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Research Article

Fine-Scale Habitat Comparison of Two Sympatric Cottontail Species in Eastern Connecticut

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Abstract

Changing landscapes in the Northeastern United States over the past century have had a profound effect on the abundance and distribution of native wildlife species that prefer early successional habitat, including New England cottontail (*Sylvilagus transitionalis*). Populations of New England cottontail have been in decline for several decades, whereas during this same time period the nonnative eastern cottontail (*S. floridanus*) range has expanded. We conducted intensive vegetation analyses at 17 known locations of New England cottontail and 19 known locations of eastern cottontail in Connecticut to better describe their chosen habitat and identify any difference in habitat used by the two species. Sites that were occupied by New England cottontail had greater canopy closure (73.7%) and basal area (12.3 m2/ha) than sites occupied by eastern cottontail (45.3% and 6.8 m2/ha). Our findings suggest management plans to create habitat for New England cottontails should include retaining more basal area and canopy closure than what is currently prescribed in southern New England; however, further fine-scale research is required to determine if this recommendation applies throughout the range of New England cottontail.

Keywords: Basal Area; Canopy Closure; Early Successional Habitat; Eastern Cottontail (*Sylvilagus floridanus*); New England Cottontail (*Sylvilagus transitionalis*); Nonnative

Introduction

The changing landscape in the Northeastern United States over the past century has had a profound effect on the abundance and distribution of native wildlife species that prefer early successional habitats. In the mid 20th century many of these species experienced an increase in population numbers as abandoned agricultural fields matured into early successional habitats [1]. However, lands previously dominated by early successional forests have transitioned to mature forests [2-4] and are becoming more fragmented by development and infrastructure [4-6]. This affects many wildlife species that depend on large patches of early successional forests [7], such as bobcat (*Lynx rufus*), ruffed grouse (*Bonasa umbellus*), American woodcock (*Scolopax minor*), and New England cottontail (*Sylvilagus transitionalis*) [1,8].

The historic range of the New England cottontail decreased by more than 80% over the past 50 years [9,10]. This dramatic decline prompted the United States Fish and Wildlife Service to nominate the New England cottontail as a candidate for threatened or endangered status under the Endangered Species Act in 2006 [11]. However, a decision was made in 2015 to not list New England cottontail. There are currently five distinct populations of New England cottontail throughout their historic range and although it is unknown what the current population sizes are, these distinct populations are evidence of a significant decline [10,12].

During this same time period marked by a decline in New England cottontail populations, the distribution of nonnative eastern cottontail (*S. floridanus*) has increased [13,14]. Beginning in the 1920s and continuing at least into the 1950s, eastern cottontails from states including Kansas, Minnesota, West Virginia, and Missouri were introduced to southern New England states to supplement cottontail populations for hunting [13]. This resulted in many different subspecies of eastern cottontail becoming established throughout the landscape [13,15].

Throughout much of their current range, New England cottontails are sympatric with eastern cottontails [10,16]. There are several hypotheses behind the shift in abundance of these two species, including New England cottontail habitat change and loss [1,3], differences in their relative abilities to avoid increased predator populations [17,18], interspecific competition for resources [14,19,20], and the adaptability of eastern cottontails to occupy a wider variety of habitat types [13,14,18,19,21,22], possibly as a result of hybridization among eastern cottontail subspecies [15].

The most apparent cause for the decline of the New England cottontail is the loss of early successional habitat and habitat fragmentation [23,24]. In an attempt to better understand the habitat requirements of the species, there have been many habitats related studies that have focused on New England cottontail in the past. However, these studies either examined the northern portion of the New England cottontail's historic range (e.g., [20]) where the vegetation can be very different both structurally and in species composition from other parts of its range, or study areas where eastern cottontail is not present (e.g., [6]). Recent studies on cottontail habitat that include southern New England (e.g., [25]) focus on broad scale analyses that neglected key habitat variables, such as shrub cover, as information on the spatial distribution and extent of these shrubland habitats is not widely available [26]. Although the two species of rabbits are often sympatric, each species has a relatively small annual home range (4.1 ha for New England cottontail and 2.6 ha for eastern cottontails) [27] that could have significant differences at a finer scale. A fine-scale habitat survey could allow researchers to separate out differences in microhabitat feature use between the two species. Identifying any possible differences in habitat use is important because it will allow land managers to favor habitat characteristics that are ideal for New England cottontail rather than eastern cottontail.

To develop more effective habitat management plans for areas where New England and eastern cottontails are sympatric, more needs to be known about the fine-scale habitat qualities used by each species; therefore, our objectives were to: (1) characterize microhabitat use by eastern and New England cottontail; and (2) identify differences in habitat use between the two species in their core use areas.

Methods

Field Site Description

This study was conducted in Windham and New London counties in eastern Connecticut. Vegetation survey plots were located on four properties: 1) a 61 ha portion of Pachaug State Forest in the Town of North Stonington, CT (41°29′34″N, 71°51′33″W); 2) a 45 ha farm in the Town of Scotland, CT (41°42′38″N, 72°05′15″W); 3) a 33 ha private property in Scotland (41°42′02.14″N, 72°05′21.56″W); and 4) a 3 ha highway department property in Scotland (41°42′02.89″N, 72°05′14.99″W). The Pachaug State Forest property includes a 36 ha area of young forest created by even-aged timber management in 2006. All four properties have a matrix of shrub thickets, young, and mature forests. These properties were chosen because rabbit signs (pellets, browse, tracks) were detected during previous surveys.

Vegetation Survey Site Selection

Telemetry data collected by the Connecticut Department of Energy and Environmental Protection Wildlife Division from December 2008 to May 2012 [27] was used to determine the locations for our vegetation survey sites. Data were provided for 19 eastern cottontail individuals and 11 New England cottontail individuals within the study area (Figure 1). Locations for individuals were collected six times a week, including three evening and three daytime location points [27]. Home range sizes varied between winter and breeding seasons [27]; therefore, all data points for each individual were divided in two seasons as follows: telemetry records collected from 1 November to 31 March were labeled as "winter season" and records collected from 1 April to 31 October were labeled as "breeding season." The telemetry data was limited by the year it was collected (2009-2011) to ensure that the current habitat conditions during the time of the vegetation surveys (2011-2012) reflected the conditions at the time the telemetry data were collected.

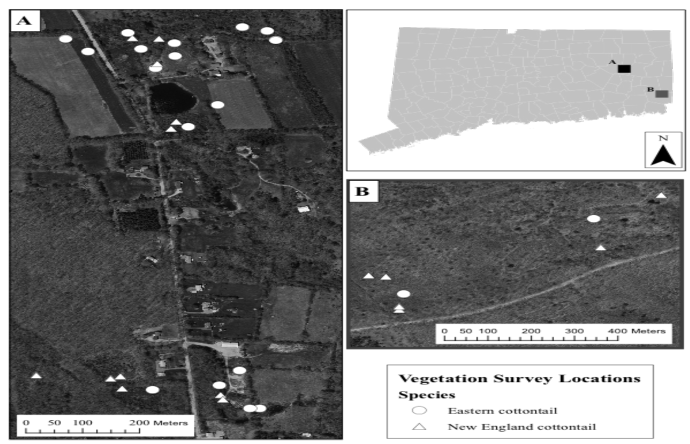

Figure 1: Map of study area with vegetation survey locations. Points represent vegetation survey locations based on previous telemetry studies for New England cottontail (*S. transitionalis*) and eastern cottontail (*S. floridanus*).

The areas with the highest density of points (core use area) for each individual during each season of available data was identified using ArcMap10 and the kernel density tool (Environmental Systems Research Institute, Inc., Redlands, California). The geographic center of the telemetry fixes in the core use area was calculated using the mean center tool to serve as the center point of the vegetation survey plots. Because several of the home ranges for individuals overlapped, a distance rule was developed to avoid overlapping vegetation surveys for more than one individual. In the event that the center point for one individual was ≤10 m from another individual of the same species' center point, the telemetry fixes within the core use areas for those individuals were combined and the geographic center of these combined fixes were used as the center point for the vegetation survey plot.

Vegetation Data Collection

Fine-scale vegetation surveys were conducted within 50 x 50 m survey plots. We measured stem density, herbaceous cover, shrub cover, basal area, tree height, and canopy closure. Species names of all shrub, herbaceous, and tree species were recorded. For plant species that could not be identified in the field, sample clippings were collected and later identified by a botanist at the University of Rhode Island.

Stem density was estimated by conducting stem counts in 1 m^2 quadrats [28] at three random locations in each quadrant of the 50 x 50 m plot for a total of 12 quadrat measurements. Each rooted stem of a woody shrub species 0.5-2 m tall in the quadrat was counted as one stem. Cover in the herbaceous layer, all plants <0.5 m tall, was estimated within the same 12 quadrats and the cover percentage was recorded using a Daubenmire scale [29].

Estimates of horizontal shrub cover were measured by using the line-intercept method [30] along two 50 m transects in each plot, one in the North-South direction and one in the East-West direction. Species and heights (high or low) of all shrub plants ≥50 cm tall that intercepted the transects were recorded. During the second field season, we also measured visual obstruction by shrub cover using a modified Robel pole [31,32]. Measurements were taken at a random location in each quadrant of the main plot. Visual obstruction and minimum height of the vegetation were recorded from 4 m away and 1 m above ground in each of the four cardinal directions at each location.

Basal area and canopy closure measurements were taken at the same locations as visual obstruction measurements and averaged to get basal area and canopy closure estimates for the plot. Canopy closure was measured using a convex spherical densiometer (Forest Densiometers, Rapid City, South Dakota) [33] and basal area was measured using a 10-factor basal area prism (Cruise Master Prisms, Inc., Sublimity, Oregon). The distance to, diameter at breast height (DBH), and species of each basal area tree were recorded, as well. The closest tree to the center point that also was counted in the basal area estimation in each plot was selected for height measurements using a clinometer (Suunto, Vantaa, Finland). A total of four trees in each main plot were measured to give an estimate of overall tree height in the plot.

NED-2 forest inventory software [34] was used to generate additional variables on the forest characteristics. We used the DBH and species of trees recorded while measuring basal area to generate values of quadratic mean DBH, percentage of basal area consisting of coniferous or hardwood tree species, and stand density for large (DBH ≥12.5 cm) and sapling trees (DBH <12.5 cm).

SAS Software version 9.2 (SAS Institute, Inc., Cary, North Carolina) was used to complete a logistic regression (PROC GENMOD, PROC LOGISTIC) to compare the probability of a site being occupied by New England cottontail versus being occupied by Eastern cottontails based on the habitat variables measured at the site. The general equation for the logistic regression model used was $\log\left[\frac{p_i}{1-p_i}\right] = \alpha + \beta_1 x_{i1} + \beta_2 x_{i2} + \cdots + \beta_k x_{ik}$ [35]. A univariate logistic regression was used to identify significant variables ($P < 0.05$) to select variables to test in the multivariate model [36]. We compared the tolerance (TOL) and variance of inflation factors (VIF) of each variable to exclude variables that showed signs of multicollinearity. If multicollinearity was detected, Akaike's Information Criterion [37] was used for goodness of fit and corrected for small sample bias (AIC_c) [38] to select variables to include in the multivariate logistic regression models. Multivariate models were compared by evaluating the delta AIC_c (Δ) and AIC_c weights (w) [38]. Values of area under the receiver operating characteristic curve (AUC), or ROC curve, also were generated to explain variability in each model and provide further evidence in support of a final model [39].

Results

Fine-scale vegetation surveys were completed for 36 plots (New England cottontail n = 17; eastern cottontail n = 19) representing 19 individual eastern cottontails and 11 individual New England cottontails. The individual sample size differs from the plot sample size because several of the core use area center points were within 10 m of another individual's core use area center point. Two of the eastern cottontail vegetation plot centers were determined by combining the winter and breeding season core use areas for each individual. A third eastern cottontail plot combined the winter and breeding season core use areas of two eastern cottontail individuals. Two of the New England cottontail plots were determined by combining the mean centers of multiple plots due to close proximity to one another. One plot contained points from the winter season of two different individuals, and the other combined plot contained points from both the winter and breeding points of one individual. The habitat characteristics of the breeding and winter core use areas for both species were compared using an analysis of variance. There were no significant differences in the habitat characteristics ($P > 0.05$) between New England cottontail winter and breeding sites, and no significant differences ($P > 0.05$) for all characteristics, except for the high shrub ($P = 0.04$) at eastern cottontail winter and breeding sites. Because the majority of characteristics did not differ significantly between winter and breeding core use areas, for all subsequent analysis data were separated by species only.

In a univariate logistic regression, canopy closure (P = 0.01) and basal area (P = 0.01) were the only significant variables (Table 1), and thus the only two variables that remained in the multivariate logistic regression model (P = 0.015) (Table 2). Although the AUC value for this model was high, 0.774, neither variable was significant (P ≥ 0.05) (Table 3). A correlation analysis indicated slight multicollinearity (VIF = 2.59) between the two variables, which may explain the reason why the AUC value was high (0.774), although the variables were not significant in the model.

Habitat variable code	Description	P
ShrAll	Proportion of total area covered by shrubs	0.52
ShrHigh	Proportion of total area covered by high shrubs (>1 m)	0.39
ShrLow	Proportion of total area covered by low shrubs (0.5-1 m)	0.73
StmDen	Average number of stems per m^2	0.06
HerbCov	Average percent of area covered by herbaceous plants	0.06
Canopy	Average percent canopy closure	0.01
BA	Average basal area (m^2/ha)	0.01
AvgDBH	Average DBH (cm)	0.12
BAconif	Average percent of total basal area that is coniferous	0.41
BAhardw	Average percent of total basal area that is hardwood	0.41
TreeDenL	Number of trees >12.5 cm per ha	0.41
TreeDenS	Number of trees <12.5 cm per ha	0.08
TreeHt[a]	Average tree height (m)	0.94
VOhigh[a]	Average percent visual obstruction by low vegetation (<1 m)	0.81
VOlow[a]	Average percent visual obstruction by high vegetation (>1 m)	0.98
VOht[a]	Average height of visual obstruction (m)	0.89
[a]Data were not available for all measured plots, so variable was excluded in multivariate analysis.		

Table 1: Description of habitat variables measured in the survey to identify important variables associated with the presence of New England cottontail (*Sylvilagus transitionalis*) or eastern cottontail (*S. floridanus*), and the results of a univariate logistic regression analysis. Significant variables (P < 0.05) were considered for inclusion in a multivariate logistic regression analysis.

Variable Code	Coefficient	Odds ratio	SE	P
Canopy	0.024	1.024	0.019	0.22
BA	0.074	1.077	0.092	0.42

Table 2: Results of logistic regression analysis of survey sites in Connecticut where eastern cottontail (*Sylvilagus floridanus*) was present (n = 19) versus sites where New England cottontail (*S. transitionalis*) was present (n = 17). Variables with odds ratios >1 are positively associated with New England cottontail presence, and those <1 are positively associated with eastern cottontail presence in Connecticut.

	Eastern Cottontail	New England Cottontail
Variable Code	Mean ± SE	Mean ± SE
ShrAll	0.3 ± 0.05	0.34 ± 0.05
ShrHigh	0.32 ± 0.05	0.38 ± 0.05
ShrLow	0.27 ± 0.05	0.29 ± 0.05
StmDen	3.53 ± 0.58	5.42 ± 0.7
HerbCov	54.66 ± 6.27	36.89 ± 6.03
Canopy	45.28 ± 7.04	73.66 ± 6
BA	6.77 ± 1.23	12.31 ± 1.52
TreeHt	14.07 ± 1.99	13.84 ± 2.15
VOhigh	65.23 ± 4.65	67.09 ± 7.54
VOlow	44.78 ± 7.38	44.49 ± 9.03
VOht	0.79 ± 0.11	0.77 ± 0.17
AvgDBH	20.58 ± 3.63	13.16 ± 2.5
BAconif	4.24 ± 2.4	1.84 ± 1.49
BAhardw	95.76 ± 2.4	98.16 ± 1.49
TreeDenL	173.43 ± 38.87	219.94 ± 41.84
TreeDenS	1400.13 ± 495.1	3545.23 ± 997.27

Table 3: Comparison of habitat variables for known locations of eastern cottontail (*Sylvilagus floridanus*; n = 19) and New England cottontail (*S. transitionalis*; n = 17) in Connecticut.

Logistic regression plots showed a positive relationship between probability of presence of New England cottontail and amount of canopy closure and basal area (Figure 2 and Figure 3). Although not statistically significant, we observed positive trends between the probability of New England cottontail presence and stem density (P = 0.057), high shrub cover (>1 m tall; P = 0.386), and stand density of both large trees and saplings (P = 0.413 and P = 0.079, respectively), and negative trends between the probability of presence of New England cottontail and herbaceous cover (P = 0.058) and average DBH (P = 0.123).

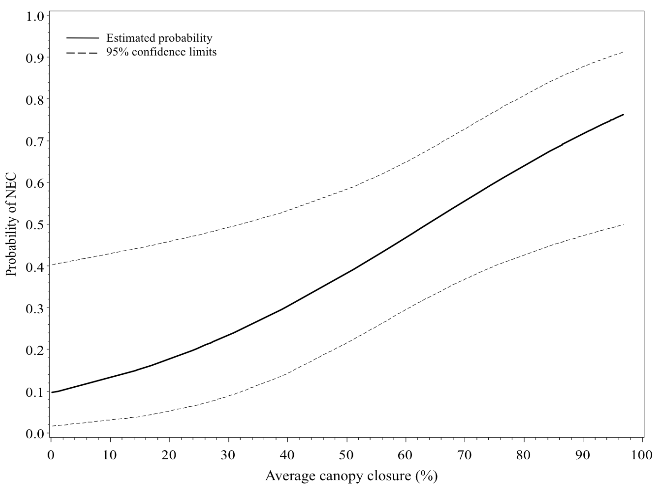

Figure 2: Logistic regression of the probability of New England cottontail (*Sylvilagus transitionalis*; NEC) presence versus eastern cottontail (*S. floridanus*) presence based on average percentage of canopy closure measured in 50 x 50 m plots.

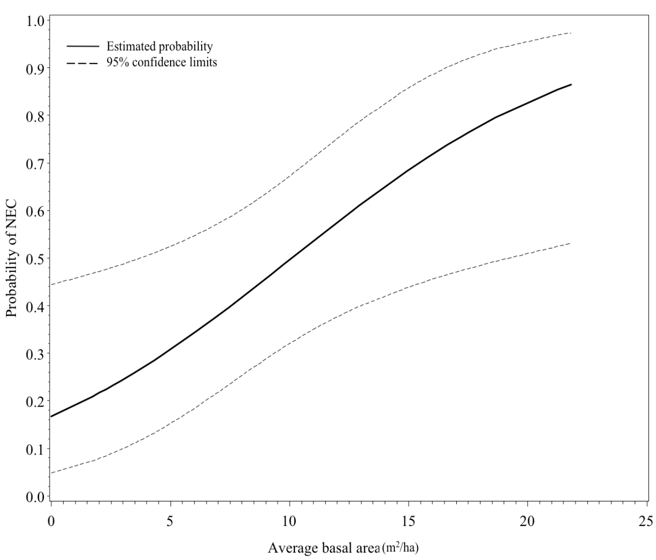

Figure 3: Logistic regression of the probability of New England cottontail (*Sylvilagus transitionalis*; NEC) presence versus eastern cottontail (*S. floridanus*) presence based on average basal area (m^2/ha) measured in 50 x 50 m plots.

Each shrub and herbaceous species was ranked from most to least abundant based on the measurements recorded using the line-intercept method, stem counts, and herbaceous cover estimates. We compared the ranking of plant species composition in plots occupied by New England cottontail compared to those occupied by eastern cottontail. Multiflora rose (*Rosa multiflora* Thunb.), autumn olive (*Elaeagnus umbellata* Thunb.), and fox grape (*Vitis labrusca* L.) were the most common high shrub species recorded in both New England cottontail and eastern cottontail sites, and multiflora rose and Asiatic bittersweet (*Celastrus orbiculatus* Thunb.) were the most commonly recorded low shrubs for both site types. Multiflora rose, Asiatic bittersweet, greenbrier (*Smilax* spp.), and *Rubus* spp. were stem count species with the highest average occurrence for both New England cottontail sites and eastern cottontail sites, and both sites had various grasses (Family *Poaceae*) as the most common plant in the herbaceous layer.

Discussion

In a comparison of fine-scale habitat features of core use areas for New England cottontail and eastern cottontail, basal area and canopy closure were the only two variables that were significant in a logistic regression analysis. Both basal area and canopy closure estimates were higher in the core use areas of New England cottontail than in eastern cottontail core use areas. In a recent region-wide analysis on tree canopy cover at sites occupied by New England or eastern cottontails, Buffum et al. [40] found that New England cottontail were more likely than eastern cottontail to occupy areas with high tree canopy (61 - 80% canopy cover). These results coincide with our findings of average estimate of 73.7% canopy closure for sites used by New England cottontail. Basal area has not been reported in previous habitat studies relating to New England cottontail, so direct comparisons to values observed in other parts of the species' range cannot be made, but references to this variable have been discussed in relation to other early successional wildlife species. Ideal basal area for bobwhite quail (*Colinus virginianus*) early successional habitat management in the Southeastern US has been reported as 7 - 21 m^2/ha [41]; however, in central US hardwood forests, basal areas >4.6 m^2/ha on managed lands were found to have reduced stem density and were therefore considered poor quality habitat for early successional wildlife species [42]. The average basal area measured in this study on sites with New England cottontail present (12.31 m^2/ha) agreed with the range presented for the Southeastern US, but was higher than the value presented by Thompson III and Dessecker [42] and would be considered poor quality habitat based on that metric.

Even-aged timber management, or clear-cutting, on small patches of habitat is often recommended as a management tool to provide habitat for early successional species [3,8,43], including New England cottontail [44,45]. In our study area, New England cottontail used habitats with a higher basal area and canopy closure than would be achieved using traditional even-aged timber management. Shelterwood cuts, on the other hand, retain 9 - 11m^2/ha of basal area that provides adequate residual canopy shading for seedling development in northern hardwoods [46]. Probert and Litvaitis [14] found that if eastern cottontails are able to colonize a habitat patch first, they will exclude New England cottontail from inhabiting that patch, so eliminating the majority of the canopy closure/basal area through a clearcut in a habitat patch may create habitat that is initially more ideal for eastern cottontail, which could prevent New England cottontail from eventually colonizing these managed habitat patches. Results from our study area suggest that shelterwood cuts may be a more appropriate silvicultural approach than clearcuts for creating habitat for New England cottontail in southern New England.

In our study area, the most common shrub species observed were multiflora rose, fox grape, and Asiatic bittersweet. These plant species are known to provide food for cottontails [47,48] and have the structure to provide cover; however, the manner in which the stems grow from the ground leads to artificially low stem density measurements with high variability. Litvaitis et al. [6] consider habitat suitable for New England cottontail if the woody stem density is >9,000 stems/ha, and Barbour and Litvatis [20] report that New England cottontail generally use patches with dense understory of >50,000 stems/ha. The stem density for New England cottontail sites in Connecticut was 54,167 stems/ha (SE ± 7,018), and although this number agrees with past studies, the variability was very high. Understory shrub cover and shrub density are important habitat variables for New England cottontail, but given the vine-like structure of the understory plant communities in southern New England, stem density is not the most accurate measure of cottontail habitat suitability. In established shrub habitats, stem counts should only be used along with other habitat measurements to accurately evaluate cottontail habitat in southern New England.

There were some limitations in this study stemming from the low population sizes of New England cottontails in the region, which had an effect on the sample size and the distribution of survey sites. Because the locations of the vegetation plots were determined by telemetry locations and not based on a random survey, the plots were clustered on four distinct properties where New England cottontail was known to occur. Although the vegetation survey plots for New England and eastern cottontails did not overlap, the vegetation characteristics of the entire properties were very similar. Had we surveyed more areas, there is a chance that we would have detected more significant differences in the habitat characteristics between the two-cottontail species, but with a steadily declining population of New England cottontail the opportunities for additional surveys of this nature are becoming increasingly more limited. Additionally, within our study area the two species are sympatric, and we did not have sites where only New England cottontail occur; therefore, we were limited to interpreting results based on habitat use. It is unclear whether the sites identified for New England cottontail in Connecticut are what the species is choosing based on preference, or if these sites are less desirable but are being used due to competition from eastern cottontail. It also is possible that the sites occupied by New England cottontail are in transition from an ideal early successional habitat to a more forested habitat -New England cottontail may not be able to persist in this marginal habitat over the long term. Alternatively, New England cottontail may be better adapted than eastern cottontail to this type of marginal habitat.

Ultimately, to be able to test what habitats are ideal for New England cottontail in southern New England, habitat characteristics need to be measured on New England cottontail populations that are allopatric to eastern cottontail populations to identify which habitats are being chosen based on preference. However, our results highlight the need to examine more habitat characteristics, such as basal area and canopy closure, rather than only shrub and stem density when evaluating habitats for New England cottontail management.

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