High individual variability in space use by translocated, imperiled New England cottontail (*Sylvilagus transitionalis*)

Wales Carter[1], Thomas J. McGreevy Jr.[1], Bill Buffum[1], Roland J. Duhaime[1], Nicholas T. Ernst[2], Dylan Ferreira[3], Thomas P. Husband[1], Brian C. Tefft[3], Andrea M. Petrullo[1], Brian D. Gerber[1]

1. University of Rhode Island, 1 Greenhouse Road, Kingston, RI 02881, USA
2. Rhode Island National Wildlife Refuge Complex, U.S. Fish and Wildlife Service, 1040 Matunuck School House Road, South Kingstown, RI 02813, USA
3. Rhode Island Department of Environmental Management, 277 Great Neck Road, West Kingston, RI 02892, USA

Correspondence: Wales Carter, University of Rhode Island, 1 Greenhouse Road, Kingston, RI 02881, USA. Email: wales_carter@uri.edu

Abstract

Translocations are an established element of restoration plans for threatened species, but success in establishing new populations is often limited, highlighting the need for careful evaluation of translocation efforts. Variation among individuals may contribute to poorly placed translocations, particularly when there is variation in the spatial ecology of target species. As a test of this we investigated the spatial ecology of imperiled New England cottontail (*Sylvilagus transitionalis* Bangs, 1895) in Rhode Island, USA. We combined telemetry data with remotely-sensed vegetation data to evaluate the home ranges, resource selection, and survival of translocated cottontails at three sites, including one where we also tracked resident cottontails. Despite instances of alignment among individuals, we found a wide span of home range estimates and high individual variability on resource selection. Both of these results suggest that population-level inferences of translocated individuals may fail to capture important aspects of animal ecology at the individual level. Further, we found lower survival compared to residents at one of our sites and literature values for other resident populations. Our results suggest that there are benefits to considering variation among individuals when designing management plans to support translocations.

Keywords

GPS telemetry, home range, LiDAR, New England cottontail, resource selection, survival, *Sylvilagus transitionalis*, translocation

Introduction

As awareness has grown about widespread species population declines, reintroductions and other translocations have been increasingly applied as conservation strategies for threatened populations (Seddon et al. 2014). However, reintroductions can have low success rates (Griffith et al. 1989; Fischer and Lindenmayer 2000), indicating the need for careful evaluation of individual restoration plans as efforts progress. Likewise, understanding the drivers of variation in translocated animal behavior and success provides important feedback to further improve translocation methodologies and release site selection (Seddon et al. 2007). One potentially important factor is the well-established observation of individual-level behavioral variation in numerous species (Smith and Blumstein 2013; Merrick and Koprowski 2017), and multiple studies have documented substantial variation in resource selection and use of space (e.g., Montgomery et al. 2018; Harris et al. 2019; Milligan et al. 2020). The presence of unacknowledged variability among individuals can undermine the value of population-level inferences for conservation planning, as average parameter estimates can misrepresent the behavior of many individuals (Dzialak et al. 2011; Merrick and Koprowski 2017; Montgomery et al. 2018; Milligan et al. 2020). In extreme cases, ignoring individual differences can lead to a substantial misalignment between used and protected areas (Perrig et al. 2020). Accordingly, when tracking the progress of translocation efforts, it is critical to evaluate the variation among individuals in key ecological parameters.

One key ecological parameter is space use, with estimates of home range size for relocated individuals providing value to translocation managers by assessing the spatial requirements and, in aggregate, territoriality of the focal species (Burt 1943; Spencer 2012; Fozzi et al. 2023). This information can then inform future conservation efforts by helping to estimate appropriate reserve sizes (Bruinderink et al. 2003) and to project target species densities (Kramer and Chapman 1999). Another factor potentially limiting the success of translocation efforts is habitat quality (Cook et al. 2010, Bubac and Johnson 2019, Berger-Tal et al. 2020). Habitat use and corresponding quality have been effectively evaluated for mammalian species ranging from elk (*Cervus canadesis* Erxleben 1777) to anteaters (*Myrmecophaga tridactyla* Linnaeus, 1758) and bats (*Myotis evotis* H. Allen 1864) using a resource selection framework (e.g., Johnson et al. 2004; Blanco et al. 2015; Anthony and Sanchez 2019; Smith et al. 2019). These and other such studies have been able to confirm the use of conservation areas maintained for translocated individuals and to identify environmental features that are favored and can serve as targets for habitat management efforts. Home range size and resource selection have commonly been estimated as averages across populations (Gillies et al. 2006; Thomas and Taylor 2006), and so evaluating these patterns at the individual level may offer novel insights into their variability and lead to more robust inferences.

The New England cottontail (*Sylvilagus transitionalis* Bangs, 1895) is a species of greatest conservation need in the Northeastern United States and the focus of a large scale reintroduction and translocation effort by state biologists, federal biologists, and numerous other partners (Young Forest and Shrubland). The New England cottontail is an obligate shrubland species, the only rabbit native to the Northeastern United States, and has experienced an estimated 86% decline from its historic range due to habitat loss and fragmentation (Litvaitis et al. 2004). This reduction has restricted the species to just five geographically isolated populations spread across the states of New York, Connecticut, Rhode Island, Massachusetts, New Hampshire, and Maine (Litvaitis et al. 2004; Fenderson et al. 2011) and led to the species being considered for Endangered Species Act listing in 2006 (USFWS 2006). More recent occupancy analyses of New England cottontail distribution show a 50% decline in occupied sites during the decade preceding 2017/2018 (Rittenhouse and Kovach 2020). Moreover, the declines have made New England cottontail the focus of a large proactive regional effort to conserve the species by restoring approximately 15,000 ha of early successional habitat and releasing captive-bred individuals into certain areas (Fuller and Tur 2012). In Rhode Island, a state with very low occurrence of New England cottontail (only two positive detections in 1235 pellet samples; Sullivan et al. 2019), conservation plans have prioritized the translocation of individuals to establish an island breeding colony as a source of rabbits to reestablish and augment populations at mainland sites.

Our goal was to assess individual variation in the home range size and fine-scale resource selection of radio-collared translocated captive-bred and wild-caught New England cottontails, with a secondary goal of estimating survival times of translocated rabbits. Evaluating the spatial ecology of the New England cottontail may offer valuable insights into the design and progress of recovery efforts for this species and by evaluating home range size and resource selection at the individual level, this study provides an excellent opportunity to consider the potential role of variation among individuals in the success of a translocation program. Moreover, although other rabbit species have been the focus of translocation efforts (e.g., lower keys marsh rabbit [*Sylvilagus palustris hefneri* Lazell, 1984]: Faulhaber et al. 2006; European rabbit [*Oryctolagus cuniculus* Linnaeus, 1758]: Cabezas and Moreno 2007; swamp rabbit [*Sylvilagus aquatics* Bachman, 1837]: Watland et al. 2007; pygmy rabbit [*Brachylagus idahoensis* Merriam, 1891]: Lawes et al. 2013; Gallie and Hayes 2020), our study is one of few to investigate the animals' third order selection of resources in translocation sites, and, to our knowledge, the only one to use the high-resolution data on individuals afforded by Geographic Positioning System (GPS) collars. Studies on fine scale resource selection also are often limited by the availability of high-resolution data on vegetation structure (Ciuti et al. 2018). We used a novel combination of LiDAR data and traditional GIS datasets to characterize the combinations of resources available to New England cottontail for selection.

Previous studies on resident New England cottontail have in select cases documented, but rarely focused on individual variation in behavior. For home range size, translocated animals will be occupying unfamiliar areas, and so we predict that they will use space less efficiently and therefore exhibit larger home range size than previously found (< 2 ha, Litvaitis et al. 2008, Cheeseman et al. 2019, but see larger estimates in Kilpatrick and Goodie 2020). Similarly, Eline et al. (2023) found translocated New England cottontail displayed more time vigilant and moving than resident animals during the initial period post release. For resource selection, previous studies in other areas occupied by remaining resident New England cottontail populations have found that their preferences for areas with dense understory and relatively high, closed overstory are relatively consistent (Litvaitis et al. 2003; Buffum et al. 2015; Cheeseman et al. 2018; Mayer et al. 2018), and so we expected to find similar preferences. Finally, estimates of the survival rates of New England cottontail are scarce in southern New England (Barbour and Litvaitis 1993; Brown and Litvaitis 1999; Kilpatrick and Goodie 2020), but there is evidence translocated New England cottontail initially have higher level of activity and movement compared to resident animals (Eline et al. 2003), which could increase their exposure to predators if they have larger home range sizes. Thus, we expected to observe shorter lifespans for translocated animals than in prior studies on resident animals.

Materials and Methods

Ethics Statement

All efforts followed ASM guidelines (Sikes 2016) and have been conducted under the approval of the University of Rhode Island's Institutional Animal Care and Use Committee (AN11-012-11). The authors declare no conflicts of interest.

Study Area

The three study sites, two mainland (Great Swamp Management Area and Ninigret National Wildlife Refuge) and one island (Patience Island), were all located in Rhode Island (Figure 1). Great Swamp Management Area is approximately 1,406 ha, located in South Kingstown, and owned by the state of Rhode Island and managed with a combination of mowing and timber harvests. Common tree species there include red maple (*Acer rubrum* L.), red oak (*Quercus rubra* L.), white oak (*Quercus alba* L.), Atlantic white cedar (*Chamaecyparis thyoides* L.), white pine (*Pinus strobus* L), and American holly (*Ilex opaca* Aiton). The Division of Fish and Wildlife actively manages the habitat for early successional forest (approximately 40 ha) and annually stocks pheasants for hunting, which may support predator populations. Mammalian species documented depredating New England cottontails include coyote (*Canis latrans* Say, 1823), bobcat (*Lynx rufus* Schreber, 1777), red (*Vulpes vulpes* Linnaeus, 1758*)* and gray foxes (*Urocyon cinereoargenteus* Schreber, 1775), fisher (*Pekania pennanti* Erxleben, 1777), raccoon (*Procyon lotor* Linnaeus, 1758), skunk (*Mephitis mephitis* Schreber, 1776), mink (*Neogale vision* Schreber, 1777), and weasels (*Mustela* spp.). The elevation at Great Swamp Management Area ranges from approximately 30 to 50 m above sea level (asl). Ninigret National Wildlife Refuge (NWR; Salt Pond Unit) is approximately 347 hectares, located in Charlestown, and owned by the United States Fish and Wildlife Service. Common tree species include red maple and black cherry (*Prunus serotina* Erhr.), while the understory includes bush honeysuckle *(Lonicera spp.*), Asiatic bittersweet *(Celastrus orbiculatus* Thunb.), viburnum (*Viburnum spp.*), shadbush (*Amelanchier spp.*), and green briar (*Smilax spp.*). The United States Fish and Wildlife Service manages Ninigret NWR with prescribed fires and mastication to maintain early successional habitat. The range of mammalian predators present at the site is similar to Great Swamp Management Area. The elevation at Ninigret NWR ranges from approximately 1 to 5 m asl. Patience Island is approximately 85 ha, located in upper Narragansett Bay, and is almost entirely owned by the state of Rhode Island. Common tree species include red maple, black cherry, oak, red cedar *(Juniperus virginiana* L.), and pitch pine (*Pinus rigida* Mill.), while the understory includes bayberry (*Morella pennsylvanica* Mirbel), blueberry (*Vaccinium spp*.), northern arrowwood (*Viburnum dentatum* L.), and shadbush, greenbrier, and bittersweet (Explore Important Bird Areas). Mammalian predators on the island are similar to the mainland, but lack bobcat, foxes, fisher, and skunk. The elevation at Patience Island ranges from approximately 1 to 12 m asl. The average annual temperature in Rhode

Island was typically 8.9° C, while the average annual precipitation was approximately 117 cm (State of Rhode Island Department of Environmental Management).

The three translocation sites were chosen based on 1) their status as conserved lands with little development and 2) availability of densely vegetated early successional forest as a result of coastal effects (Patience Island and Ninigret NWR) or active management (Great Swamp MA). No New England cottontail were documented at any of these sites for at least ten years prior to initial translocations and only one individual from a previous translocation was detected at Great Swamp Management Area prior to the deployment of GPS collars. However, an unsupervised breeding colony was established on Patience Island between 2012 and 2018 by translocating wild-caught founders of a zoo-based breeding program (n = 4, see below) and captive born offspring (n = 82) to the island. Eastern cottontail (*S. floridanus* J.A. Allen 1890) were detected at Great Swamp Management Area and Ninigret NWR. The small number of translocation sites, as well as their opportunistic placement and confounding with year, render them unsuitable contrasts for inferences about New England cottontail spatial ecology.

Field Methods

The University of Rhode Island (URI), Rhode Island Department of Environmental Management (RIDEM) and the New England Cottontail Technical Committee have conducted translocation efforts for New England cottontail in Rhode Island from 2012 to present. From 2018 to 2022 a subset of translocated rabbits (N = 57) were equipped with GPS collars to track their movements and habitat use (Table 1). Translocations in each year were conducted opportunistically based on the number of available rabbits and recent management and translocation history at target sites, which renders contrasts between years unsuitable for producing reliable inferences. The tracked rabbits were sourced from 1) captive breeding colonies housed and cared for at either the Roger Williams Park Zoo (Providence, RI) or Queens Zoo (Corona, NY), or 2) the breeding colony established on Patience Island. The captive colonies at the

Roger Williams Park Zoo and Queens Zoo were established in with wild-caught individuals in 2010 and 2015, respectively. Wild-born individuals descended from colony founders were trapped on Patience Island using single-door wire traps baited with apple slices. In the final year of our study, we also tracked 10 resident animals (six female, four male, all wild-born adults) on Patience Island to increase numbers for that site and contrast individual variability between translocated and resident individuals. Tracked individuals were a mixture of adults (n = 44) and juveniles (n = 23), males (n = 41) and females (n = 26; Table 1). The adults were predominately from Patience Island, whereas the juveniles were first generation captive born animals that were only released when they achieved a minimum mass of 650 g. The sex of each individual was confirmed by polymerase chain reaction amplification using a Y chromosome marker V326 (Chantry-Darmon et al. 2005).

Translocations to Great Swamp Management Area took place in March–April. Translocations to Patience Island took place in September–November. Resident rabbits on Patience Island (n = 10) were captured in December of 2021 and released immediately after they were processed. Translocations to Ninigret NWR also took place in September–November, with the exception of two rabbits released at the refuge in July 2020. At Ninigret NWR, weaned, zoo-born juveniles were acclimated to outdoor life for at least one week prior to release in a predator-proofed enclosed pen where they were provided with supplemental food and water. Additionally, six supplemental feeding stations were spread throughout the release area at Ninigret NWR in the winter of 2019, which were available to translocated rabbits.

We deployed two models of GPS collars to track the locations of released cottontails: FLR V GPS collars (Telemetry Solutions, Concord, CA, USA; n = 21) and LiteTrackRF 20 GPS collars (Lotek Wireless, Newmarket ON, CA; n = 46). The manufacturer-reported accuracy for these models is 10-15 m and testing by Mayer et al. (2021) with the same GPS receiver on a different collar type found an accuracy of 10.5 m (SE = 0.5 m) in a variety of habitats. The LiteTrackRF 20 collars had a mass of approximately 20 g

(≤ 3% of body mass), while the FLV R collars had a mass of approximately 28 g and were only deployed on adults (≤ 5% of body mass). GPS collars were most commonly programmed to collect a maximum of one location per hour, although the specific schedules differed between collars and years (see supporting information for additional detail about GPS programs and settings). Each collar was equipped with a VHF transmitter (included in above masses) and GPS locations were remotely downloaded approximately once per week until the animal died or the collar reached the end of its battery lifetime. When possible, mortality was confirmed by recovering collars that recorded a mortality event and entered recovery mode.

Habitat data

We used fine scale Geographic Information System (GIS) datasets previously developed for the state of Rhode Island (Buffum et al. 2021) to characterize the habitat that was available or used by released New England cottontail. Although we expected general relationships between aspects of vegetation structure and cottontail habitat use based on previous findings (e.g., stem density, Litvaitis et al. 2003; canopy closure, Mayer et al. 2018; canopy cover and height, Buffum et al. 2015), it was unclear how rabbits would perceive and respond to specific measures related to vegetation. Therefore, we initially considered all available datasets potentially related to vegetation, including measures of canopy height and cover, density, reflectance, vegetation type, soil type, agricultural use, and age, as well as distance to feeding stations for rabbits translocated to Ninigret in 2019. After screening potential datasets to eliminate variables lacking variation within release sites, we used the following variables in subsequent analyses of resource selection at all sites: percent cover of low canopy forest (< 1 m), percent cover of intermediate canopy forest (1 – 6 m), percent cover of high canopy forest (> 6 m), percent cover of deciduous vegetation vs. mixed coniferous and deciduous vegetation, and percent cover of poorly-drained soils vs. well-drained soils. Percent cover in each of these layers was calculated for the area within an 18 m radius of the center points of a grid with 1 x 1 m resolution because it was available from a previous study on American woodcock (*Scolopax minor* Gmelin, 1789; Buffum et al. 2021). For Great Swamp Management Area, there was also sufficient variation for inclusion in a layer measuring the distance to young forest, again calculated for center points of a 1 x 1 m grid. To characterize variation in vegetation as indicated by reflectance of different wavelengths of light (Xiao et al. 2014), we also accessed four-band aerial imagery produced by the National Agricultural Imagery Program (NAIP) in August of 2018 (available through USGS TNM Download v1.0).

Finally, to describe vegetation structure for Ninigret NWR and Patience Island, we calculated vegetation density at different height classes (< 1 m, 1 m – 3 m, 3 m – 6 m, 6 m – 10 m, > 10 m) from LiDAR point cloud data produced in September 2011 as part of the USGS 3D Elevation Program (available through USGS TNM Download v1.0). Vegetation density was calculated for each cell of a 1 m x 1 m grid as the percentage of LiDAR points passing through a vegetation height class that were returned from that height class rather than continuing towards the ground (see supporting information for additional information on LiDAR data processing). We did not characterize vegetation density for Great Swamp Management Area because vegetation at that site was substantially restructured by active management between the collection of available LiDAR data and the translocation of New England cottontail. Vegetation structure may have changed between LiDAR data collection and rabbit tracking, but there is reason to expect that coastal sites such as Ninigret NWR and Patience Island may have relatively more stable vegetation communities and structures than inland areas (Latham 2003). All environmental data layers were resampled into 10 x 10 m cell raster layers before analysis to match the spatial resolution of GPS telemetry data.

Data analysis

All analyses were conducted in R version 3.6.2 (R Core Team, Vienna Austria). Before analyses, we filtered all GPS location data to remove points with poor quality GPS fixes, defined as points with an altitude greater than 100 m above sea level and/or with a horizontal dilution of precision (HDOP) value of 10 or greater. To standardize data and avoid autocorrelation in resource selection analyses, we filtered data to a minimum interval of one hour between locations. We also cross-referenced mortality events recorded by collars with logged collar temperatures and removed any locations that were recorded after the rabbit died.

We estimated home range area as the 95% utilization distribution of a fitted autocorrelated kernel density estimator (Fleming et al. 2015; Fleming and Calabrese 2017). First, we evaluated changes in net squared displacement over time for unusual behavior following release. Finding no evidence of dispersal movements, we then fit the data for each individual to a range of continuous time movement models and incorporated HDOP values by simultaneously estimating user equivalent range error using the R package ctmm (Calabrese et al. 2016). The ctmm method uses a continuous-time stochastic process model, which allows the method to be used with autocorrelated geographic location data (Calabrese et al. 2016). We selected the top movement model based on AIC score corrected for small sample sizes (Table S-1), and estimated home range sizes using the *akde* function. We restricted this analysis (and subsequent analyses of resource selection) to individuals with > 50 total GPS locations following filtering to 1) help ensure that rabbits were tracked for at least several weeks, 2) to avoid overfitting models (Fleming and Calabrese 2017), and 3) to enable the detection of moderately small resource selection parameters (Street et al. 2021). We used separate linear models to test for differences in estimated 95% home range based on age, sex, collar type, and home range model.

We evaluated the selection of translocated New England cottontail for and against environmental variables within their home ranges using a used-available framework (Manly et al. 2002). We used the random_points function in the R package amt (Signer et al. 2019) to randomly place 'available' points throughout the estimated home range of each individual at a ratio of 100 available points for each used location (Northrup et al. 201;, Gerber and Northrup 2020) and the function extract_covariates to find the values of environmental variables for each used and available point. To reduce the complexity of selection models, given the relatively low numbers of used locations, and facilitate the prediction of habitat selection, we scaled all extracted environmental variables and then conducted a principal components analysis (PCA) for each site to identify associations among variables and reduce the dimensions of the predictor variables (Haerdle and Simar 2015). PCA is a form of statistical regularization that is related to ridge regression, which is useful for dealing with multicollinearity and constraining model complexity to avoid overfitting (Hastie et al. 2008, Gerber et al. 2015). Furthermore, PCA provided the added benefit of more accurately representing the way animals can encounter multiple habitat characteristics simultaneously and allowed us to avoid making assumptions about the connections between specific remote-sensing variables and rabbit perception. We retained all components that accounted for a greater proportion of cumulative variance than expected assuming an even distribution and for interpretation we used a broken-stick model to determine significant loadings of environmental variables on retained components (Peres-Neto et al. 2003). We then calculated PCA scores for each used and available point and used logistic regression with the glm function in R to approximate a spatial point process and fit a resource selection model separately for each individual. Each model contained an intercept and fixed effects for all principal components retained for that site and used points were given a weight of one and available a weight of 5,000 (Fithian and Hastie 2013). To contrast the inferences of individual- and population-level models, we pooled individual data for each site and then fit a population-level mixed-effects glm, which included fixed effects for all principal components and with random slopes and intercepts corresponding to individuals. Random slopes were included to allow population-level models to describe individual responses to environmental variables that differed in intensity and direction. We then tested the significance of variance components associated with individuals with likelihood ratio tests comparing nested models that did and did not include random effects. We did not group our population-level analyses by sex or age due to our limited sample size for these categories at individual sites and corresponding issues with model convergence.

We analyzed the combined and site-specific survival of GPS collared rabbits released at all three sites. We estimated daily survival using a non-parametric Kaplan-Meier estimator (Kleinbaum and Klein 2012) and used pairwise log-rank tests to conduct pairwise comparisons of survival at different sites and between translocated and resident rabbits at Patience Island. We did not explicitly consider the effect of source population in this analysis because it was confounded with site.

Results

Home ranges

We collected sufficient data to estimate home range size for 34 of the 67 collared individuals, which included eight animals from Great Swamp Management Area, 13 animals from Ninigret NWR, and 13 animals from Patience Island. Estimated 95% home range size was between 1.3 and 85 ha in size with a mean and standard error of 9.3 ± 2.7 ha (Figure 2, Table S-1). The largest home range (85 ha) was observed in an individual that repeatedly moved between multiple core use areas (Figure S-2). Estimated home range areas were unrelated to sex, age, collar type, or continuous time movement model ($P > 0.35$ in all cases). The New England cottontail released at Patience Island had the lowest average home range (3.2 ± 1.6 ha), while the average home range for Patience Island resident cottontails were slightly larger (4.5 ± 0.8 ha). Animals released at Great Swamp Management Area had the highest average home range (22.0 ± 10 ha) whereas values estimated from Ninigret NWR were more intermediate (5.2 ± 0.7 ha). However, we did not test for statistical differences in home range estimates between sites. See supporting information for additional detail about home ranges.

Principal Components Analysis and resource selection

The associations between environmental variables differed among sites (Table 2). For Great Swamp Management Area, we retained three components, which accounted for 72.7% of the variance in all variables. The first component described the prominence of areas lacking woody vegetation with high reflectance, loading on the red, blue and green bands of NAIP imagery, whereas the second and third components reflected the prominence of young forest with well drained soils and wetter shrublands, respectively. For Ninigret NWR we retained five components, which accounted for 75.5% of the variance in environmental variables. The first component at Ninigret NWR was correlated with increasing unforested, high reflectance areas similar to the first component at Great Swamp Management Area. The second component at Ninigret NWR described the prominence of very low canopy areas with sparse vegetation, whereas the third component reflected mature forest with a high canopy. Finally, the fourth component was specifically associated with increasing deciduous vegetation and the fifth component was correlated with wetlands with dense overstory as well as dense understory below 1 m in height. At Patience Island we retained four components accounting for 73.9% of the variance in environmental variables. Here, the first component primarily was highest in areas with low, sparse littoral vegetation, whereas the second component described the prominence of areas with more mature forest and sparse understory. Meanwhile, the third component was more indicative of increasingly dense thickets below 6 m in height, and the fourth component was most correlated with low coastal shrubland with well-drained soils.

Despite some qualitative agreement, individual rabbits often differed in their selection of the various combinations of vegetation characteristics represented by principal components (Figures 3–5). At Great Swamp Management Area, seven out of eight individuals selected for high values of PC2, but only five out of eight showed negative selection for PC1 and the eight rabbits were split regarding PC3, with two selecting for, two selecting against, and four showing no selection towards that component (Figure 3). At Ninigret NWR, five out of thirteen individuals selected against PC2, but selection was mixed for PC1, PC3, PC4, and PC5, with at least one individual selecting for each component and one individual selecting against each component (Figure 4). Although a majority of rabbits showing clear selection favored PC3 (5 to 3) and PC4 (5 to 1), and avoided PC1 (7 to 1) and PC5 (5 to 1), the outlying individual(s) who selected differently from the majority was different for each component. At Patience Island (Figure 5) all of the individuals displaying a significant preference regarding PC2 (5 to 8) selected for lower values, but preferences regarding PC1, PC3 and PC4 were mixed, with at least one individual selecting for and against each of those components. Selection was particularly mixed regarding PC1, with three individuals selecting for higher values of that component, five individuals selecting for lower values, and four individuals displaying no preference.

Population-level resource selection models included significant variance components associated with individuals (Table 3, Great Swamp Management Area: X^2_{10} = 476.65, $P < 0.001$; Ninigret NWR: X^2_{21} = 464.1, $P < 0.001$; Patience Island: X^2_{15} = 255.9, $P < 0.001$), but often qualitatively differed from individual-level selection at all three sites. At Great Swamp Management Area, six out of eight individuals for PC1 and three out of eight individuals for both PC2 and PC3 had their estimated resource selection parameters fall outside of the 95% confidence interval of the population-level parameter estimate, with two individuals each for PC2 and PC3 having no overlap in confidence intervals (Figure 3). At both Ninigret NWR and Patience Island, estimated selection parameters for between seven and nine out of thirteen individuals fell outside 95% confidence intervals of population-level estimates for all five components (Figures 4–5). For each component at those sites, between one and five individuals showed no overlap between individual-level and population-level parameter confidence intervals. However, we recognize our population-level results may have been different if we had grouped individuals by sex and age and conducted analyses separately for these different categories.

Survival

Of the 67 rabbits released and tracked over the course of this study, only 38 survived longer than the lifetime of their collar and we were able to record the time of death for 34 individuals, some after their collar ceased recording locations. The median survival time of released rabbits was 44 days (95% CI: 18 – 126 days) and the maximum recorded lifespan was 324 days after release. There was some variation in survival among sites for translocated rabbits, with a median survival time of 44 days (95% CI: 14 – >200 days) at Great Swamp Management Area, 102 days (95% CI: 36 – >200 days) at Ninigret NWR and 25 days (95% CI: 2 – >200 days) on Patience Island. However, none of these differences was significant in a paired log-rank test ($P > 0.3$ in all cases). Survival of resident rabbits on Patience Island in 2021 was significantly higher than that of rabbits translocated to the island in 2018, with a median survival time of greater than 200 days in 2021 ($C^2 = 5.8$, df = 1, $P = 0.016$).

Discussion

Our primary goal was to assess individual variation in the home range size, fine-scale resource selection, and survival of radio-collared translocated New England cottontail individuals. We observed a 65-fold difference between the largest and smallest estimated home ranges as well as numerous instances of qualitative disagreement in fine-scale resource selection, although in several cases a preponderance of individuals behaved consistently with previous observations for this species. State and federal agencies were quick to recognize the potential benefits of translocations for the conservation of New England cottontail in Rhode Island and early on prioritized the creation of breeding populations to bolster the limited and fragmented distribution of the species in the state. Accordingly, time and resources were primarily devoted to the transfer of rabbits to sites selected based on the location and availability of state and federal lands. The numbers and timing of translocations were pragmatically based on the timing and success of captive breeding programs and later trapping efforts at the Patience Island breeding colony and selected rabbits were tracked to monitor survival with the collection of telemetry data being a secondary goal. In this context, important factors including site, timing, and source population were confounded with one another and consequently impossible to relate to the spatial ecology of translocated rabbits. Nevertheless, our telemetry dataset is somewhat unique among studies on New England cottontail and consequently offers valuable insights into the conservation of this species, despite limitations to inferences involving year, site, and season. Due to the reduced population and fragmented range of New England cottontail, our study is one of only several to assess their fine-scale resource selection and effectively the only one to do so for translocated individuals. This value is enhanced by the importance of translocations from Patience Island to conservation efforts throughout New England. Finally, our study is a reminder of the potential scope and impact of individual variation, an undervalued, yet broadly applicable factor in conservation.

Variation among individuals

Studies investigating the spatial requirements and resource selection of animals, and particularly studies motivated by conservation goals, have traditionally focused on finding population-level trends (Thomas and Taylor 2006; Aarts et al. 2008). Although findings at the population-level are often more straightforward to translate into conservation practices, they do not always accurately reflect the behavior of all or most individuals in focal populations, creating the potential for misguided conclusions (Leclerc et al. 2016; Perrig et al. 2020). Thus, there is increasing appreciation for the benefits of considering individual variation when studying animal spatial ecology (Gillies et al. 2006; Merrick and Koprowski 2017; Montgomery et al. 2018). Accordingly, we analyzed home range size and resource selection of translocated New England cottontail at the individual level and, contrary to expectations, we found an unexpectedly large amount of variation among individuals.

Home range estimates varied over a 65-fold range from less than two to nearly 85 ha. Differences in patch and vegetation structure have been proposed to influence home range size of New England cottontail (Barbour and Litvaitis 1993; Cheeseman et al. 2019) and may have contributed to differing results among study locations. Another possible explanation for differences in home range size is the density of cottontails on the landscape. The small size of Patience Island and correspondingly higher density of New England cottontail may explain the smallest average home range size for the animals released there. Eastern cottontail have been documented at both Great Swamp Management Area and Ninigret NWR, but their detection based on pellet surveys have been less at Great Swamp Management Area (McGreevy, unpublished data). The higher home range estimates for Great Swamp Management Area New England cottontail could be due to less interaction with eastern cottontail (Probert and Litvaitis 1996); however, the higher average at that site was mainly driven by three individuals with the one with the highest home range having two core areas occupied. The managed area at Great Swamp Management Area was smaller than the amount of early successional habitat available at Ninigret National Wildlife Refuge and Patience Island, which also could explain New England cottontails' larger home range estimates at that site. Rabbits in the mature forest surrounding the managed area could have been in more marginal habitat and continually seeking more dense habitat or need a larger area to meet their nutritional needs. Although, we recognize that these are only general comparisons because different technologies and techniques were used to generate the home ranges in the different studies and we did not separate our home range estimates by season.

Resource selection by individual rabbits we tracked was not reliably consistent within sites, with rabbits showing varied directions of selection and regularly differing from population-level estimates both directionally and quantitatively. Beyond mixes of significant and non-significant selection, in many cases different individuals displayed conflicting selection, with some selecting for and others against combinations of environmental variables. There is some evidence that selection towards patch structure is weak in New England cottontail (Barbour and Litvaitis 1993; Cheeseman et al. 2018), but our study appears to provide the clearest evidence of qualitatively different fine-scale resource selection among individuals of this species thus far. As with estimated home range size, there were no clear patterns of selection based on broad characteristics, such as age or sex.

The existence of such notable variation among translocated individuals broadly suggests that there may be limits to our ability to make inferences about fine-scale spatial ecology for entire populations of New England cottontail, but it also may suggest that we need to consider other factors that might influence the use of space and resources. One possibility is that there is a broad disconnect between the remote-sensing data we used to characterize habitats and the way that New England cottontail perceive and navigate their environment despite instances of significant selection. Such a disconnect could have been compounded by the imperfect cumulative variance covered by our principal components (72.7 – 75.5%, depending on site). If this is the case, then field-based vegetation metrics are likely necessary to reveal patterns of fine-scale resource selection in this species. Although most translocations at each site took place in the same season, it is also possible that seasonal changes in home range placement could have contributed to differences in resource selection. Alternately, there is evidence that New England cottontail alter their resource selection in response to competition with other cottontail species (Probert and Litvaitis 1996; Cheeseman et al. 2018), and so it may be possible that social dynamics (e.g. territoriality) also are an important driver of spatial organization and resource use within this species. This idea is supported by the fairly distinct partitioning of core use areas among our study animals (50% kernel density estimates, see supplementary figures S-5 – S-7) and would be consistent with the observed influence of intraspecific competition and social interactions on habitat selection and use of space in other mammal species (including translocated individuals) ranging from rats (*Rattus lutreolus* Gray, 1841; Fox and Monamy 2007; Antunes et al. 2016) to ibex (*Capra ibex* Linnaeus, 1758; Scillitani et al. 2013). More coordinated observations of behavioral interactions in future studies may be useful for further explicating the extent of intraspecific competition in New England cottontail, which appeared minor in controlled behavioral trials (Probert and Litvaitis 1996). However, more recent research shows a clear impact of eastern cottontail on New England cottontail relative probability of use of a variety of vegetation characteristics along with seasonal differences (Cheeseman et al. 2018). Variation in behavioral syndromes or personalities is gaining recognition as an important feature of animal ecology (Merrick and Koprowski 2017; Webber and Wal 2018), which could contribute to the inconsistent resource selection and use of space among our study animals. Differences in movement behavior could especially contribute to the high individual variation observed here, although such variation might be somewhat unexpected given the potential homogenizing effects of captive breeding in a common environment (Smith and Blumstein 2013). For wild-born and dispersing rabbits, fine-scale resource selection would occur within the context of broader-scale selection among landscapes, which may be much more homogenous across individuals.

Translocation, spatial ecology, and survival

A major concern for conservation plans involving translocations is the potential for unexpected complications resulting from altered behavior in new areas (Smith and Blumstein 2013; Bamber et al. 2020; Berger-Tal et al. 2020). However, to the extent that our results are comparable to those of previous studies, we did not see a strong contrast in behavior between the translocated individuals in our study and resident New England cottontail in our study or in previous studies. Most of the home range sizes estimated for translocated individuals were larger than historical estimates (0.2 - 0.7 ha, Litvaitis et al. 2008) and estimates from New York (0.8 - 1.7 ha; Cheeseman et al. 2019), but 31 out of 34 of our estimated home range sizes fell within the broad range of recent estimates from Connecticut (1.0 - 24.5 ha depending on site and season; Kilpatrick and Goodie 2020). Thus, although some individuals exhibited exceptionally large home range sizes, there was no reliable expansion of home ranges following translocation as seen in other species (Scillitani et al. 2013; Ebrahimi and Bull 2014) and, in fact, residents on Patience Island had larger home ranges, thus contradicting our prediction that translocated New England cottontail would use space less efficiently.

Any potential impact of translocation on resource selection may have been obscured by variation among individuals, as individuals frequently displayed contradictory selection. However, the fact that every individual selected for or against at least one principal component does suggest that exploratory behavior among New England cottontail was not extensive enough to override all resource selection. Moreover, in the several cases where trends did emerge across individual-level analyses at single sites, those patterns were largely consistent with previous studies on resident New England cottontail suggesting preferences for dense understory (Barbour and Litvaitis 1993; Litvaitis et al. 2003; Cheeseman et al. 2018). At Great Swamp Management Area seven out of eight individuals selected for PC2, which was associated with increasing low to medium-canopy young forest, and at Patience Island eight out of thirteen individuals selected for both PC3 and PC4, which were associated with dense understory thickets and low canopy shrubland, respectively. Both of these trends match an expected preference for areas with substantial shelter, as low, dense vegetation provides good cover and young forest is similarly associated with high stem densities (Warren et al. 2015; Mayer et al. 2018). However, the vast majority (10 of 13) of Patience Island New England cottontail were resident animals. Meanwhile, at Ninigret NWR a majority of individuals selected against PC1, which represented open, high-reflectance areas with poor cover. Thus, where inter-individual trends did exist, they were generally consistent with the findings of previous studies, suggesting that translocations do not substantially impact fine-scale habitat selection by New England cottontail.

The median survival time of translocated rabbits in our study (44 days) is considerably shorter than both our estimate for residents on Patience Island (>200 days) and a recent estimate of 183 days alive for resident New England cottontail in eastern Connecticut (Kilpatrick and Goodie 2020). The lower number of days the translocated New England cottontail survived compared to the survival of residents could have been due to a high density of rabbits on the island and resident rabbits restricting new arrivals to more marginal habitat. Our estimate was more similar to an estimated median survival time of 42 days for resident New England cottontail during the winter in New Hampshire (Weidman and Litvaitis 2011). Thus, although the scope of our results is quite limited, it appears that translocated New England cottontail had substantially lower survival than resident individuals at other locations, similar to other rabbit translocation efforts (Cabezas and Moreno 2007; Watland et al. 2007). Overall, our results suggest that translocation influences New England cottontail survival more strongly than it influences New England cottontail spatial ecology.

Conclusion

Our study highlights the need to consider variation among individuals when creating restoration plans, and adjust site selection and translocation numbers accordingly when there is robust evidence for substantial variation in habitat preferences. In such cases, it may be beneficial to choose translocation sites that contain a mosaic of fine-scale habitat characteristics so that individuals are able to sort themselves according to different preferences. Alternately, in cases where other factors such as social dynamics have a large impact on habitat selection, it may generally be inefficient to manage and select sites based on fine-scale environmental features rather than landscape-level features where preferences may be more homogeneous. To the extent that habitat variation is beneficial, conservation planners also could consider selecting for variation among sites as well as habitat variation within sites to achieve a larger mosaic. However, in the absence of a strong understanding of the sources of variation in selection, such as an observed link between personality or territoriality and habitat preferences, it will remain difficult to predict which individuals will prefer and succeed in which habitats. Consequently, conservation planners may need to expect a poor fit for many individuals when there are large differences in selection and compensate by increasing the number of translocated individuals. Similar adjustments should be made for other factors known to influence translocation success. Overall, translocations require well-informed and careful decision-making, and our study provides an example of an approach towards collecting valuable information that can be used to guide management decisions for other translocated species of interest.

Acknowledgments

We thank Lou Perrotti, Scott Silver, and the staffs of the Roger Williams Park and Queens Zoos for their efforts maintaining the captive New England cottontail breeding colonies and their support for translocation efforts. We thank Rand Herron and Mary Sullivan for assistance with genetic analyses.

Competing interests statement

The authors declare no conflicts of interest

Author Contributions: The study was conceived by TJM, TPH, and BCT and funding was acquired by TJM, NTE, TPH, and BCT. Methodology for the study was designed by WC, TJM, and BDG while TJM, NTE, DF, and AP conducted field work and WC, TJM, BB, RJD, and NTE contributed to data curation. Formal analysis was carried out by WC, TJM, and RJD with WC drafting the original manuscript. WC, TJM, and BDG revised and edited the manuscript and all authors provided approval for the final version.

Funding Statement

Funding was provided by the Rhode Island Department of Environmental Management, Division of Fish and Wildlife through the Pittman-Robertson Federal Aid in Wildlife Restoration Act. Additional funding was provided by the U.S. Fish and Wildlife Service DNRCP, Inventory and Monitoring effort. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the US Fish and Wildlife Service.

Data archiving statement

Data will be provided by the corresponding author on request.

Supplementary Material

Supplementary data on Geographic Positioning System programs, LiDAR data processing, and home ranges models is available at: <to be confirmed upon acceptance>

References

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., and Matthiopoulos, J. 2008. Estimating space-use and habitat preference from wildlife telemetry data. Ecography (Cop.). **31**(1): 140–160. doi:10.1111/j.2007.0906-7590.05236.x.

Anthony, C.R., and Sanchez, D.M. 2019. Resource selection and space use of Myotis evotis in a western juniper woodland in Oregon. J. Mammal. **100**(November 2018): 239–248. doi:10.1093/jmammal/gyy150.

Antunes, P.C., Oliveira-Santos, L.G.R., Tomas, W.M., Forester, J.D., and Fernandez, F.A.S. 2016. Disentangling the effects of habitat, food, and intraspecific competition on resource selection by the spiny rat, Thrichomys fosteri. J. Mammal **97**(6): 1738–1744. doi:10.1093/jmammal/gyw140.

Bamber, J.A., Shuttleworth, C.M., and Hayward, M.W. 2020. Do differing levels of boldness influence the success of translocation? A pilot study on red squirrels (Sciurus vulgaris). Animals **10**(10): 1–11. doi:10.3390/ani10101748.

Barbour, M.S., and Litvaitis, J.A. 1993. Niche dimensions of New England cottontails in relation to habitat patch size. Oecologia **95**(3): 321–327. doi:10.1007/BF00320983.

Berger-Tal, O., Blumstein, D.T., and Swaisgood, R.R. 2020. Conservation translocations: a review of common difficulties and promising directions. Anim. Conserv. **23**(2): 121–131. doi:10.1111/acv.12534.

Blanco, Y.E. Di, Pérez, I.J., and Bitetti, M.S. Di. 2015. Habitat selection in reintroduced giant anteaters: the critical role of conservation areas. J. Mammal. **96**(5): 1024–1035. doi:10.1093/jmammal/gyv107.

Brown, A.L., and Litvaitis, J.A. 1999. Habitat features associated with predation of New England cottontails: what scale is appropriate? NCASI Tech. Bull. **1**(781 I): 61.

Bruinderink, G.G., Van Der Sluis, T., Lammertsma, D., Opdam, P., and Pouwels, R. 2003. Designing a coherent ecological network for large mammals in northwestern Europe. Conserv. Biol. **17**(2): 549–557. doi:10.1046/j.1523-1739.2003.01137.x.

Bubac, C.M., and Johnson, A.C. 2019. Conservation translocations and post-release monitoring: identifying trends in failures, biases, and challenges from around the world. Biol. Conserv. **238**(September): 108239. Elsevier. doi:10.1016/j.biocon.2019.108239.

Buffum, B., Masse, R., and McWilliams, S.R. 2021. Novel Use of Species Distribution Modeling to Identify High Priority Sites for American Woodcock Habitat Management. Northeast. Nat. **28**(3): 233–247. doi:10.1656/045.028.0301.

Buffum, B., McGreevy, T.J., Gottfried, A.E., Sullivan, M.E., and Husband, T.P. 2015. An analysis of overstory tree canopy cover in sites occupied by native and introduced cottontails in the Northeastern United States with recommendations for habitat management for new England Cottontail. PLoS One **10**(8): 1–17. doi:10.1371/journal.pone.0135067.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. **24**(3): 346–352.

Cabezas, S., and Moreno, S. 2007. An experimental study of translocation success and habitat improvement in wild rabbits. Anim. Conserv. **10**(3): 340–348. doi:10.1111/j.1469-1795.2007.00119.x.

Calabrese, J.M., Fleming, C.H., and Gurarie, E. 2016. ctmm: an R package for analyzing animal relocation data as a continuous-time stochastic process. Methods Ecol. Evol. **7**(9): 1124–1132. doi:10.1111/2041-210X.12559.

Chantry-Darmon, C., Urien, C., Hayes, H., Bertaud, M., Chadi-Taourit, S., Chardon, P., Vaiman, D., and Rogel-Gaillard, C. 2005. Construction of a cytogenetically anchored microsatellite map in rabbit. Mamm. Genome **16**(6): 442–459. doi:10.1007/s00335-005-2471-z.

Cheeseman, A.E., Cohen, J.B., Ryan, S.J., and Whipps, C.M. 2019. Determinants of home-range size of imperiled New England cottontails (Sylvilagus transitionalis) and introduced eastern cottontails (Sylvilagus floridanus). Can. J. Zool. **97**(6): 516–523. doi:10.1139/cjz-2018-0277.

Cheeseman, A.E., Ryan, S.J., Whipps, C.M., and Cohen, J.B. 2018. Competition alters seasonal resource selection and promotes use of invasive shrubs by an imperiled native cottontail. Ecol. Evol. **8**(22): 11122–11133. doi:10.1002/ece3.4580.

Ciuti, S., Tripke, H., Antkowiak, P., Gonzalez, R.S., Dormann, C.F., and Heurich, M. 2018. An efficient method to exploit LiDAR data in animal ecology. Methods Ecol. Evol. **9**(4): 893–904. doi:10.1111/2041-210X.12921.

Cook, C.N., Morgan, D.G., and Marshall, D.J. 2010. Reevaluating suitable habitat for reintroductions: Lessons learnt from the eastern barred bandicoot recovery program. Anim. Conserv. **13**(2): 184–195. doi:10.1111/j.1469-1795.2009.00320.x.

Dzialak, M.R., Webb, S.L., Harju, S.M., Winstead, J.B., Wondzell, J.J., Mudd, J.P., and Hayden-Wing, L.D. 2011. The spatial pattern of demographic performance as a component of sustainable landscape management and planning. Landsc. Ecol. **26**(6): 775–790. doi:10.1007/s10980-011-9607-1.

Ebrahimi, M., and Bull, C.M. 2014. Resources and their distribution can influence social behaviour at translocation sites: Lessons from a lizard. Appl. Anim. Behav. Sci. **156**: 94–104. Elsevier B.V. doi:10.1016/j.applanim.2014.04.013.

Eline, D. V, Cohen, J.B., McGreevy, T.J., Whipps, C.M., and Cheeseman, A.E. 2023. Behavior as a rapid indicator of reintroduction and translocation success for a cryptic mammal, the New England Cottontail (Sylvilagus transitionalis) . J. Mammal. **104**(4): 855–866. doi:10.1093/jmammal/gyad023.

Explore Important Bird Areas. Available from https://www.audubon.org/important-bird-areas/prudence-patience-islands [Accessed February 2025].

Faulhaber, C.A., Perry, N.D., Silvy, N.J., Lopez, R.R., Frank, P.A., and Peterson, M.J. 2006. Reintroduction of lower keys marsh rabbits. Wildl. Soc. Bull. **34**(4): 1198–1202. doi:10.2193/0091-7648(2006)34[1198:rolkmr]2.0.co;2.

Fenderson, L.E., Kovach, A.I., Litvaitis, J.A., and Litvaitis, M.K. 2011. Population genetic structure and history of fragmented remnant populations of the New England cottontail (Sylvilagus transitionalis). Conserv. Genet. **12**(4): 943–958. doi:10.1007/s10592-011-0197-x.

Fischer, J., and Lindenmayer, D.B. 2000. An assessment of the published results of animal relocations. Biol. Conserv. **96**: 1–11.

Fithian, W., and Hastie, T. 2013. Finite-sample equivalence in statistical models for presence-only data. Ann. Appl. Stat. **7**(4): 1917–1939. doi:10.1214/13-AOAS667.

Fleming, C.H., and Calabrese, J.M. 2017. A new kernel density estimator for accurate home-range and species-range area estimation. Methods Ecol. Evol. **8**: 571–579. doi:10.1111/2041-210X.12673.

Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P., and Calabrese, J.M. 2015. Rigorous home range estimation with movement data: a new autocorrelated kernal density estimator. Ecology **96**(5): 1182–1188.

Fox, B.J., and Monamy, V. 2007. A review of habitat selection by the swamp rat, Rattus lutreolus

(Rodentia: Muridae). Austral Ecol. **32**: 837–849. doi:10.1111/j.1442-9993.2007.01849.x.

Fozzi, I., Brogi, R., Cavazza, S., Chirchella, R., De Rosa, D., Aresu, M., Cerri, J., Apollonio, M., Berlinguer, F. 2023. Insights on the best release strategy from post-release movements and mortality patterns in an avian scavenger. iScience **26**(5): 106699. doi:10.1016/j.isci.2023.106699.

Fuller, S., and Tur, A. 2012. Conservation strategy for the New England cottontail (Sylvilagus transitionalis). Available from https://newenglandcottontail.org/resource/conservation-strategy-new-england-cottontail.

Gallie, J., and Hayes, G. 2020. Columbia basin pygmy rabbit reintroduction and genetic management plan 2019. Olympia.

Gerber, B.D., Kendall, W.L., Hooten, M.B., Dubovsky, J.A., and Drewien, R.C. 2015. Optimal population prediction of sandhill crane recruitment based on climate-mediated habitat limitations. J. Anim. Ecol. **84**(5): 1299–1310. doi:10.1111/1365-2656.12370.

Gerber, B.D., and Northrup, J.M. 2020. Improving spatial predictions of animal resource selection to guide conservation decision making. Ecology **101**(3): 1–9. doi:10.1002/ecy.2953.

Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E., and Jerde, C.L. 2006. Application of random effects to the study of resource selection by animals. J. Anim. Ecol. **75**(4): 887–898. doi:10.1111/j.1365-2656.2006.01106.x.

Griffith, B., Scott, J.M., Carpenter, J.W., and Reed, C. 1989. Translocation as a species conservation tool: Status and strategy. Science (80-.). **245**(4917): 477–480. doi:10.1126/science.245.4917.477.

Haerdle, W.K., and Simar, L. 2015. Applied multivariate statistical analysis. *In* Fourth. Springer-Verlag, Berlin Heidelberg. doi:10.1007/978-3-662-45171-7.

Harris, S.M., Descamps, S., Sneddon, L.U., Bertrand, P., Chastel, O., and Patrick, S.C. 2019. Personality predicts foraging site fidelity and trip repeatability in a marine predator. J. Anim. Ecol. (May): 1–12. doi:10.1111/1365-2656.13106.

Hastie, T., Tibrishani, R., and Friedman, J. 2008. The elements of statistical learning. *In* Second. Springer-Verlag, New York. doi:10.1007/978-0-387-84858-7.

Johnson, C.J., Seip, D.R., and Boyce, M.S. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. J. Appl. Ecol. **41**: 238–251.

Kilpatrick, H.J., and Goodie, T.J. 2020. Spatial Use and Survival of Sympatric Populations of New England and Eastern Cottontails in Connecticut. J. Fish Wildl. Manag. **11**(1): 3–10. doi:10.3996/082016-jfwm-062.

Kleinbaum, D.G., and Klein, M. 2012. Survival Analysis: a Self-Learning Text. *In* Third. *Edited By*M. Gail, K. Krickeberg, J.M. Samet, A. Tsiatis, and W. Wong. Springer, New York.

Kramer, D.L., and Chapman, M.R. 1999. Implications of fish home range size and relocation for marine reserve function. Environ. Biol. Fishes **55**: 65–79.

Latham, R.E. 2003. Shrubland longevity and rare plant species in the northeastern United States. For. Ecol. Manage. **185**(1–2): 21–39. doi:10.1016/S0378-1127(03)00244-5.

Lawes, T.J., Anthony, R.G., Robinson, W.D., Forbes, J.T., and Lorton, G.A. 2013. Movements and settlement site selection of pygmy rabbits after experimental translocation. J. Wildl. Manage. **77**(6): 1170–1181. doi:10.1002/jwmg.572.

Leclerc, M., Vander Wal, E., Zedrosser, A., Swenson, J.E., Kindberg, J., and Pelletier, F. 2016. Quantifying consistent individual differences in habitat selection. Oecologia **180**(3): 697–705. Springer Berlin Heidelberg. doi:10.1007/s00442-015-3500-6.

Litvaitis, J.A., Barbour, M.S., Brown, A.L., Kovach, A.I., LItvaitis, M.K., Oehler, J.D., Probert, B.L., Smith, D.F., Tash, J.P., and Villafuerte, R. 2008. Testing multiple hypotheses to identify causes of the decline of a lagomorph species: the New England cottontail as a case study. *In* Lagomorph Biology: Evolution, Ecology, and Conservation. *Edited by* P.C. Alves, N. Ferrand, and K. Hacklaender.

Springer, Berlin Heidelberg. pp. 167–185.

Litvaitis, J.A., Johnson, B., Jakubas, W., and Morris, K. 2003. Distribution and habitat features associated with remnant populations of New England cottontails in Maine. Can. J. Zool. **81**(5): 877–887. doi:10.1139/z03-068.

Litvaitis, J.A., Tash, J.P., Litvaitis, M.K., Kovach, A.I., and Innes, R. 2004. A range-wide survey to determine the current distribution of New England Cottontails. Wildl. Soc. Bull. **34**(4): 1190–1197.

Manly, B.F., McDonald, L., Thomas, D., McDonald, T.L., and Erickson, W.P. 2002. Resource selection by animals: statistical design and analysis for field studies. *In* 2nd edition. Springer. doi:10.1007/978-0-306-481512.

Mayer, A.E.G., McGreevy, Jr, T.J., Sullivan, M.E., Buffum, B., and Husband, T.P. 2018. Fine-scale habitat comparison of two sympatric cottontail species in eastern Connecticut. Curr. Trends For. Res. **2**(4): 1–8.

Merrick, M.J., and Koprowski, J.L. 2017. Should we consider individual behavior differences in applied wildlife conservation studies? Biol. Conserv. **209**: 34–44. Elsevier Ltd. doi:10.1016/j.biocon.2017.01.021.

Milligan, M.C., Berkeley, L.I., and McNew, L.B. 2020. Habitat selection of female sharp-tailed grouse in grasslands managed for livestock production. PLoS One **15**(6): 1–18. doi:10.1371/journal.pone.0233756.

Montgomery, R.A., Redilla, K.M., Ortiz-Calo, W., Smith, T., Keller, B., and Millspaugh, J.J. 2018. Evaluating the individuality of animal-habitat relationships. Ecol. Evol. **8**(22): 10893–10901. doi:10.1002/ece3.4554.

Northrup, J.M., Hooten, M.B., Anderson, C.R., and Wittemyer, G. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. Ecology **94**(7): 1456–1463.

Peres-Neto, P.R., Jackson, D.A., and Somers, K.M. 2003. Giving meaningful interpretation to ordination axes: assessing loading significance in principal component analysis. Ecology **84**(9): 2347–2363.

Perrig, P.L., Lambertucci, S.A., Cruz, J., Alarcón, P.A.E., Plaza, P.I., Middleton, A.D., Blanco, G., Sánchez-Zapata, J.A., Donázar, J.A., and Pauli, J.N. 2020. Identifying conservation priority areas for the Andean condor in southern South America. Biol. Conserv. **243**(January): 108494. Elsevier. doi:10.1016/j.biocon.2020.108494.

Probert, B.L., and Litvaitis, J.A. 1996. Behavioral interactions between invading and endemic lagomorphs: Implications for conserving a declining species. Biol. Conserv. **76**(3): 289–295. doi:10.1016/0006-3207(95)00127-1.

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

RIGIS. 2013. Lakes, Ponds, and Reservoirs: RI Integrated Water Quality Monitoring and Assessment Report 2012. Rhode Island Geographic Information System (RIGIS) Data Distribution System, URL: http://www.rigis.org, Environmental Data Center, University of Rhode Island, Kingston, Rhode Island (last date accessed: 7 October 2020).

Scillitani, L., Darmon, G., Monaco, A., Cocca, G., Sturaro, E., Rossi, L., and Ramanzin, M. 2013. Habitat selection in translocated gregarious ungulate species: An interplay between sociality and ecological requirements. J. Wildl. Manage. **77**(4): 761–769. doi:10.1002/jwmg.517.

Seddon, P.J., Armstrong, D.P., and Maloney, R.F. 2007. Developing the science of reintroduction biology. Conserv. Biol. **21**(2): 303–312. doi:10.1111/j.1523-1739.2006.00627.x.

Seddon, P.J., Griffiths, C.J., Soorae, P.S., and Armstrong, D.P. 2014. Reversing defaunation: restoring species in a changing world. Science (80-.). **345**(6195): 406–412.

Signer, J., Fieberg, J., and Avgar, T. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecol. Evol. **9**: 880–890. doi:10.1002/ece3.4823.

Sikes, R.S. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. J. Mammal. **97**(3): 663–688. doi:10.1093/jmammal/gyw078.

Smith, B.R., and Blumstein, D.T. 2013. Animal personalities and conservation biology: the importance of behavioral diversity. *In* Animal personalities: behavior, physiology, and evolution. *Edited by* C. Carere and D. Maestripieri. University of Chicago Press, Chicago, IL. pp. 379–411.

Smith, T.N., Rota, C.T., Keller, B.J., Chitwood, M.C., Bonnot, T.W., Hansen, L.P., and Millspaugh, J.J. 2019. Resource selection of a recently translocated elk population in Missouri. J. Wildl. Manage. **83**(2): 365–378. doi:10.1002/jwmg.21584.

Spencer, W.D. 2012. Home ranges and the value of spatial information. J. Mammal. **93**(4): 929–947. doi:10.1644/12-MAMM-S-061.1.

State of Rhode Island Department of Environmental Management. Available from https://dem.ri.gov/climate/climate-overview-ri.php [Accessed February 2025].

Street, G.M., Potts, J.R., Börger, L., Beasley, J.C., Demarais, S., Fryxell, J.M., McLoughlin, P.D., Monteith, K.L., Prokopenko, C.M., Ribeiro, M.C., Rodgers, A.R., Strickland, B.K., van Beest, F.M., Bernasconi, D.A., Beumer, L.T., Dharmarajan, G., Dwinnell, S.P., Keiter, D.A., Keuroghlian, A., Newediuk, L.J., Oshima, J.E.F., Rhodes, O., Schlichting, P.E., Schmidt, N.M., and Vander Wal, E. 2021. Solving the sample size problem for resource selection functions. Methods Ecol. Evol. **12**(12): 2421–2431. doi:10.1111/2041-210X.13701.

Sullivan, M., McGreevy, T.J., Gottfried, A.E., Tefft, B.C., Buffum, B., and Husband, T.P. 2019. Molecular identification of three sympatric lagomorphs in the Northeastern United States. Mitochondrial DNA Part B Resour. **4**(1): 1513–1517. Taylor & Francis. doi:10.1080/23802359.2019.1601508.

Thomas, D.L., and Taylor, E.J. 2006. Study designs and dests for comparing resource use and availability II. J. Wildl. Manage. **70**(2): 324–336. doi:10.2307/3809050.

USFWS. 2006. Endangered and threatened wildlife and plants; review of native species that are candidates or proposed for listing as endangered or threatened; annual notice of findings on resubmitted petitions;annual description of progress on listing actions. United States Fish and Wildlife Service. Federal Register **71**: 53756–53835.

USGS TNM Download v1.0. Available from https://viewer.nationalmap.gov/basic/ [Accessed February 2025].

Young Forest and Shrubland. Available from https://youngforest.org/wildlife/new-england-cottontail [Accessed February 2025].

Warren, A., Litvaitis, J.A., and Keirstead, D. 2015. Developing a habitat suitability index to guide restoration of New England Cottontail habitats. Wildl. Soc. Bull. **40**(1): 69–77.

Watland, A.M., Schauber, E.M., and Woolf, A. 2007. Translocation of swamp rabbits in southern Illinois. Southeast. Nat. **6**(2): 259–270. doi:10.1656/1528-7092(2007)6[259:TOSRIS]2.0.CO;2.

Webber, Q.M.R., and Wal, E. Vander. 2018. An evolutionary framework outlining the integration of individual social and spatial ecology. J. Anim. Ecol. **87**: 113–127. doi:10.1111/1365-2656.12773.

Weidman, T., and Litvaitis, J.A. 2011. Can supplemental food increase winter survival of a threatened cottontail rabbit? Biol. Conserv. **144**(7): 2054–2058. Elsevier Ltd. doi:10.1016/j.biocon.2011.04.027.

Xiao, Y., Zhao, W., Zhou, D., and Gong, H. 2014. Sensitivity analysis of vegetation reflectance to biochemical and biophysical variables at leaf, canopy, and regional scales. IEEE Trans. Geosci. Remote Sens. **52**(7): 4014–4024. IEEE.

Figure Captions

Figure 1. Study sites in Rhode Island, USA, where New England cottontail (*Sylvilagus transitionalis*) were translocated as part of ongoing conservation efforts from 2012–2021. Resident New England cottontail were not detected at any of these sites in the ten years prior to translocations, although eastern cottontail (*S. floridanus*) were detected at Great Swamp Management Area and Ninigret National Wildlife Refuge. Map uses WGS84 coordinate system with NAD83 projection and includes geographic data for Rhode Island provided by RIGIS.

Figure 2. Estimated home range areas and 95% confidence intervals of New England cottontails (*Sylvilagus transitionalis*) translocated to southern Rhode Island, USA, from 2018–2021 or resident on Patience Island in 2021–2022. Home ranges were estimated as 95% autocorrelated kernel densities. Rabbits are arranged along the x-axis by ID and symbol color and shape indicate rabbit sex (females = grey, males = black) and age (adults = circles, juveniles = triangles), respectively. Panels indicate release site: GS = Great Swamp Management Area, NI = Ninigret National Wildlife Refuge, and PI = Patience Island.

Figure 3. Parameter estimates and 95% confidence intervals from resource selection models of New England cottontails (*Sylvilagus transitionalis*) released at Great Swamp Management Area, South Kingstown, Rhode Island, USA, in 2018, 2019, and 2021. Rabbits are arranged along the x-axis by ID and panels depict the different model terms estimated with logistic regression. Symbol color indicates rabbit sex (females = grey, males = black) and numbers next to estimates in the 'intercept' panel list the number of Geographic Positioning System locations recorded for each individual. Sex is included for reference but was not included in statistical analyses. Shaded areas depict the 95% confidence intervals for parameter estimates in a population-level model of resource selection.

Figure 4. Parameter estimates and 95% confidence intervals from resource selection models of New England cottontails (*Sylvilagus transitionalis*) released at Ninigret National Wildlife Refuge, Charlestown, Rhode Island, USA, from 2019–2021. Rabbits are arranged along the x-axis by identification (ID) and panels depict the different model terms estimated with logistic regression. Symbol color and shape indicate rabbit sex (females = grey, males = black) and age (adults = circles, juveniles = triangles), respectively, and numbers below estimates in the 'intercept' panel list the number of Geographic Positioning System locations recorded for each individual. Sex and age are included for reference but were not included in statistical analyses. Shaded areas depict the 95% confidence intervals for parameter estimates in a population-level model of resource selection.

Figure 5. Parameter estimates and 95% confidence intervals from resource selection models of New England cottontails (*Sylvilagus transitionalis*) released at Patience Island, Rhode Island, USA, in 2018 and captured as residents in 2021. Rabbits are arranged along the x-axis by identification (ID) and panels depict the different model terms estimated with logistic regression. Symbol color and shape indicate rabbit sex (females = grey, males = black) and age (adults = circles, juveniles = triangles), respectively, and numbers below estimates in the 'intercept' panel list the number of Geographic Positioning System locations recorded for each individual. Sex and age are included for reference but were not included in statistical analyses. Shaded areas depict the 95% confidence intervals for parameter estimates in a population-level model of resource selection.

Tables

Table 1. Summary counts of New England cottontail (*Sylvilagus transitionalis* Bangs, 1985) translocations tracked with GPS telemetry between 2018 and 2021. Translocated rabbits were either wild-caught on Patience Island or sourced from captive breeding programs at the Roger Williams Park Zoo and Queens Zoo. Total indicates the total number of rabbits translocated to a site in a given year and Data indicates the number of translocated rabbits for which we collected sufficient data for home range and resource selection analyses. These numbers do not include 10 non-translocated rabbits tracked on Patience Island in 2021.

		Sex		**Age**		**Source**			
Site	**Year**	**Male**	**Female**	**Adult**	**Juvenile**	**Zoo**	**Wild**	**Total**	**Data**
Patience Island	2018	2	8	6	4	10	–	10	3
Great Swamp Management Area	2018	6	3	9	–	–	9	9	3
	2019	11	–	11	–	–	11	11	1
	2021	4	2	6	–	–	6	6	4
Ninigret National Wildlife Refuge	2019	9	3	1	11	12	–	12	7
	2020	2	–	–	2	2	–	2	1
	2021	3	4	1	6	7	–	7	5
Total		41	26	44	24			57	24

Table 2. Loadings and cumulative variances of components extracted from a principal component analysis of environmental variables within home ranges of New England cottontail (*Sylvilagus transitionalis*) tracked at three sites in southern Rhode Island, USA, from 2018–2021. Values in bold text denote loadings considered to be important for given components.

	Percent Cover															
	Canopy Height				Poorly Drained	Distance to	NAIP Imagery Band				Vegetation Density					
	<1m	1m – 6m	>6m	Deciduous Vegetation	Poorly Drained Soil	Distance to Young Forest	Red	Green	Blue	Near Infrared	<1m	1m – 3m	3m – 6m	6m – 10m	>10m	
Great Swamp Management Area																*Cumulative Variance*
PC1	0.053	-0.032	-0.003	0.048	-0.013	-0.007	**0.539**	**0.540**	**0.499**	0.402						0.320
PC2	0.137	**0.485**	**-0.535**	-0.261	**-0.435**	**-0.418**	-0.020	0.027	-0.096	0.134						0.604
PC3	**-0.825**	**0.393**	0.072	0.263	-0.053	0.084	-0.089	0.012	-0.042	0.263						0.727
Ninigret National Wildlife Refuge																
PC1	0.215	-0.068	**-0.321**	-0.116	0.063		**0.447**	**0.432**	**0.427**	0.065	-0.122	-0.088	-0.213	-0.346	-0.260	0.262
PC2	**0.318**	**-0.525**	0.192	-0.101	-0.100		-0.045	-0.111	-0.033	0.229	**-0.412**	**-0.496**	-0.172	0.068	0.220	0.429
PC3	**-0.355**	0.167	**0.389**	0.136	-0.189		0.306	0.314	**0.305**	0.253	-0.211	-0.148	0.127	0.279	**0.362**	0.574
PC4	0.388	-0.177	0.023	**0.611**	-0.161		-0.100	0.101	-0.155	**0.576**	0.146	0.009	-0.120	-0.073	0.035	0.675
PC5	-0.017	-0.235	0.248	-0.217	**0.680**		0.012	0.098	0.055	0.176	**0.367**	0.076	-0.279	0.012	**0.334**	0.755
Patience Island																
PC1	0.166	0.252	**-0.391**	0.262	0.164		0.344	0.340	**0.345**	0.131	0.071	0.105	**-0.264**	-0.354	**-0.278**	0.322
PC2	-0.012	-0.361	0.239	0.140	-0.045		0.371	**0.333**	**0.364**	0.118	**-0.362**	-0.355	0.001	0.221	**0.300**	0.520
PC3	-0.186	**0.254**	0.142	-0.284	-0.019		0.078	**0.268**	0.110	**0.608**	**0.342**	0.278	**0.282**	0.225	0.125	0.651
PC4	**0.495**	-0.133	-0.051	-0.351	**-0.744**		0.105	0.079	0.076	-0.060	0.030	0.120	0.003	-0.054	-0.114	0.739

Table 3. Estimated standard deviations for random effect intercepts and slopes associated with individual in population-level models of resource selection for New England cottontail (*Sylvilagus transitionalis*) tracked at three sites in southern Rhode Island, USA, from 2018–2021.

	Parameter					
Site	**Intercept**	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Great Swamp Management Area	0.408	0.083	0.286	0.277	–	–
Ninigret National Wildlife Refuge	0.169	0.138	0.147	0.138	0.182	0.200
Patience Island	0.228	0.147	0.073	0.107	0.399	–

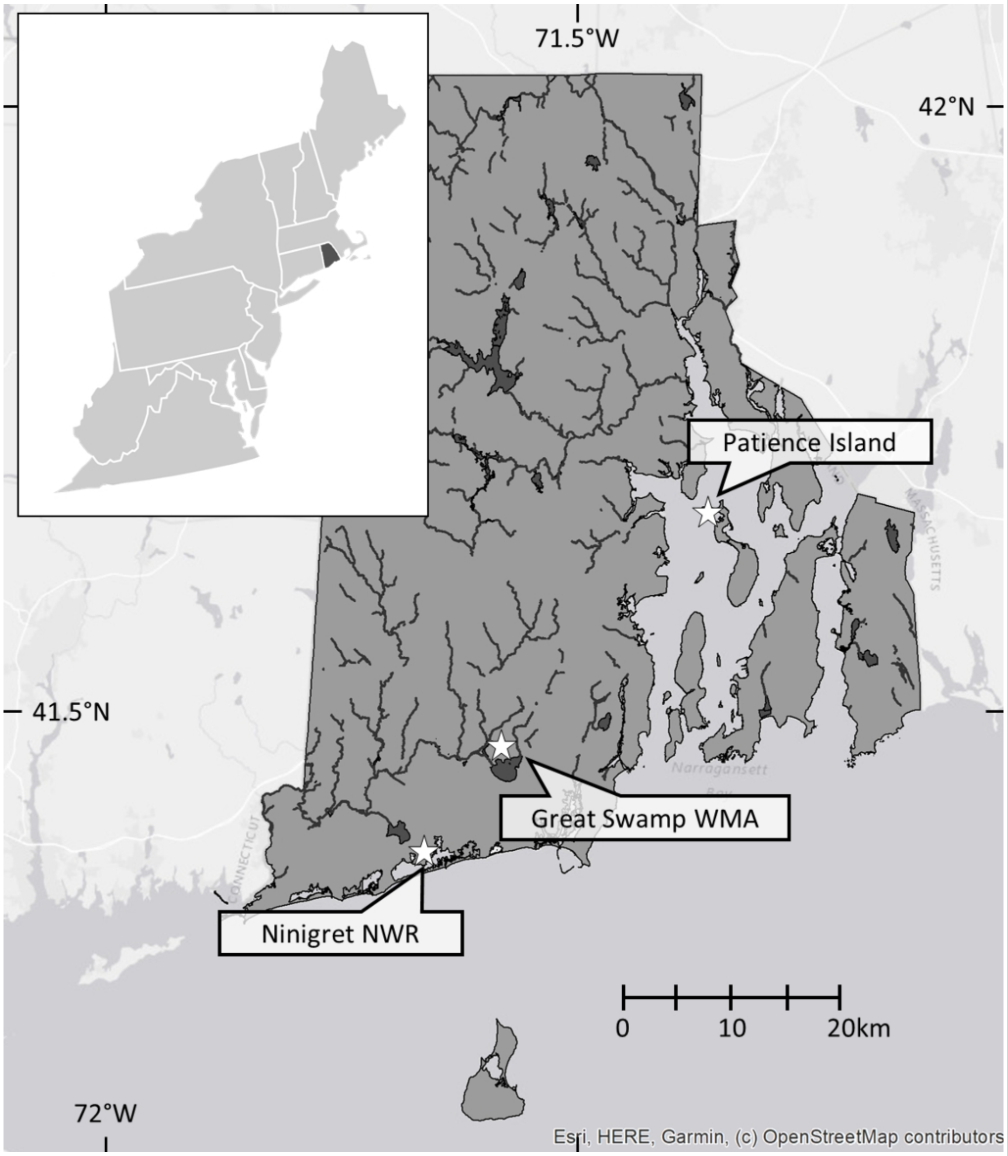

Figure 1. Study sites in Rhode Island, USA, where New England cottontail (Sylvilagus transitionalis) were translocated as part of ongoing conservation efforts from 2012□2021. Resident New England cottontail were not detected at any of these sites in the ten years prior to translocations, although eastern cottontail (S. floridanus) were detected at Great Swamp Management Area and Ninigret National Wildlife Refuge. Map uses WGS84 coordinate system with NAD83 projection and includes geographic data for Rhode Island provided by RIGIS.

98x113mm (300 x 300 DPI)

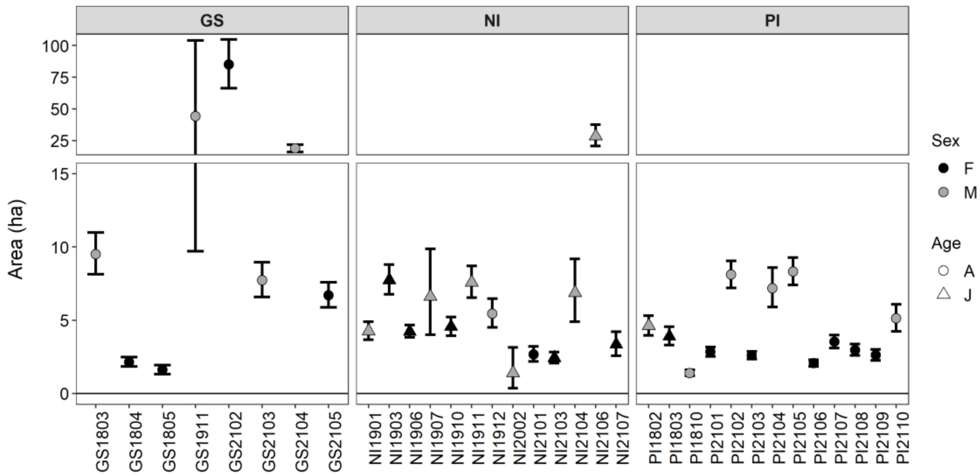

Figure 2. Estimated home range areas and 95% confidence intervals of New England cottontails (Sylvilagus transitionalis) translocated to southern Rhode Island, USA, from 2018–2021 or resident on Patience Island in 2021–2022. Home ranges were estimated as 95% autocorrelated kernel densities. Rabbits are arranged along the x-axis by ID and symbol color and shape indicate rabbit sex (females = grey, males = black) and age (adults = circles, juveniles = triangles), respectively. Panels indicate release site: GS = Great Swamp Management Area, NI = Ninigret National Wildlife Refuge, and PI = Patience Island.

254x127mm (300 x 300 DPI)

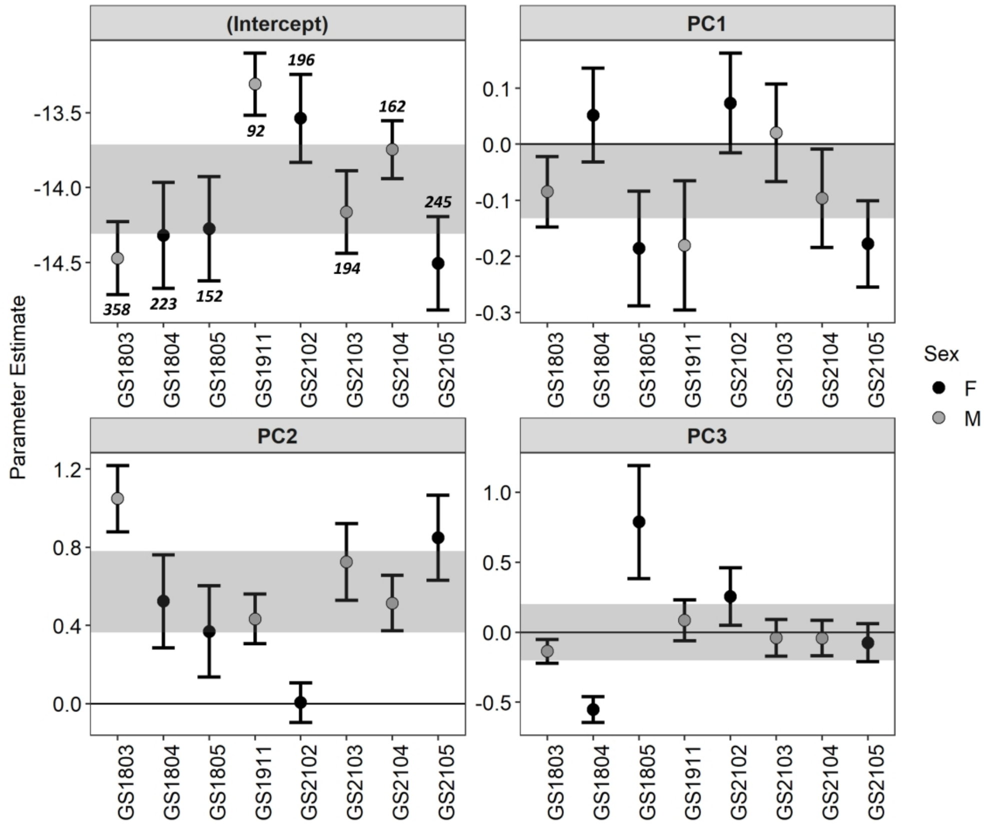

Figure 3. Parameter estimates and 95% confidence intervals from resource selection models of New England cottontails (Sylvilagus transitionalis) released at Great Swamp Management Area, South Kingstown, Rhode Island, USA, in 2018, 2019, and 2021. Rabbits are arranged along the x-axis by ID and panels depict the different model terms estimated with logistic regression. Symbol color indicates rabbit sex (females = grey, males = black) and numbers next to estimates in the 'intercept' panel list the number of Geographic Positioning System locations recorded for each individual. Sex is included for reference but was not included in statistical analyses. Shaded areas depict the 95% confidence intervals for parameter estimates in a population-level model of resource selection.

317x264mm (300 x 300 DPI)

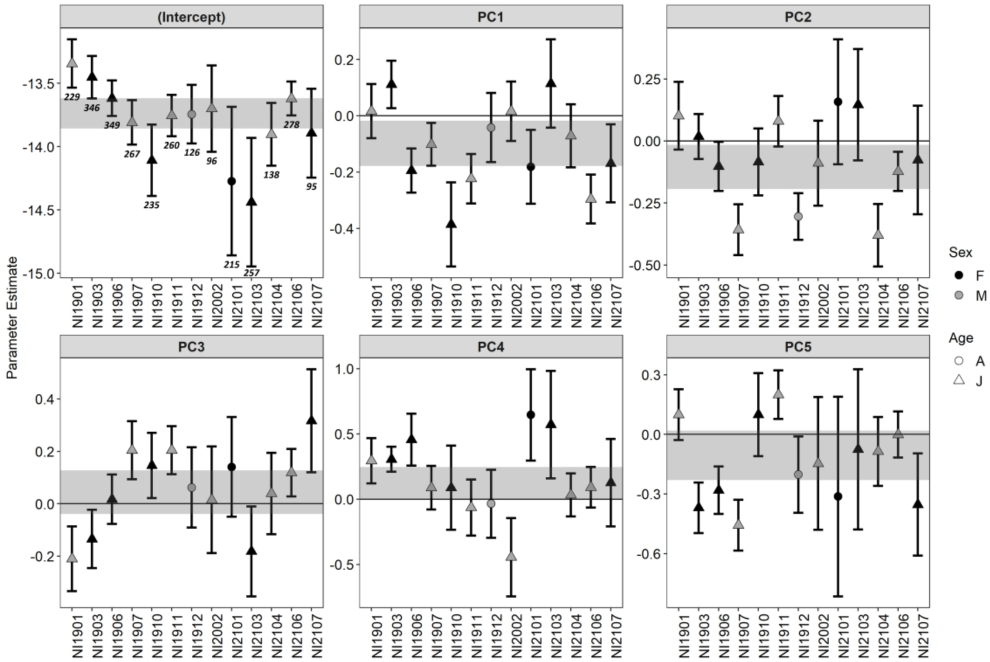

Figure 4. Parameter estimates and 95% confidence intervals from resource selection models of New England cottontails (Sylvilagus transitionalis) released at Ninigret National Wildlife Refuge, Charlestown, Rhode Island, USA, from 2019☐2021. Rabbits are arranged along the x-axis by identification (ID) and panels depict the different model terms estimated with logistic regression. Symbol color and shape indicate rabbit sex (females = grey, males = black) and age (adults = circles, juveniles = triangles), respectively, and numbers below estimates in the ‘intercept’ panel list the number of Geographic Positioning System locations recorded for each individual. Sex and age are included for reference but were not included in statistical analyses. Shaded areas depict the 95% confidence intervals for parameter estimates in a population-level model of resource selection.

476x317mm (300 x 300 DPI)

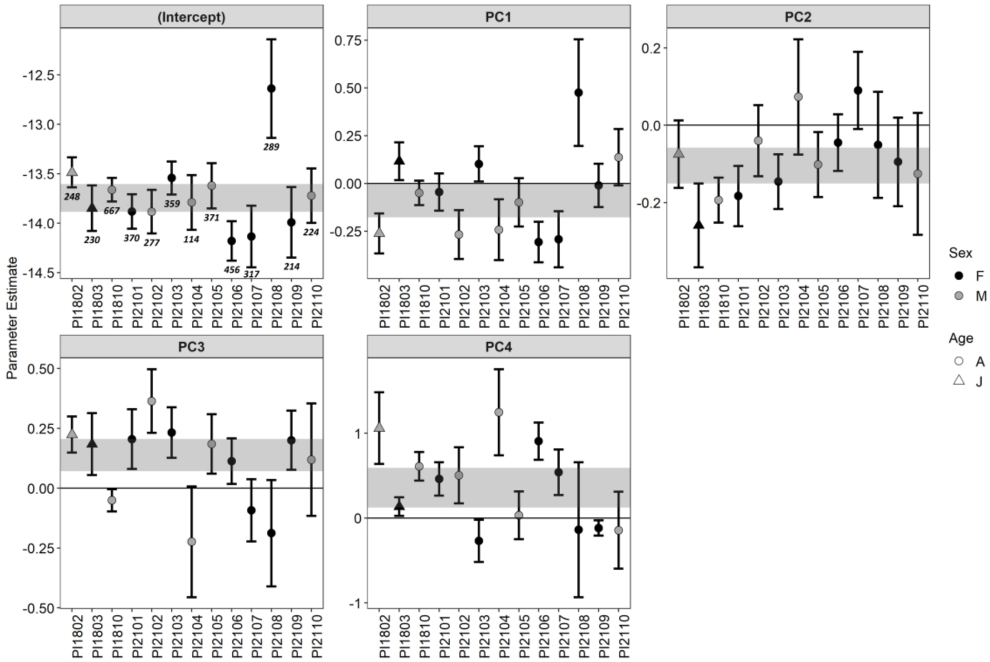

Figure 5. Parameter estimates and 95% confidence intervals from resource selection models of New England cottontails (Sylvilagus transitionalis) released at Patience Island, Rhode Island, USA, in 2018 and captured as residents in 2021. Rabbits are arranged along the x-axis by identification (ID) and panels depict the different model terms estimated with logistic regression. Symbol color and shape indicate rabbit sex (females = grey, males = black) and age (adults = circles, juveniles = triangles), respectively, and numbers below estimates in the 'intercept' panel list the number of Geographic Positioning System locations recorded for each individual. Sex and age are included for reference but were not included in statistical analyses. Shaded areas depict the 95% confidence intervals for parameter estimates in a population-level model of resource selection.

476x317mm (300 x 300 DPI)