD = 0.94$). Forested wetlands had a strong positive effect on the initial occupancy of a site (probability of effect = 1.00; Table 3; Figure 3).

A clear finding in our study was that p was very low per occasion, often less than 0.20 per occasion (i.e., 7-day period; Figure 2). However, we found that placing a camera at a site feature (e.g., stone wall or game trail) increased the probability of detecting bobcat, given they used the site. We also found that at both spatial scales, the higher percent of neighboring forested habitats—upland and wetland combined—reduced the probability of detection. This is presumably because bobcats have more cover to move through, compared to being funneled into a corridor in more fragmented areas. Further, we found that as road density and

distance from a wetland increased, the probability of detecting a bobcat decreased.

The variation of p across the study area was low, with slightly higher values along coastal areas and other bodies of water; however, the majority of the study area had detection probabilities below 0.20 (Figure 4). This was most likely due to the strong negative influence of forested habitats on detection probabilities, and the overall high amount of this landcover type within the study area (Table 3). Occupancy and colonization probabilities showed more variation across the study area, with areas surrounding urban centers and major interstates having lower probabilities of being occupied or colonized. Because both forests and forested wetlands were positively associated with occupancy in our models and the study area had a high overall percentage of these land cover types, 49% of our total study area had occupancy probabilities >0.80 . Site-turnover probabilities across the study area ranged from 0 to 0.27 (Figure 4). The majority

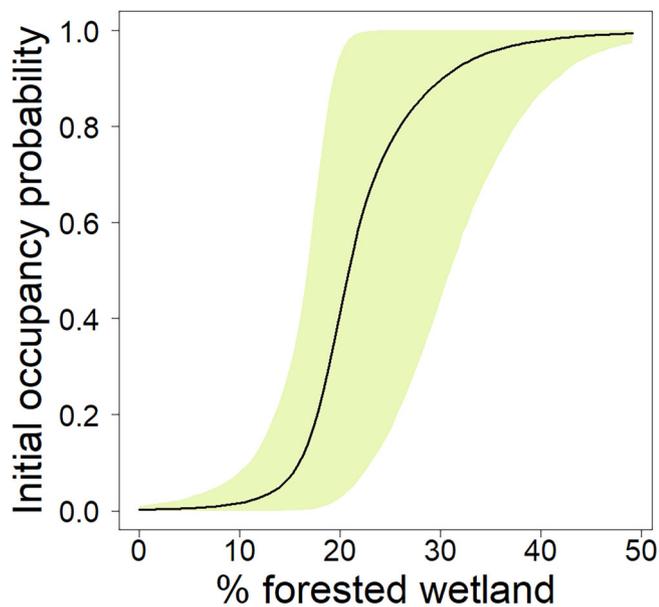


FIGURE 3 Marginal effect plot of the probability of initial occupancy (ψ_1). The covariate, percent of forested wetlands at a site, was estimated from the most supported model (via conditional predictive ordinate) at a scale of 0.25 km^2 survey grids. The solid lines indicate the estimated mean and the shaded region indicates the 95% credible intervals [Color figure can be viewed at wileyonlinelibrary.com]

of the study area (70%) had turnover probabilities near 0.27, with these locations corresponding to areas with both high occupancy and colonization probabilities.

4 | DISCUSSION

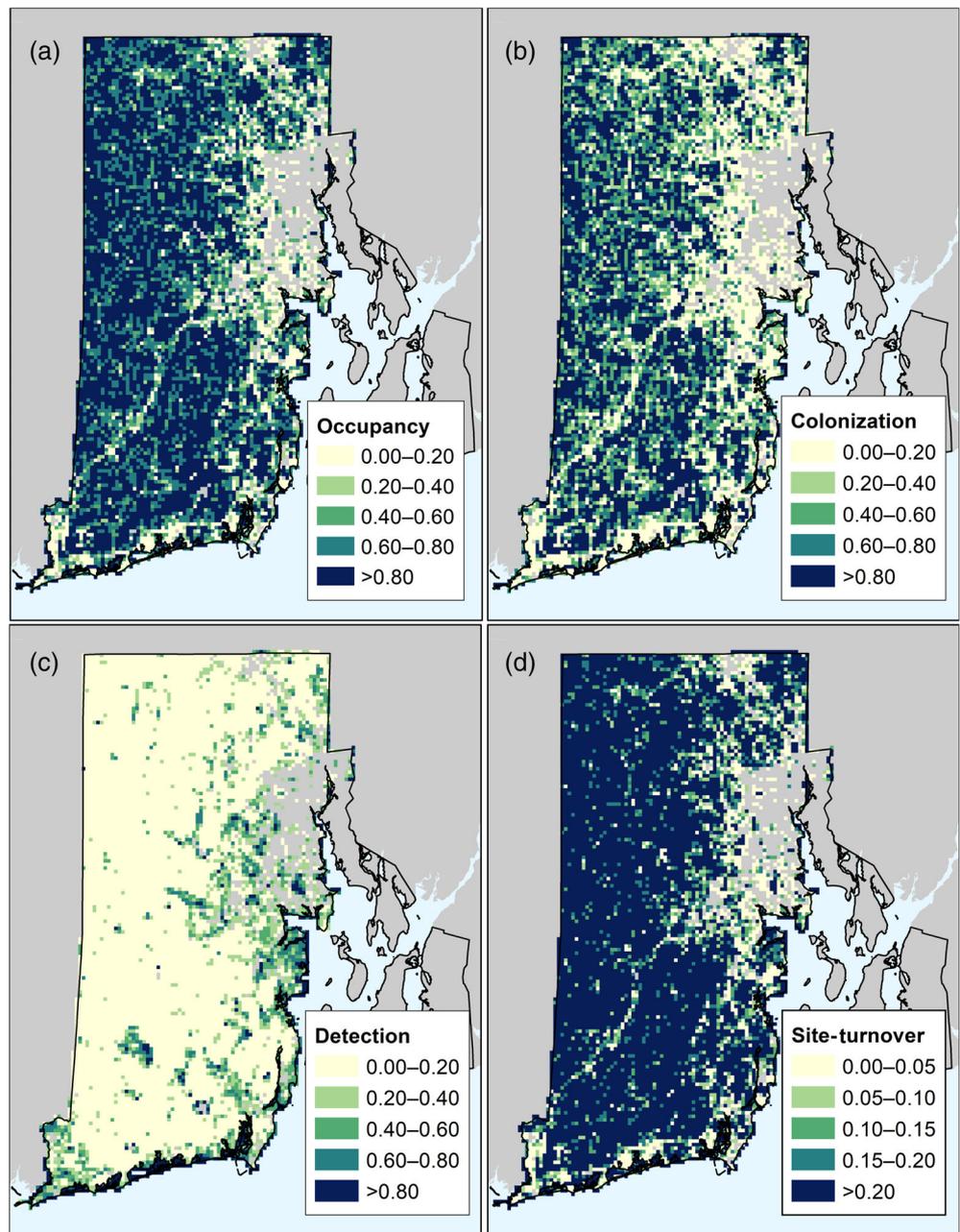
Our study aimed to identify landscape characteristics that influence bobcat occurrence, while focusing on how varying levels of road density and development affect their site-level occupancy dynamics over time in a densely populated, yet highly forested region of the northeastern United States. We hypothesized that bobcat occurrence would be positively influenced by natural landcover features including forest cover, but would be negatively influenced by road density. Bobcat landscape occupancy has been studied in many parts of the United States (e.g., Lombardi et al., 2020 [Texas]; Long et al., 2011 [Vermont]; Parsons et al., 2019 [Mid-Atlantic]; Wait et al., 2018 [Kansas]; Wang et al., 2015 [California]). However, most studies focus on the differences in occupancy between urbanized and wild or natural areas (e.g., Lewis et al., 2015; Lombardi et al., 2017; Parsons et al., 2019). Less attention has been paid to regions where the lines between natural and urbanized areas are not distinct and bobcats cannot avoid anthropogenic

features, such as roads. Previous studies on felids have found that areas with increasing road densities are associated with higher probabilities of mortality (Bencin et al., 2019; Blackburn et al., 2021; Litvaitis et al., 2015). Furthermore, natural areas surrounding areas of high road density are less suitable habitats and are generally avoided by bobcats (Donovan et al., 2011; Lovallo & Anderson, 1996; Reed et al., 2017).

We found that areas of high road density and shrub cover that were previously unoccupied by bobcats were unlikely to be colonized. In contrast, the more forested wetlands in a surrounding site had a positive influence on a site becoming colonized (Table 3). Considering the entire study area, sites that are more rural with less roads and anthropogenic development, and therefore fewer shrubby edge features caused by fragmentation, have higher likelihood of bobcat occurrence. Surprisingly, we found no hypothesized spatial or temporal drivers of site-level extirpation probability. Throughout the study area, seasonal site-level extirpation probability was estimated at a constant probability of 0.15, which across both seasons indicates an occupied site had a 0.28 probability of no longer being occupied the next year. In combining colonization and extirpation dynamics, we found the overall probability of site-occurrence at equilibrium was high, with 49% of the area having an occupancy probability >0.80 . The lowest occupancy probabilities occurred in areas surrounding urban areas with few natural areas. There was little difference in bobcat occurrence probability at equilibrium compared to predicted occurrence in the last sampling season.

We expected to observe temporal differences in site-level colonization and extirpation probabilities either seasonally (winter vs. summer) or over the course of our study (survey season 1 to survey season 6); however, neither season nor survey year was included in any of our most supported models for site-level colonization or extirpation. Prior studies have observed differences in resource selection between seasons (McNitt et al., 2020), so we expected to observe similar differences in site-level colonization and extirpation between seasons. The lack of a temporal response indicates that landcover and anthropogenic factors are the main drivers of bobcat occurrence. Litvaitis et al. (1987) found that there is significant site fidelity between seasons in resident adult bobcats, but juveniles and other transient individuals in the population do not show the same site fidelity. If the population is skewed more towards resident adults, this may explain why seasonal changes did not affect colonization or extirpation probabilities. However, this does not explain why there is relatively high site transients across the landscape. Bobcats appear to be consistently using the same features in the landscape, but not necessarily

FIGURE 4 Predictive maps of the (a) probability of occupancy at equilibrium of colonization and extirpation, (b) probability of site-level colonization (γ), (c) detection probability for a survey at a site (p), and (d) probability of site-level turnover from one season to the next. The maximum estimated probabilities were 0.87 for occupancy, 1.00 for colonization, 0.91 for detection, and 0.27 for site-turnover [Color figure can be viewed at wileyonlinelibrary.com]



the same exact sites from season to season. This suggests the possibility that home ranges or use within the home range are not stable, which could be indicative of a small dynamic population, which is more susceptible to extirpation.

Bobcats are cryptic and difficult to detect (Lewis et al., 2015), and while providing the habitat necessary for site occurrence, highly forested landscapes make detecting the species extremely difficult (Figure 3b). Our results showed that placing cameras at likely movement corridors or unique landscape features, including game trails, stone walls, or edges of two cover types (e.g., wetland/forest or forest/field edges), increased the probability of detection. While these fine-scale features

cannot be easily mapped at a larger scale and therefore were not incorporated into our predictive maps, this information is useful for maximizing detections in future surveys in areas with larger contiguous habitat patches. Lewis et al. (2015) found that detection probabilities are often higher in exurban and natural edges, rather than in larger natural patches; however, detection probabilities decrease with increasing development and human-use (Goad et al., 2014; Lewis et al., 2015; Wang et al., 2015). There also may be bias in detection probabilities due to camera placement in exurban areas where available survey locations are limited to fragmented pieces of natural habitat that wildlife use as corridors for movement. In these spaces, we would expect bobcat detection to be

higher as they are being funneled past the camera, compared to open forested space where their movement is less constrained by their environment. So although bobcats will often use areas with some development (Parsons et al., 2018; Wang et al., 2015), in many cases they are more likely to occupy natural patches (Parsons et al., 2019) where they are more difficult to detect. Additionally, the probability of detecting a bobcat decreased with increasing distance from a wetland. Wetlands and edges of these habitats generally have high increased prey density and are often selected for by bobcats (Clare et al., 2015; Stephens & Anderson, 2014). Our results may suggest that bobcats have decreased activity in areas further from wetlands and are thus more difficult to detect.

A possible contribution to our low detection probabilities may be the timing and duration of the surveys. Previous studies in the region have showed that young male bobcats have very large home ranges (Mayer et al., 2021), so while a camera may be placed within their home range, the extent of the animal's movements throughout their home range may preclude it from having the opportunity to pass by that camera within the 6-week survey period. Additionally, males typically have larger home ranges and higher frequency of movements within their home range than females as a result of breeding and kitten-rearing (Conner & Plowman, 1999; McNitt et al., 2020). These differences may affect the probability of detecting a female, and thus decrease overall detection probabilities. Given that the species is going through recent population growth following many years of being classified as rare (C. Brown, unpublished data), it is possible that low population densities are a contributing factor to low detection probabilities. An effective population size has been estimated at 82 with a 95% confidence interval of 44–329 (Mayer et al., 2021). Given the extent of our study area, 242,745 ha, this is an extremely low bobcat density. Further, our overall detections were low in general at 0.72 detections/100 trap nights over the course of the study compared to other studies that reported 3.8 detections/100 trap nights (Clare et al., 2014), 1.83 detections/100 trap nights (Clare et al., 2015), and 3.57 detections/100 trap nights (Harrison, 2006). This also suggests the population in Rhode Island is existing at low densities on the landscape.

Despite the low detection probability of bobcat throughout the study area, the probability of occupancy was relatively high in comparison (average across the study area, $\psi = 0.66$, $SD = 0.27$). Detections across seasons in this study (Figure S1) indicate that bobcat distribution is widespread. Forested wetlands, a natural landcover type that was found to be selected for by bobcats in a resource-selection model in the region (Mayer

et al., 2021), was positively associated with site occupancy and the probability of colonization of a new site. This is consistent with prior research showing forested areas, and forested wetlands in particular, are important habitats for bobcats (Broman et al., 2014; Donovan et al., 2011; Mayer et al., 2021; Reed et al., 2017), and that occupancy is positively influenced by forested areas (Wait et al., 2018). The average road density in our study area was 2.70 km/km² ($SD = 2.76$), and when comparing occupancy probabilities only in areas with higher than average road densities, the probability of occupancy at equilibrium reduced to 0.44 ($SD = 0.29$). These results indicate that bobcats are widespread throughout the fragmented landscape in this region, likely due to their preference for forested edges (Clare et al., 2015; Donovan et al., 2011; Tucker et al., 2008); however they are less likely to occur where the anthropogenic footprint is high and are thus sensitive to human development.

Overall, our results highlight both the adaptability of a mesocarnivore in an urbanized and fragmented landscape, as well as its sensitivity to areas with high road densities. Because bobcats are unlikely to colonize previously unoccupied sites if the road density is high (e.g., 6 km/km²), this could have conservation implications given the trend of increasing development in the region. Further, the expansion of the bobcat population throughout much of Rhode Island, after decades of landscape change and habitat loss (Novak & Wang, 2004), indicates that the species is able to survive in a highly altered landscape. Longer-term monitoring that directly compares changes to the landscape with changes to occupancy would provide more insight into the direct effect increasing road densities have on the population. Although unfragmented patches of natural habitat are better suited for supporting biodiversity in the region—particularly unfragmented forested areas to promote bobcat populations—species persistence is possible in high-human density regions. Conservation planning should focus on ensuring forest fragments are well connected with road densities that are less than 2 km/km² to support long-term occupancy of bobcat populations.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

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