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RESEARCH ARTICLE

Muskrat occurrence in Rhode Island shows little evidence of land use change driving declines

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Abstract

Muskrat (*Ondatra zibethicus*) populations have been in apparent decline across their native range in North America for decades. Several hypotheses exist for the causes of these declines, including loss of wetlands. We used time-to-detection data from 925 surveys from 276 sites across Rhode Island, USA, between 2021–2023 to fit an occupancy model that related the probability of muskrat occupancy at a site to land cover classification. We found that muskrat occupancy was higher in areas with more open water, urban land cover, or a second-order or larger stream, and lower in areas with salt water. We estimated changes in wetland area throughout Rhode Island using the National Land Cover Database classifications from 2001 and 2019 and found a net loss in wetland cover of 219 ha. We calculated the distance between wetland patches in each of these periods and found that patches were closer together than the dispersal distance of muskrats, suggesting isolation is unlikely to be driving muskrat declines. Additionally, when we used our model to predict changes in muskrat occupancy between 2001 and 2019, both mean and median predicted occupancy changed by <0.005. These results indicate that muskrat declines are not driven by habitat loss, and suggest future research is needed that focuses on other hypothesized mechanisms of muskrat declines such as disease, declining habitat quality, predation, and competition.

KEYWORDS
habitat loss, muskrats, occupancy, *Ondatra zibethicus*, Rhode Island, time-to-detection, wetland

Muskrats (*Ondatra zibethicus*) are an economically (White et al. 2015) and ecologically (Erb and Perry 2003, Kua et al. 2020) important semi-aquatic mammal species widely distributed throughout most of the United States and Canada, but they are currently declining in large portions of their native range (Ahlers and Heske 2017). Muskrats can live in a wide variety of wetland types, reproduce quickly, and develop a winter pelt that is economically valuable; these traits have historically made them one of the most widely harvested furbearer species in North America (White et al. 2015). Although muskrats preferentially consume plants such as cattails (*Typha* spp.), they can exploit a variety of food resources in wetlands that include most aquatic plants and some bivalves (Errington 1963). Muskrats have been declining throughout their native range in the last several decades (Roberts and Crimmins 2010, White et al. 2015, Ahlers and Heske 2017, Sadowski and Bowman 2021). These declines are concerning for the health and continued function of wetlands (Nyman et al. 1993) because muskrats are often the dominant herbivore in North American wetlands, where their population cycles can drive aquatic plant dynamics (Bomske and Ahlers 2021). Additionally, muskrats can be common, widespread, and urban-adapted (Cotner and Schooley 2011, Laurence et al. 2013). As wetland obligates (Errington 1963, Willner et al. 1980) their habitat has been more protected from conversion in the decades in which they have declined than in the previous 2 centuries, when wetland loss was relatively rapid and extensive (Davidson 2014), which makes their declines surprising. Ahlers and Heske (2017) proposed 5 hypotheses for declines in muskrat abundance including habitat loss or isolation, habitat degradation, changing hydrology, competition or predation, and shifting fur-harvest culture. Additionally, they considered the possibility that declines in trapping effort are driving declines in harvests but do not reflect an underlying change in muskrat abundance, although Sadowski and Bowman (2021) showed that muskrat declines in Ontario, Canada, were true declines in population rather than changes in harvest effort. These hypotheses are not mutually exclusive; changes in harvest effort (Roberts and Crimmins 2010, Ahlers et al. 2016*a*, Ahlers and Heske 2017; Figure 1) could co-occur with changes in muskrat population size. Further, habitat loss, degradation, and changing hydrology may be linked to climate change and land use change for wetland species such as muskrats (Mantyka-Pringle et al. 2012, Ahlers et al. 2015, Segan et al. 2015).

Although declines in muskrat harvest are largest in the southeast and western United States (Ahlers and Heske 2017), muskrat harvest declines in the northeastern United States have been evident for at least a decade (Roberts and Crimmins 2010). The northeastern United States has undergone several large shifts in land use in the past 2 centuries, with widespread conversion of forests to agriculture followed by reforestation as human populations increasingly concentrated in coastal cities. Muskrat populations persisted in the region through these changes despite trapper harvests more than an order of magnitude greater than present-day harvests (White et al. 2015, Ahlers and Heske 2017; Figure 1), indicating that while harvests may have significant impacts on muskrat populations today, trapping pressure alone is unlikely to have caused muskrat declines in the region.

Rhode Island is the smallest and second-most densely populated state in the United States (U.S. Census Bureau 2020) and is broadly similar to other northeastern states. Rhode Island is heavily urbanized, highly forested, and contains many coastal and inland wetlands. Muskrat harvests have declined in the state as in other areas of the northeast United States; continuous records of harvests collected by the state go back to 1952 and demonstrate that muskrat populations were large enough at the time to sustain annual harvests of as many as 10,000 (Figure 1), but harvests declined over the last half of the twentieth century and have not exceeded 1,000 since 1987. Major changes in Rhode Island wetland communities in recent decades include the invasion of common reed (*Phragmites australis*; Saltonstall 2002), the reintroduction of beavers (*Castor canadensis*) beginning in 1976, and the colonization of coyotes (*Canis latrans*) into the state starting in the 1960s. Wetlands in the Great Lakes region have experienced significant changes due to the invasion of narrowleaf cattail (*Typha angustifolia*) and the hybrid *Typha* × *glauca*; however, these invasions are not as extensively documented in New England and may have occurred earlier (Shih and Finkelstein 2008). These changes have likely altered the food available to muskrats and the predation and competition regime in Rhode Island wetlands. However, given that these changes were simultaneous with declining trapping effort, it is difficult to separate their effects on muskrat population and distribution. Until the turn of the century, the pattern in annual muskrat harvest mirrored the pattern in trapper license sales in the state (Figure 1),

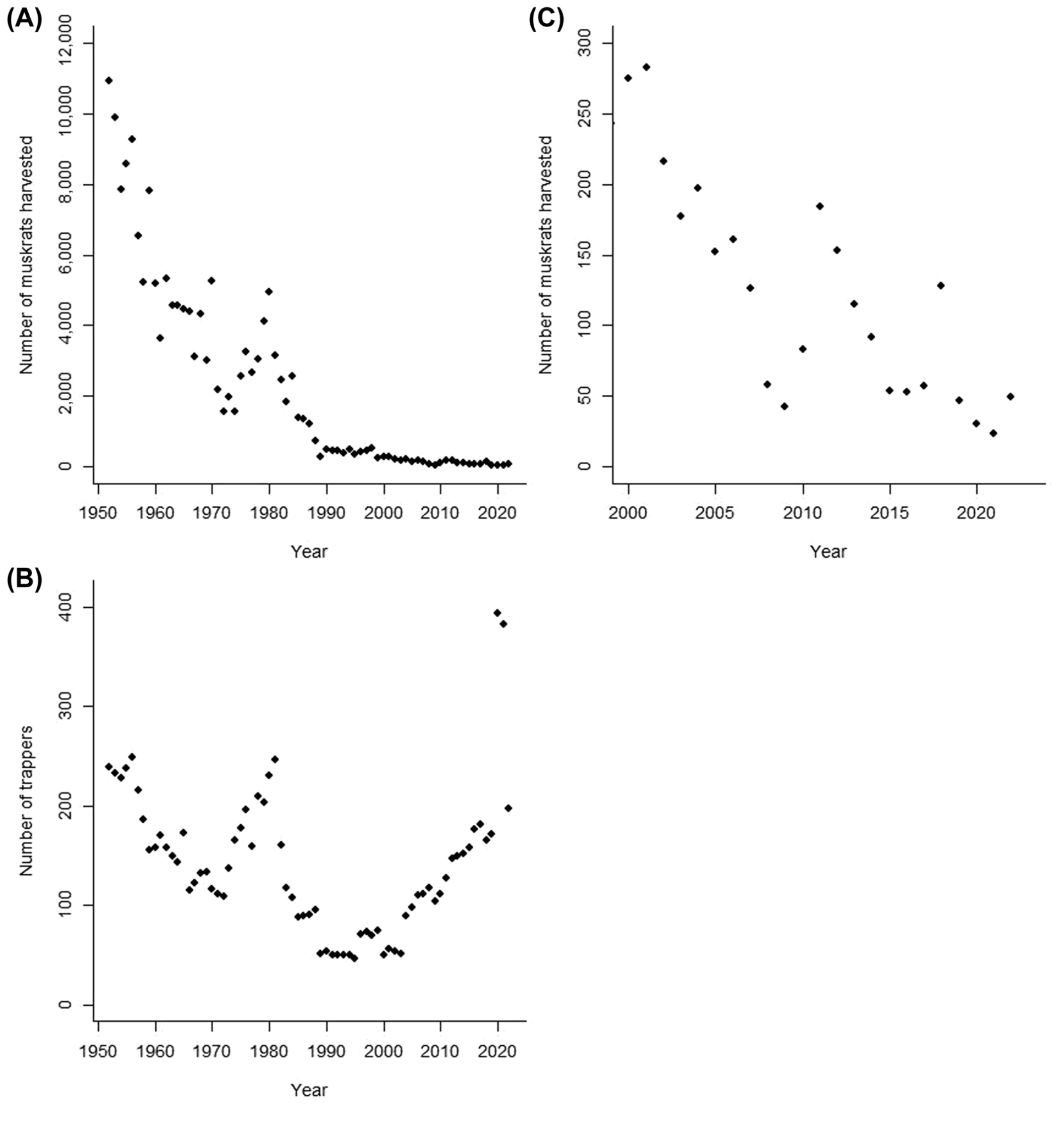

FIGURE 1 The number of muskrats harvested (A) and trapper license sales (B) in Rhode Island, USA, by year from 1952 to 2022. Panel (C) shows the number of muskrats harvested in Rhode Island during our study period from 2000 to 2023.

but since then trapping license sales have increased while muskrat harvests have not; this shift may be due to higher interest in beaver and fisher (*Pekania pennanti*) trapping, 2 species that have increased in population during this time.

Rhode Island's small size provides an opportunity to survey a large proportion of the state, allowing for a statewide assessment of relationships between muskrat occurrence and predictors, such as land cover, while Rhode Island's similarities to neighboring states should allow inferences to be broadly applicable to other northeastern states. Wildlife management benefits from an understanding of species distributions (Elith and Leathwick 2009), and an understanding of the current distribution of muskrats in Rhode Island would benefit land managers in prioritizing areas for conservation and would provide a baseline for future monitoring that could be linked to harvest levels or other management decisions. Additionally, understanding muskrat distribution would allow us to test the hypothesis that habitat loss is driving muskrat declines in the state by evaluating whether areas associated with muskrat occurrence have declined along with muskrat harvests.

We used a time-to-detection occupancy model (Garrard et al. 2008) to assess the impact of land cover variables on the probability of muskrat occupancy in mainland Rhode Island, predicting that muskrat occupancy would be higher in areas with a greater proportion of wetland land cover (Errington 1963) and a lower proportion of urban land cover. We also estimated the amount of wetland lost in our study area from 2001 to 2019, hypothesizing that if habitat loss is driving muskrat population declines, then we should see a decline in wetland areas. We were unable to test for population declines directly, but we assessed declines indirectly by assuming habitat loss would result in declines in occurrence, which is well known to generally relate to regional abundances (Gaston et al. 2000, Noon et al. 2012).

STUDY AREA

We sampled wetlands and waterbodies throughout the contiguous terrestrial landscape of Rhode Island, including all parts of the state draining into Block Island Sound (excluding Block Island) or Narragansett Bay via the Blackstone River or streams to its west and south (Figure 2), an area of 236,288 ha. The northern and western portions of the study area are in the Southern New England Coastal Plains and Hills ecoregion, while the eastern portion is in the Narragansett/Bristol Lowland and the southern portion is in the Long Island Sound Coastal Lowland (Griffith et al. 2009). The study area is dominated by forest (48% of the study area) and urban (28%) land cover types, but extensive wetlands exist throughout the state (forested wetlands, open wetlands, and water cover 15% of the study area). Elevation varies from sea level to 247 m, with higher elevation areas in the north and west. Most of the study area has a cold winter, warm summer climate without a dry season (Koppen classification Dfb), but some of the more coastal regions have a hot summer climate (Dfa; Peel et al. 2007). Precipitation is relatively constant throughout the year, with the lowest mean monthly precipitation in June (7.62 cm) and the highest in March (10.36 cm; Lawrimore et al. 2011). We established a grid covering the sampling area with each grid cell being square with sides of 0.5 km in length. Sites (i.e., cells from this grid) were available for selection if they had ≥5% of their

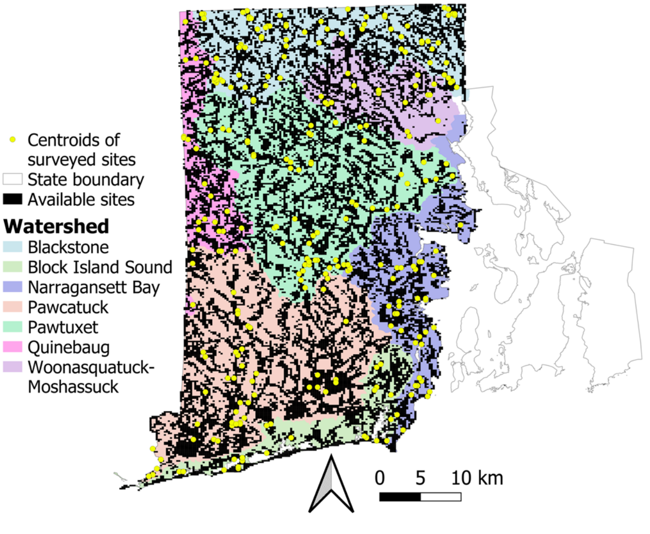

FIGURE 2 The sampling frame for muskrat sampling within Rhode Island, USA, in 2021–2023. The state boundary is outlined in light gray. We used watersheds to stratify the selection of sites. Small black squares indicate a site available for sampling and yellow circles indicate the centroids of sampled sites.

area covered by wetland or water and <95% of their area covered by water. Because of concerns about excluding streams, we also included sites that did not meet these criteria but had at least a second-order stream flowing through them. The resulting sampling frame consisted of 17,101 sites.

METHODS

Data collection

We stratified by watershed and randomly selected sites within each watershed. We surveyed the Pawcatuck River, Block Island Sound, and Quinebaug River watersheds in 2021, Pawtuxet River and Narragansett Bay watersheds in 2022, and Blackstone River, Woonasquatucket River, and Moshassuck River watersheds in 2023. Each year we selected 150 sites in each watershed and surveyed as many as we could access. We surveyed sites once in winter and once again in summer, allowing for 4 surveys of most sites, with at least 2 observers and 2 visits.

We surveyed for muskrats on foot and kayak by searching for muskrat sign along the shoreline of wetland areas at each site. Two observers were present on each survey, in which they noted the time and sign type of each muskrat sign encountered (i.e., scat, lodges, or feeding platforms). Surveys continued until the observers had covered all of the accessible wetland area in the site (i.e., excluding areas that could not safely be reached by foot on walking surveys, or which would have required extensive mid-survey portages on kayak surveys). We used these data to calculate the time from the start of the survey to the first detection of muskrats by each observer in each survey (TTD_{ij}, the time to first detection at site i on survey j). To avoid misclassification, observers photographed muskrat signs when they encountered them and recorded uncertainty in species assignment; if reviewing the photograph at a later date was insufficient to resolve uncertainty, we dropped the record from the data. We also removed from the data signs that we believed were older than one year (i.e., muskrat lodges that did not appear to be actively maintained).

In the initial selection of sites from the sampling frame, we calculated the proportion of sites covered by land cover classes using the land use and land cover (2011) dataset available from the Rhode Island Geographic Information System (RIGIS 2014), which provided a land cover class for every part of the state. To understand the relationship between muskrat occupancy and land cover, we used the National Land Cover Database (NLCD; U.S. Geological Survey 2003, Dewitz 2021). The NLCD has land cover classifications for the state from 2001 to 2019 using similar methodologies and classification and a consistent 30-m resolution, which allows valid comparisons between different time frames (Dewitz 2021). We reclassified the NLCD data from 2019 and 2001 into 9 classes: open water, urban, barren land, forest, shrub or scrubland, grassland, agricultural, forested wetland, and open wetland. We then calculated the proportion of each site in our sampling frame covered by each land cover class using the exactextractr package in R (Baston 2023). We predicted that the proportion of a site covered by open water, open wetlands, and forested wetlands would be positively associated with muskrat occupancy, as these are all wetland types that muskrats can occupy (Willner et al. 1980). We did not expect to encounter muskrat sign in truly open water, but our site selection criteria excluded sites that were more than 95% open water; sites with a large amount of open water always had some other land cover type in them. Additionally, because of classification difficulties, we expected that some areas considered open water in the NLCD data may be open wetland. Muskrats can tolerate urban areas (Cotner and Schooley 2011, Laurence et al. 2013), but we expected that there would be a small negative relationship between the proportion of a site covered by urban areas and muskrat occupancy.

Because the NLCD does not distinguish between fresh and salt water, we also considered an indicator variable that was equal to 1 for sites that contained salt water, intertidal rivers and creeks, salt marsh, or intertidal areas in the RIGIS 2011 data, and a 0 otherwise. We expected a negative association of muskrat occurrence with salt water because the coastal wetlands have daily fluctuations in water level, many forage plants preferred by muskrats are negatively correlated with salinity (Dozier et al. 1948, Daiber 1972), and sheltered coastal waters of Rhode Island (especially southern Rhode Island) are highly saline. We calculated the presence of second-order or greater streams based on the statewide rivers and streams dataset also available from RIGIS. Muskrats often use bank dens along streams (Willner et al. 1980, Erb and Perry 2003), so we predicted that the presence of streams would be positively associated with muskrat occupancy.

We expected that muskrat detection would be easier in sites surveyed by kayak because we found most muskrat sign along the edge of the water. We obtained weather variables using the openmeteo package in R (Pisel 2023) to access Open-Meteo (Zippenfenig 2023). We used the first recorded location of an observer in a site as the time and location for the openmeteo query and obtained the temperature and cloud cover at the start of the survey (rounded to the nearest hour) and the total precipitation in the previous 24 hours. We expected lower detection after heavy precipitation, and on cloudy days because precipitation could either cover up (in the case of snow) or wash away (in the case of rain) signs of muskrat presence. If detection was dramatically different in summer or winter, or if detection was lower on particularly cold days, we would expect temperature at the start of the survey to affect time to detection. We matched the global positioning system locations of each observer, taken once per minute, to the RIGIS land use and land cover 2020 dataset (RIGIS 2022) to calculate the proportion of time the observer spent in wetlands, water, or urban areas. We expected that areas with high predicted muskrat occupancy might have larger populations and more sign available for detection, so we expected shorter times to detection in wetlands and water and longer times to detection in urban areas.

To evaluate whether the total amount of muskrat habitat in the state had declined and if habitat patches were becoming more isolated, we compared wetland areas (i.e., emergent herbaceous wetland and woody wetland) throughout Rhode Island between 2001 and 2019 using the NLCD. We hypothesized that if muskrats were declining because of habitat loss, we would observe a decline in the total amount of wetlands available or that many wetland areas would be converted into land cover classes that do not provide habitat for muskrats. Habitat isolation could drive muskrat declines even if the isolation of habitat patches occurred in years before the year range of our data (Tilman 1994, Hylander and Ehrlén 2013), but if isolation is driving muskrat declines, we would expect wetlands to be more isolated in 2019 than they were in 2001, and habitat patches to be farther apart than maximum dispersal distances of muskrats.

Data analysis

Muskrat occupancy

We implemented a time-to-detection occupancy model (Garrard et al. 2008, Kéry and Royle 2015) where the realized presence ($z_i = 1$) or absence ($z_i = 0$) of muskrats at site i followed a Bernoulli distribution with a probability of occupancy ψ_i, where $\text{logit}(\psi_i) = \boldsymbol{\beta} \times \boldsymbol{w_i} + \gamma_w$. In this equation, $\boldsymbol{w_i}$ is a vector of site-specific covariates such as the proportion of the site covered by each land cover class, $\boldsymbol{\beta}$ is a vector of associated coefficients, and γ_w is the effect of watershed w and is treated as a random effect, where $\gamma_w \sim \text{Normal}(0, \tau_w)$.

Given muskrat presence, we considered time to detection at site i during survey j (TTD_{ij}) to follow a Weibull distribution with shape v and scale λ. The scale parameter λ was related to site- and survey-specific covariates such that $\log(b_{ij}) = \boldsymbol{\alpha} \times \boldsymbol{x_{ij}}$, where $\boldsymbol{x_{ij}}$ is a vector of covariates associated with a survey, $\boldsymbol{\alpha}$ is a vector of associated coefficients, and $b = \lambda^{-v}$. Non-detections of muskrats in our survey could indicate either absence of muskrats or that they were present but not detected, which the time-to-detection model treats as having an estimated time to detection that exceeds the length of the survey. To link the detection and occupancy components of the model, we included a censoring equation in which $d_{ij} \sim \text{Bernoulli}(\theta_{ij})$, where d_{ij} is equal to 0 if the observer detected muskrats during the survey and 1 if not. Following Kéry and Royle (2015), θ_{ij} was an indicator that was equal to 1 if $TTD_{ij} > TMax_{ij}$ and equal to $1 - z_i$ if $TTD_{ij} \leq TMax_{ij}$. Here, $TMax_{ij}$ is the total time spent on the survey. Although surveys were initially separated by season, we did not retain this structure in the analysis; however, season effects would likely be apparent in the effect of temperature.

We implemented this model in a Bayesian context using prior distributions intended to be relatively uninformative (Northrup and Gerber 2018). We used logistic priors on each β, normal priors on each α, and gamma priors on τ_w and v. For logistic priors, the location parameter was 0 and the scale parameter was 1. Normal priors had a mean of 0 and a variance of 3.33. Gamma priors had a shape of 1 and a rate of 1. We fit models with Markov chain Monte Carlo (MCMC) methods in JAGS (Plummer 2003) via the runjags (Denwood 2016) package in R version 4.2.1 (R Core Team 2022). We report coefficient estimates as posterior medians ($\hat{\beta}$) and 95% highest posterior density intervals (HPDI) and we estimated the probability of support for each prediction by calculating the proportion of posterior samples in which the coefficient was estimated in the same direction as the prediction; a probability of >0.90 indicates strong statistical support, >0.70 but <0.90 indicates moderate support, and >0.50 but <0.70 indicates weak support. Probabilities of support <0.5 indicate no support for the predicted effect.

Wetland change

To understand whether wetland loss or isolation is driving muskrat declines in Rhode Island, we analyzed whether wetland extent or isolation has changed in the past 2 decades using NLCD data. To test for wetland declines, we reclassified the NLCD data from 2001 to make a raster that was equal to 1 if the land cover classification was 90 (woody wetland) or 95 (emergent herbaceous wetland) and 0 otherwise. We multiplied this raster by the 2019 NLCD data to get a raster showing only land cover in 2019 that had been wetland in 2001. We summed the number of pixels in each land cover class and multiplied by 0.09 (the proportion of a hectare covered by a single 30-m pixel) to convert the number of pixels to area in hectares of each land cover class. To understand whether wetland losses were offset by gains, we also did this same operation in reverse to find the land cover classification in 2001 of areas that were classified as wetland in 2019. We performed all raster manipulations in R using the raster package (Hijmans 2022). To test whether wetlands were becoming more isolated (by straight-line distance), we used the landscapemetrics package (Hesselbarth et al. 2019) to find the mean and standard deviation of the Euclidean distance (measured from patch edge to patch edge) from a patch to its nearest neighbor of the same class for 2001 and 2019.

To more directly test whether cover types associated with muskrat occurrence have declined, we used the estimated coefficients from our occupancy model and land cover classifications from the 2001 NLCD data to obtain predicted muskrat occupancy in 2001 and 2019. Assuming stable relationships between muskrat occupancy and land cover classifications in this period, we estimated the expected change in muskrat occupancy due solely to changes in land cover.

RESULTS

Muskrat occupancy

We surveyed 90 sites in winter 2021, 65 in summer 2021, 95 in winter 2022, 69 in summer 2022, 94 in winter 2023, and 68 in summer 2023. We did not re-survey some sites in summer because they lacked deep water or wetlands of any kind and thus did not provide habitat for muskrats. The survey length ranged from 4–133 minutes, with a median length of 29 minutes.

We found strong support that muskrat occupancy was higher in sites with second-order or greater streams ($\hat{\beta}_{\text{stream}}$ = 0.66, HPDI = −0.31, 1.7) and sites with more of their area covered by water ($\hat{\beta}_{\text{water}}$ = 0.49, HPDI = −0.18, 1.5) but no support for our prediction that muskrat occupancy was lower in sites with more of the grid cell covered by urban areas ($\hat{\beta}_{\text{urban}}$ = 0.70, HPDI = −0.014, 1.8; Figure 3; Table 1). Given other variables were held at their mean

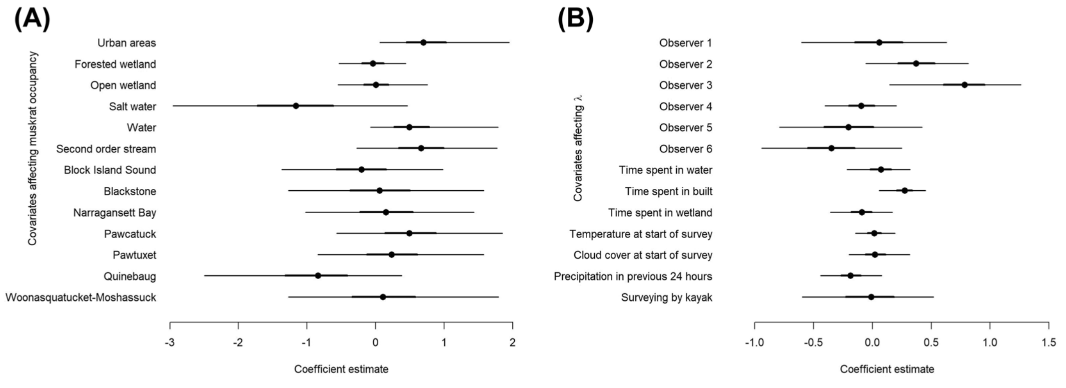

FIGURE 3 Posterior estimates of coefficients affecting muskrat occupancy (A) and the Weibull scale parameter (λ; B) throughout Rhode Island, USA, in 2021–2023. The circles indicate the posterior median, while the thin lines show the 95% credible intervals and the thick lines show the 50% credible intervals. Occupancy coefficients (A) are on the logit scale; positive numbers indicate a higher probability of muskrat occupancy. Larger Weibull scale parameter coefficients (B) correspond to shorter times to detection and higher probabilities of detection. Coefficients for observers represent differences from the grand mean.

TABLE 1 Site-level covariates used to predict muskrat occupancy in Rhode Island, USA, in 2021–2023, including data from the National Land Cover Database (NLCD) and Rhode Island Geographic Information System (RIGIS).

Site-level covariate	Description	Predicted effect on muskrat occupancy	Probability of support[a]
Water	Proportion of site covered by water in NLCD 2019 data	Positive	0.952
Second-order stream	Presence of a second-order or larger stream in RIGIS freshwater rivers and streams data	Positive	0.917
Urban areas	Proportion of site covered by urban areas in NLCD 2019 data	Negative	0.014
Salt water	Proportion of site covered by salt water, estuaries, or tidal rivers and streams in RIGIS 2011 data	Negative	0.923
Open wetland	Proportion of site covered by open wetlands in NLCD 2019 data	Positive	0.509
Forested wetland	Proportion of site covered by forested wetland in NLCD 2019 data	Positive	0.433

[a]Calculated as the proportion of posterior samples in which the coefficient was estimated in the same direction as the prediction.

levels and the site had neither salt water nor second-order streams, increasing proportion of urban land cover from 0 to 1 resulted in an increase in predicted occupancy from 0.43 to 0.89; increasing water cover from 0 to 0.95 resulted in an increase in predicted occupancy from 0.50 to 0.93. A site with mean land cover values that had a second-order or greater stream had a predicted occupancy of 0.77, while a site without a stream had a predicted occupancy of 0.55. We also found strong support that muskrat occupancy was lower in sites with salt water ($\hat{\beta}_{salt}$ = −1.2, HPDI = −2.9, 0.53; a site without a second-order or larger stream that had salt water had a predicted occupancy of 0.28 versus 0.55 for a similar site without salt water. Occupancy also varied by watershed, although the effects were small for most watersheds (Figure 3). Predicted muskrat occupancy varied throughout our sampling frame across Rhode Island from 0.20 to 0.97 (Figure 4) with a median of 0.56 (HPDI = 0.44, 0.70).

We found strong support that the time to first detection for muskrats varied by observer (Figures 3 and 5) and precipitation, and a strong effect (in the opposite direction of our prediction) of time observers spent in urban areas (Figure 3; Table 2). We found moderate support for variation in time to detection by the time observers spent in open water or wetland (i.e., woody wetland or emergent herbaceous wetland, but this effect was in the opposite direction of our prediction), and weak or no support for an effect of temperature, mode of survey, or cloud cover on time to detection. It took less time to detect muskrats if observers spent more time in urban areas (α_{urban} = 0.28, HDPI = 0.068, 0.46). It took longer to detect muskrats if observers spent more time in wetlands ($\alpha_{wetland}$ = −0.091, HPDI = −0.354 , 0.174) or if there was more precipitation in the previous 24 hours (α_{precip} = −0.186, HPDI = −0.443, 0.075). The overall probability of detecting muskrats was low; averaging across covariates (including observers), a walking survey that lasted an hour would have a 0.36 probability of detecting muskrat sign, given occurrence (Figure 5). The shape parameter was <1 (v = 0.579, HPDI = 0.509, 0.653), indicating that the hazard for detection of muskrat sign declines further into the survey.

Wetland change

Most areas of Rhode Island that were classified as wetland in 2001 remained wetland in 2019 (Table 3); 98% of areas that were wetland in 2001, or 29,508 ha, remained wetland in 2019. Across our study area, there was a gross loss of 481 ha and a net decrease of 219 ha of wetland from 2001 to 2019. Areas that were wetland in 2001 and not wetland in 2019 tended to be converted to open water, and most areas that were wetland in 2019 but not in 2001 were open water in 2001. Barren land and forest were more likely to be converted into wetland than to have

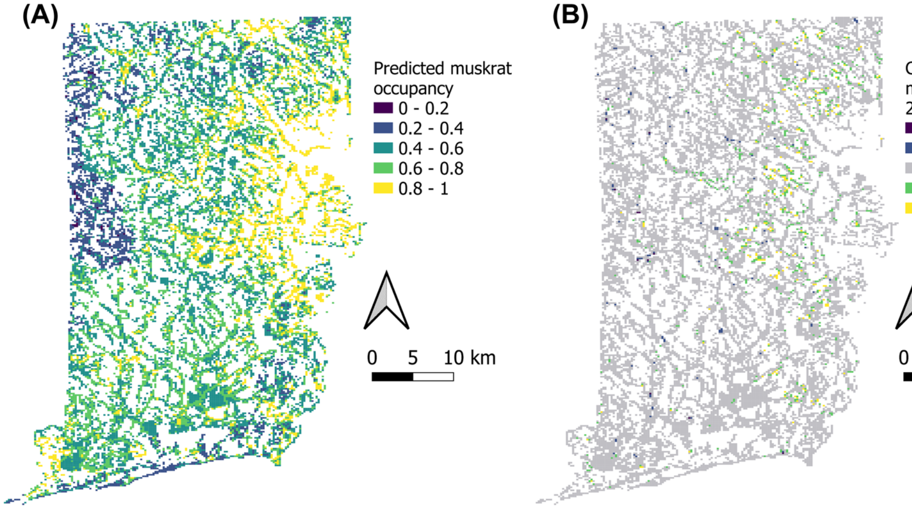

FIGURE 4 Predicted probability of muskrat occupancy (A) across the sampling frame in Rhode Island, USA, using the median value for all coefficients and 2019 land cover data and changes in predicted muskrat occupancy (B) from 2001 to 2019, using the median values for all coefficients. In frame A, blue shading indicates lower predicted occupancy, while yellow shading indicates higher predicted occupancy. In frame B, blue shading indicates areas where predicted occupancy declined between 2001 and 2019, yellow areas are where it increased, and gray areas are where the magnitude of the change was <0.05.

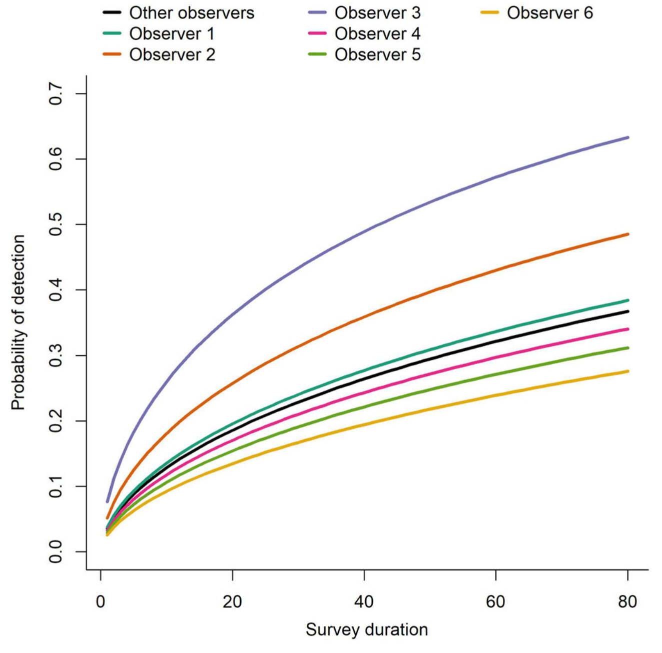

FIGURE 5 The cumulative probability of detection of muskrat sign over time (minutes) for surveys conducted on foot by each observer, keeping all other covariates at their median values. Sampling for muskrat sign occurred between 2021 and 2023 in Rhode Island, USA.

TABLE 2 Survey-specific covariates used to predict time to detection of muskrats in Rhode Island, USA, in 2021–2023.

Survey-level covariate	Description	Predicted effect on muskrat detection	Probability of support[a]
Urban	Proportion of time the observer spent in urban areas	Negative	0.007
Water	Proportion of time the observer spent in water	Positive	0.706
Wetland	Proportion of time the observer spent in wetlands	Positive	0.239
Temperature	Temperature in Celsius at the start of the survey	Positive	0.565
Cloud cover	Proportion of the sky covered by clouds at the start of the survey	Negative	0.429
Precipitation	Total precipitation in the previous 24 hours	Negative	0.919
Kayak	Whether the survey was done by kayak	Positive	0.485

[a]Calculated as the proportion of posterior samples in which the coefficient was estimated in the same direction as the prediction.

TABLE 3 Change in land cover classification in our study area in Rhode Island, USA, given that it was classified as wetland in either 2001 or 2019. The gain column shows the area in hectares in each land cover class in 2001, given that it was either forested wetland or open wetland in 2019. The loss column shows the area in hectares in each land cover class in 2019, given that it was classified as either forested wetland or open wetland in 2001. For both columns, the forested wetland and emergent wetland rows reflect areas that remained wetland from 2001 to 2019.

Land cover class	Gain from 2001 to 2019	Loss from 2001 to 2019
Open water	244.71	256.50
Forested wetland	1545.03	1,516.32
Emergent wetland	27,963.54	27,992.25
Shrub scrub	0.90	0.90
Grassland	0.54	1.35
Barren land	2.61	0.81
Agriculture	0.90	0.18
Forest	12.24	0.81
Urban	0.00	220.77
Total	29,770.47	29,989.89

wetland converted into them, but no areas that were classified as urban in 2001 became wetland by 2019, while 220 ha that were wetland in 2001 were converted to urban land.

Open wetlands in 2019 had a slightly higher mean (209.9 m) and standard deviation (298.8) of Euclidean distance between patches than in 2001 (mean = 194.3 m, SD = 271.7). Similarly, forested wetlands had a higher mean (127.8 m) Euclidean distance between patches than in 2001 (125.9 m), although the standard deviation of distance between patches was lower in 2019 (104.5) than in 2001 (103.6).

Most sites in our sampling frame had similar predicted muskrat occupancy when using 2001 and 2019 land cover classifications (Figure 4); 94.6% of sites had a change in predicted occupancy between −0.05 and 0.05. Most sites saw very small decreases in predicted occupancy from 2001 to 2019 (the median change was −0.0039), but a few saw large increases, and the mean change (0.0006) was very slightly positive.

DISCUSSION

Our results indicate that declines in muskrat harvest in Rhode Island during the study period were not primarily caused by habitat loss. Land cover classes associated with higher muskrat occupancy have not seen large declines in the past 2 decades (Table 3), and predicted muskrat occupancy based on those land cover classes has remained constant in most of our sampling frame (Figure 4). Of course, occupancy is not a direct measure of abundance. Within-site population dynamics can lead to declines in abundance without extirpation, such that occupancy does not decline. However, these declines cannot be attributed to habitat loss without habitat loss occurring.

Although more wetland area was lost than was gained between 2001 and 2019, both the net change and total wetland loss were small (net change of 219 ha, or <1% of the wetlands in the study area in 2001; gross wetland loss of 481 ha), and areas with increasing urbanization had higher predicted occupancy in 2019 than in 2001. Wetlands continue to decline globally (Fluet-Chouinard et al. 2023), but wetland loss in North America has slowed in recent decades (Davidson 2014). Our analysis treats all wetlands gained and lost as the same, which ignores the potential for time lags between the loss or gain of a habitat and the resulting extinction or colonization (Watts et al. 2020). Because muskrats are wetland obligates that reproduce quickly and have a short lifespan, they are unlikely to exhibit long time lags between habitat loss and local extinction (Figueiredo et al. 2019), but there may be a significant lag between wetland creation and colonization by muskrats. Treating wetland lost and gained as equal may also not reflect differences in habitat quality between newly created wetlands and lost wetlands. Human-created wetlands such as mitigation wetlands may have a much lower value to muskrats than the wetlands lost (Brown and Veneman 2001, Walker et al. 2009). However, natural processes such as beaver dams leading to pond formation and ponds converting to open wetland may lead to high-quality new habitat for muskrats. Additionally, in areas where the land cover classification changed between wetland and water, this may represent misclassification in one year or the other rather than a true change in the landscape. Open wetland and open water in particular may be hard to distinguish between (Wickham et al. 2017) when the open water has large amounts of submerged aquatic vegetation. Muskrats often prefer habitats where wetland and open water are interspersed at a finer scale than the NLCD is able to capture (Proulx and Gilbert 1983), and may themselves influence shifts in the classification of an area (i.e., muskrats can reduce vegetation sufficiently for an area to shift from being classified as open wetland to being classified as water). Similarly, our results do not show that wetlands in Rhode Island have become more geographically isolated; the average distance between wetland patches was greater in 2019 than 2001 but remained small relative to the home range size (500–800 m in restricted linear habitats, Ahlers et al. 2010; 0.24–3 ha depending on the estimator used, Ganoe et al. 2021; 2.5 ha for translocated muskrats, Matykiewicz et al. 2021) and dispersal capability of muskrats (10–20 km in Finland, Artimo 1960; 30 m–5 km, Errington 1963; significant gene flow and no isolation between watershed in a ~10-km^2 landscape, Laurence et al. 2013; 2 km post-release for translocated muskrats, Matykiewicz et al. 2021), suggesting that the average wetland patch had other wetland patches within easy dispersal distance. However, connectivity between patches is not merely a function of distance (Fahrig et al. 2021) but is affected by the matrix between habitat areas; areas of open water with high fetch (Larreur et al. 2020) and urban or forested land (Laurence et al. 2013) may expose muskrats to higher predation risk (relative to sheltered wetlands and streams) when attempting to cross them, and increasing urban and forest cover in Rhode Island therefore may lead to decreasing functional connectivity, which we did not attempt to measure.

Urban wetlands are frequently characterized as low-quality (Walsh et al. 2005, McGrane 2016), but we found a positive relationship between muskrat occupancy and the proportion of a site covered by urban areas, and faster times to detection on surveys when the observer spent more time in urban areas. This supports the idea that muskrats are tolerant of urbanization (Cotner and Schooley 2010, Laurence et al. 2013, Magle et al. 2021). Sadowski and Bowman (2021) also found no evidence of habitat loss as a driver of declining muskrat abundance in Ontario, suggesting this pattern is consistent across large parts of the native range of muskrats.

Surprisingly, we found no support for a positive effect of the proportion of wetlands in a site on muskrat occupancy. However, our sampling frame only included sites with at least 5% of their area covered by wetlands (or a second-order or larger stream), and muskrat home ranges can be smaller than 5% of a site's area (Ahlers et al. 2010, Ganoe et al. 2021, Matykiewicz et al. 2021). Muskrat preference for water depths >0.5 m (Allen and Hoffman 1984) may lead to stronger associations between muskrat occupancy and open water or large streams than either of the wetland classifications in the NLCD. Some wetland areas were frozen solid (i.e., they were shallow enough that when frozen had no liquid water remaining in the wetland) when visited in winter, which would render them unsuitable as muskrat habitat (Allen and Hoffman 1984), while larger lakes and streams maintain open water in the winter (and most rivers in the state have warm effluent inputs).

Given the lack of evidence of extensive habitat loss in our study period, and therefore lack of support for habitat loss as a driver of muskrat declines in Rhode Island, we suggest that muskrat declines in the region are linked to other changes, such as a decline in habitat quality, shifting predation and competition regimes, and changing hydrology (Ahlers and Heske 2017). Muskrat habitat quality could be declining without the overall amount of wetlands decreasing. This could be due to environmental contaminants, such as heavy metals or herbicides and pesticides from lawns and agricultural areas (Ganoe et al. 2020), or invasive plant species such as narrowleaf cattail or the hybrid *Typha* × *glauca*, which along with the native broadleaf cattail (*Typha latifolia*) form an invasive complex (Shih and Finkelstein 2008, Ciotir et al. 2013, Freeland et al. 2013). However, Larreur et al. (2020) found positive effects of an invasive plant species on muskrat occupancy, and invasive *Typha* hybrids are more common in the Great Lakes region than in New England (Freeland et al. 2013). In some areas, changing hydrology has been implicated in muskrat declines (Ouellet and Morin 2006, Greenhorn et al. 2017). Rhode Island's streams and rivers are extensively dammed, leading to many changes from natural flow regimes; however, the historical (steadier summer flows to power mills) and modern (steady supplies of drinking water in large reservoirs and flood control) uses of Rhode Island's dams tend to lead to steady releases of water rather than the dramatic daily changes in water levels associated with hydropower installations. Changes in water level in Rhode Island streams or wetlands hydrologically connected to streams are more likely due to precipitation, or to tides in wetlands connected to the ocean.

Higher muskrat occupancy in urban areas could be due to decreased predation risk in these areas; coyotes (Way et al. 2004, Mitchell et al. 2015), foxes (LeFlore et al. 2019), and American mink (*Neogale vison*; Wolff et al. 2015, Ahlers et al. 2016*b*) avoid these areas, and trapper pressure is likely lower in urban areas relative to rural areas (Poudyal et al. 2008, Cotner and Schooley 2011). This pattern may suggest support for the shifting predation and competition hypothesis, although many predators of muskrats have remained present before and after their declines, including mink, which saw similar declines in apparent abundance as muskrats (Ahlers et al. 2021). The shifting competition hypothesis of Ahlers and Heske (2017) focuses on the introduction of nutria (*Myocastor coypus*), which do not occur in Rhode Island. However, beavers have been reintroduced into Rhode Island in the past half century and these introductions may have altered wetlands in rural areas of Rhode Island, although the expected shift from forested wetland or forests to open water should be expected to produce higher muskrat occupancy. Beaver introductions have had significant impacts on both the land cover and hydrology of wetlands; their dam-building leads to more open water, lower nutrient export from small streams and wetlands into larger streams, and decreased canopy cover (Brazier et al. 2021). However, these beaver-driven impacts on hydrology may be offset by shifts in the precipitation regime driven by climate change (Horton et al. 2014) and by increasing urbanization in the region (Feng et al. 2021), both of which may make wetlands more flood-prone.

Our results suggested that researchers interested in muskrat occupancy should be prepared to conduct multiple surveys to ensure detection because the overall probability of detection on a 1-hour survey was low; to reach an overall probability of detection of 0.85, as recommended by MacKenzie and Royle (2005), we would need to conduct 5 hour-long walking surveys. However, shorter surveys may be preferable because we estimated the shape parameter (v) to be <1, such that the cumulative probability of detection at an occupied site reaches 0.2 after the first 20 minutes but doesn't reach 0.4 until 80 minutes of surveying (Figure 5). This may mean that observers were giving up early on sites that had muskrat sign (either leaving before they had surveyed the whole site thoroughly, in the case of sites with partial accessibility, or by losing focus and looking less carefully later in surveys). Additionally, the probability of occupancy was higher and the time to detection lower in urban areas, indicating that a sampling scheme could include fewer, shorter surveys in urban areas.

The lower time to detection we found in urban areas, and to a lesser degree in water, may reflect the lack of complexity in those land cover classes and the higher speeds the observers could achieve in them; observers kayaking along a lake shore or walking along a paved shoreline are able to focus on the shoreline and move quickly from one point that looks promising to another, while observers walking through a swamp may take much longer to get to an area that looked like it might have muskrat sign. Muskrats maintain high activity levels in cold months (MacArthur 1980), so we should not expect lower rates of sign deposition in cold weather, but longer times to detection in cold weather may reflect the difficulty of accessing and moving through iced-over sections of wetlands.

We suggest additional research focused on the underlying mechanisms limiting muskrat distribution in rural areas. Mark-recapture studies that more closely link wetland characteristics to survival or recruitment in populations or radio-tracking studies to understand the sources of mortality may be better able to discriminate between remaining hypotheses for muskrat declines.

CONSERVATION IMPLICATIONS

Our results highlight a need to conserve urban wetlands and streams and more natural landscapes in rural areas; despite their frequent characterization as poor quality, urban wetlands provide a refuge for muskrats. Our results further indicate that maintaining wetland area on the landscape, particularly without regard to wetland quality, is not sufficient to maintain muskrat populations given that declines in harvests continued throughout our study area despite little change in wetland area. Effective muskrat conservation will require a better understanding of the drivers of declines within populations.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

We carried out data collection on publicly accessible lands in Rhode Island or with permission from relevant landowners. No animals were handled in the course of this project, which was observational in nature and received appropriate approval from the funding agencies.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at https://zenodo.org/doi/10.5281/zenodo.12208226.

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