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Habitat management to reduce competitive interactions: case study of native and invading cottontails

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Abstract

Habitat management recommendations are often based on best available science determined through retroductive and inductive hypotheses. Such recommendations are not frequently tested, potentially resulting in the implementation of unreliable practices for management of imperiled species. The New England cottontail (*Sylvilagus transitionalis*) is an imperiled shrubland-obligate species whose recovery efforts include habitat management and restoration. Researchers suggest former best management practices for the species may result in ecological traps and new recommendations have been developed. We evaluated these newly revised best management practices designed to retain higher tree canopy closure to promote New England cottontails without encouraging eastern cottontails (*Sylvilagus floridanus*). We compared New England and eastern cottontail density between management plots (tree canopy thinned with all downed trees left on the ground, with or without invasive shrub treatment) and control plots (unmanaged) and examined the influence of management on resource selection and survival. Management strategies retaining higher canopy closure promoted stronger selection by New England cottontails than by eastern cottontails. Catch per unit effort of New England cottontails was greater than for eastern cottontails in management plots ($P = 0.002$). For both species, the proportion of the 95% home range overlapping managed areas was greater than the proportion of managed area in the habitat patch; however, for the 50% core area of the home range, this was only true for New England cottontails. When post-treatment canopy cover was >75%, New England cottontails selected canopy-thinning treatments without invasive shrub removal over unmanaged areas, but selection by eastern cottontails was unaffected by management treatment or canopy cover. Survival probability of both species was high and uncorrelated with time spent in management areas. Survival probability decreased as the average distance a rabbit moved in a 7-day period increased. Our results illustrate the need to revise management strategies that emphasize eliminating canopy cover when improving New England cottontail habitat is an objective, particularly where they are sympatric with eastern cottontails.

KEYWORDS

habitat selection, invasive species, New England cottontail, shrubland, survival, *Sylvilagus floridanus*, *Sylvilagus transitionalis*, young forest

Habitat management and restoration are important tools for the conservation of imperiled species. Management recommendations for such species are often based on best available science (Doremus 2004, Murphy and Weiland 2016) determined through retroductive and inductive hypotheses, which are not frequently tested and are thereby limited in their usefulness for drawing reliable conclusions (Romesburg 1981, Nichols and Williams 2006, Seddon et al. 2007, Guthery 2010). In such cases, habitat restoration efforts may fail to meet their objectives for population growth or abundance, and without evaluations of hypothesized effects of management actions on resource selection and fitness, the reasons for failures may not be apparent or rectifiable (Parma 1998, Cheeseman et al. 2021). Some restorations could even create perceptual or ecological traps for target species (Hale and Swearer 2017).

The relationships among management actions, habitat selection, vital rates, and population response are typically obscured by uncertainties that observational studies alone cannot resolve (Romesburg 1981, Guthery 2010). Frequently research comprises isolated, single studies that may not provide a considerable increase in knowledge or conclusive evidence; thus, recommendations now call for researchers to shift from isolated studies and instead focus on contributing to the bigger picture of accumulating evidence through continual studies (Nichols et al. 2021). Deriving retroductive hypotheses from a study in a particular location and then conducting an experimental evaluation in the same location is the first step to generalizing knowledge that is useful for management, with the next step being to replicate the experiments in other relevant settings. If decisions are made iteratively until uncertainty is reduced to an agreed-upon level, then the experimental and monitoring processes can form the part of a true adaptive management framework. The conservation effort for the imperiled New England cottontail (*Sylvilagus transitionalis*) provides an example of how enacting management using best available science when there is high uncertainty (e.g., effect of invasive competitors and hybridization, recently-naturalized predators, invasive plants, and parasites such as ticks on habitat selection and fitness; Litvaitis et al. 2008, Fuller and Tur 2012, Cheeseman et al. 2021) can lead to detrimental outcomes. Uncertainties can be reduced through experimental management and subsequent evaluation to improve species management.

A shrubland obligate and the only native cottontail found east of the Hudson River, the New England cottontail experienced drastic population declines after the mid-1900s due largely to habitat loss and fragmentation

(Litvaitis 1993, Litvaitis et al. 2006). As a result, the New England cottontail has been of significant conservation focus including its consideration for listing through the Endangered Species Act. The United States Fish and Wildlife Service (USFWS) concluded that listing was not warranted in 2015 because ongoing restoration efforts were considered sufficient for recovery (USFWS 2015). Since the listing decision on the New England cottontail, populations have continued to decline, with recent estimates indicating an additional 50% decline in occupied sites in the past decade (Rittenhouse and Kovach 2020), suggesting current strategies may be insufficient to ensure recovery.

Habitat restoration targeting early-successional stages of shrubland, characterized by low overstory canopy and high shrub stem density (Cheeseman et al. 2018:appendix 1), has been the primary focus of conservation for New England cottontails (New England Cottontail Regional Technical Committee 2017). Yet widespread invasion in New England and eastern New York, USA, by eastern cottontails (*Sylvilagus floridanus*), an introduced competitor that occupies similar habitat, and invasive shrubs may affect the efficacy of traditional management practices (Litvaitis and Probert 1996, Cheeseman et al. 2018). Cheeseman et al. (2021) suggest that some management strategies may act as ecological traps, particularly in the presence of eastern cottontails or invasive shrubs. These authors reported that management for early-successional shrubland (e.g., clear cutting) was associated with low survival and density of New England cottontails. There were also complex trade-offs in habitat quality (e.g., amount of cover and forage present relative to the amount needed to sustain a stationary or growing population) for the species based on the abundance of eastern cottontails, as eastern cottontails appeared to competitively exclude New England cottontails from early to mid-successional shrublands (Cheeseman et al. 2018, 2021). Because traditional management for the New England cottontail aims to create conditions of early and mid-successional shrublands, these results indicate a serious risk of promoting the non-native species while creating an ecological trap for the native New England cottontail. An evaluation of approaches to conserve New England cottontails in the presence of eastern cottontails is therefore needed.

We tested retroductive hypotheses regarding the effectiveness of revised best management practices for New England cottontails using experiments in the same location at which the hypotheses were originally derived. Based on the research by Cheeseman et al. (2018, 2021), we designed management treatments for New England cottontails in New York to test competing hypotheses of resource selection in the face of species competition (Cheeseman and Cohen 2019). We developed management treatments to retain a higher degree of canopy closure than was called for in pre-existing protocols and to promote the growth of native shrubs to simulate mid- and late-successional shrublands (Cheeseman et al. 2018:appendix 1), rather than early to mid-successional shrublands preferred by eastern cottontails. Habitat selection and estimates of population density are valuable tools for understanding an individual's relationship with its environment, and for gauging species-specific responses to habitat management (Manly et al. 2002). But inter- and intraspecific competition and other ecological interactions, whether direct or indirect, can lead to a mismatch between selection or density and what we understand as a species' optimal habitat (Van Horne 1983, Ginger et al. 2003, Cheeseman et al. 2018, Reif et al. 2018). In these instances, using direct indicators of fitness (i.e., survival) leads to more accurate inferences of habitat quality (Bock and Jones 2004, Johnson 2007).

Specifically, we tested the hypothesis that managing habitat to retain higher canopy closure similar to that of mid- to late-successional shrublands could selectively promote use by New England cottontails without encouraging use by eastern cottontails. Our objective was to evaluate the responses of New England and eastern cottontails to these management treatments by comparing an index of density between management and control plots, determining if managed areas were incorporated into home ranges and core areas out of proportion to their availability in habitat patches, determining within-home-range factors that affected selection within managed and unmanaged areas, and examining the relationship between survival and ecological and management covariates. We predicted that New England cottontails would have higher survival and densities within management plots than in control plots and would select for managed areas while eastern cottontail would show no response (survival, density, or selection) to managed areas.

STUDY AREA

Our study took place in Dutchess and Putnam counties within the Hudson Valley in New York (latitude 41.5429°, longitude −73.6635°). This area was characterized by a 4-season temperate climate and highly variable snowfall. Average monthly temperature during the study period from November 2018–April 2019 and October 2019–March 2020 was 3.1 ± 4.6 (SD)°C and average monthly precipitation was 8.1 ± 4.1 cm (National Oceanic and Atmospheric Administration [NOAA] 2021). Daily snow depth varied across winters (Nov through Mar), ranging from 0 cm to 20.3 cm (2018–2020; NOAA 2021). The topography in the area is low-lying and hilly, with study sites ranging in elevation, from approximately 125 m to 400 m. Land uses in the Hudson Valley area were a mix of residential, commercial, agricultural, nature preserves, and recreational areas. Study sites contained a mixture of successional shrublands, forested shrub wetlands, and deciduous coniferous mixed forest. Shrublands were typically dominated by invasive Japanese barberry (*Berberis thunbergii*), multiflora rose (*Rosa multiflora*), oriental bittersweet (*Celastrus orbiculatus*), autumn olive (*Elaeagnus umbellata*), and bush honeysuckle (*Lonicera tatarica*), with lower densities of native species such as blackberry and raspberry (*Rubus* spp.), viburnums (*Viburnum* spp.), and dogwoods (*Cornus* spp.). Forested wetlands were often dominated by native shrubs including sweet pepperbush (*Clethra alnifolia*) and blueberry (*Vaccinium* spp.). Mixed deciduous-coniferous forests were generally dominated by eastern red cedar (*Juniperus virginiana*), oaks (*Quercus* spp.), maples (*Acer* spp.), and shrubs or small trees such as autumn olive, privet (*Ligustrum sinense*), Japanese barberry, and prickly ash (*Zanthoxylum americanum*). The study area contained a high diversity of terrestrial and aquatic wildlife characteristic of temperate mixed forests, including resident and migrant birds, small and large mammals, and reptiles and amphibians. White-tailed deer (*Odocoileus virginianus*) were among the most abundant large mammals, occurring in densities to affect vegetation composition. Study sites commonly included other mammals such as black bear (*Ursus americanus*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*), eastern gray squirrel (*Sciurus carolinensis*), American red squirrel (*Tamiasciurus hudsonicus*), and North American deer mice (*Peromyscus* spp.). Common bird species included turkey (*Meleagris gallopavo*), American crow (*Corvus brachyrhynchos*), blue jay (*Cyanocitta cristata*), American woodcock (*Scolopax minor*), gray catbird (*Dumetella carolinensis*), veery (*Catharus fuscescens*), and eastern towhee (*Pipilo erythrophthalmus*).

METHODS

Field methods

We implemented habitat management at 4 sites with known New England and eastern cottontail presence at the site level based on previous trapping efforts and pellet surveys (Cheeseman 2017). Although all sites had historical occupancy, not all managed areas were known to be used by New England and eastern cottontails at the time of the study. To evaluate the effect of management recommendations for higher canopy retention and removal of invasive shrubs on cottontail interactions, habitat use, and survival, we selected from previously managed sites or created 100-m × 100-m management plots treated with canopy thinning ranging from approximately 10% to 60% at the plot level and leaving downed trees *in situ* (Figure 1). Managers conducted all tree cutting between 2013 and 2019. Each site had 2–6 experimental units, defined as a paired 100-m × 100-m control plot and a management plot. We established paired plots within 150 m of each other and kept them small to help ensure both plot types would be accessible to resident cottontails given the short movement distances (e.g., 75 m) and home range size (e.g., 0.84–1.81 ha) of New England cottontails (Cheeseman 2017, Cheeseman et al. 2018). We selected control plots that were similar in plant species and composition to management plots prior to treatment. Within management plots, invasive shrubs were either left untreated ($n = 6$), treated throughout the plot ($n = 4$), or treated in 50-m × 50-m blocks comprising 50% of the plot area ($n = 4$). Invasive shrub treatments included spraying,

FIGURE 1 Example of management area before (pre-treatment) and after (post-treatment) selective thinning of canopy trees for New England cottontail habitat management in New York, USA, 2018–2020.

mechanical removal, or both, subject to local restrictions and landowner preference. We considered sites to be treated for invasive species immediately after mechanical removal or 14 days after spraying to allow for plant die-off for the purpose of analyses (T. Lewis, Trillium Invasive Species Management, personal communication).

We live-trapped New England and eastern cottontails from November 2018 through April 2019 and October 2019 through March 2020 using single door box traps (Havahart, Lititz, PA, USA; Tomahawk live traps, Tomahawk, WI, USA) baited with apple slices. We set 40 traps for each experimental unit near cover or rabbit sign (e.g., scat, browsed plants, small pathways through vegetation): 10 were approximately 25 m apart within each management and control plot, and 10 were in locations with high cover or sign of rabbits within a 75-m buffer around each plot. Trapping sessions for experimental units were 2–3 weeks long and separated by a >3-month interval. We made initial species determinations in the field by morphological traits (Cheeseman et al. 2018) and confirmed species genetically. We marked individuals with a uniquely numbered metal ear tag and used a scalpel to collect an approximately 0.3-cm × 0.3-cm tissue sample from an ear for species confirmation, which we stored in 100% ethanol for genetic analysis. We extracted DNA for species identification from biopsied tissue using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Germantown, MD, USA) following the methods described by Whipps et al. (2020), and implementing methods from earlier studies (Litvaitis and Litvaitis 1996, Kovach et al. 2003, Kilpatrick et al. 2013). We conducted confirmation of species identification on a subset of samples and any ambiguous results by DNA sequencing as described by Whipps et al. (2020).

We outfitted adult cottontails weighing ≥800 g with a 20-g very high frequency (VHF) radio-transmitter (Advanced Telemetry Systems, Isanti, MN, USA), a 20-g VHF radio-transmitter with a 4-g PinPoint global positioning system (GPS) tag (Lotek Wireless, Newmarket, ON, Canada, discontinued in study because of antenna breakage), or a 20-g LiteTrack 20 RF GPS collar (Lotek Wireless), all with zip-tie closures. Total collar mass did not exceed 28 g, which was <5% of the body mass of any individual.

We obtained locations for collared rabbits beginning 3 days after capture to allow for an adjustment period (Bond et al. 2001). We located rabbits with VHF collars 3 times/week, twice during active (2 hr before sunset to 2 hr after sunrise) and once during resting periods (2 hr after sunrise to 2 hr before sunset) via triangulation and homing (Bond et al. 2002, Cheeseman et al. 2018). We used homing for approximately 90% of resting locations, where we approached each rabbit and obtained GPS coordinates (Garmin, Olathe, KS, USA; accuracy = 5 m) of its resting spot. We estimated locations from triangulations using Location of a Signal 4.0 (LOAS™) software (version 4.0.3.8; Ecological Software Solutions, Hegymagas, Hungary). We estimated triangulation error using trials of VHF transmitters in known locations in the field (average accuracy = 26 ± 19.8 m [SD]), and we included azimuth error in our triangulation calculations for rabbit locations. The GPS collars were programmed to attempt locations every 31.33 hours, with 3 or 5 locations taken within a 6-minute or 12-minute window, respectively. This program allowed the collar to obtain locations that cycled through active and resting periods. The GPS collars were prone to large errors when initially obtaining satellites, possibly because of high cover at rabbit locations. To be considered a successful location attempt and included in analyses, we required the GPS unit to have captured a minimum of 2 GPS points in a 12-minute window that were within 30 m of all other points in the set. To obtain the final location for each group, we took the centroid of all points that met these criteria. All GPS and VHF transmitters were equipped with an 8-hour mortality switch and we investigated, confirmed, and recorded mortality events.

We sampled vegetation between November and April, when deciduous plants are without leaves, in both field seasons. We established 50-m × 50-m grids at each site and collected data at the center of every grid cell. We measured canopy closure from a height of 1 m with a spherical densitometer (Forestry Suppliers, Jackson, MS, USA) at the grid cell center. Within each cell, we assessed stem density by counting the number of stems of each woody plant with a diameter breast height of <7.5 cm at a height of 0.5 m along 10-m transects with a width of 1 m (Barbour and Litvaitis 1993, Cheeseman et al. 2018). From these transects, we separately classified stem density of Japanese barberry and native palatable stems, as determined by New England cottontail feeding trials (Pringle 1960), to allow us to quantify cottontail selection of these vegetation types. We imported data into ArcMap 10.8.0 (Esri, Redlands, CA, USA), and resampled vegetation metrics to 10-m resolution across sites using bilinear interpolation (Bonnot et al. 2009, Stabach et al. 2009, Cheeseman et al. 2018).

Data processing and analysis

Low recapture rates and dense vegetation make estimation via mark-recapture or distance surveys difficult for New England cottontail (Cheeseman et al. 2021). We thus modeled catch per unit effort (CPUE) as an index of density for New England and eastern cottontails (Barbour and Litvaitis 1993, Lancia et al. 1996, Schmidt et al. 2005, Allen et al. 2020, Cheeseman et al. 2021). We estimated CPUE as a function of plot type (e.g., management or control); thus, we included only captures that occurred within management or control plots and excluded captures that occurred outside of those boundaries. We fit models using a mixed effect zero-inflated Poisson regression in the glmmTMB package (Brooks et al. 2017) in Program R version 3.6.3 (R Core Team 2020). We used the trapping session and experimental unit combination as a random effect to account for rabbits recaptured multiple times within a trapping session and experimental unit. We included the log of the number of trap nights as an offset in the model and predicted captures per 100 trap nights.

To evaluate the inclusion of managed areas within cottontail home ranges, we estimated 95% isopleths (home range) and 50% isopleths (core area) using the adaptive local convex hull method (a-LoCoH) in package adehabitatHR (Calenge 2006) in program R version 3.6.3 (Getz et al. 2007, Cheeseman et al. 2019, R Core Team 2020). This approach performs better than kernel models when there are abrupt edges (e.g., roads, field edges, residential areas; Getz et al. 2007). We estimated home ranges and core areas for each individual by field season combination for which we had ≥30 locations, as home range size stabilized above 30 locations (Figure S1, available in Supporting Information). We excluded rabbits with <30 locations from the home range and resource selection analyses. We then calculated the proportion of each rabbit's home range within managed areas (i.e., management plots in addition to management conducted outside of plot boundaries), and the proportion of the habitat patch composed of management. We defined habitat patches by delineating shrublands in ArcMap 10.8.0 (Esri) based on remote sensing of aerial imagery and ground surveys of vegetation structure. Features such as mowed fields, water bodies, roads, or loss of dense understory vegetation (e.g., mature forest) also defined patch boundaries (Barbour and Litvaitis 1993, Cheeseman et al. 2018). We compared the proportions of home ranges and core areas within a management plot to the proportion of the patch within a management plot using multi-response permutation procedure for blocked data in the statistical software Blossom (Cade and Richards 2001). This procedure is a non-parametric analog of multivariate analysis of variance that is useful for small sample sizes and allows for block effects. In our case, the blocks were combinations of rabbit and field season.

We assessed resource selection using resource selection functions (RSFs; Lele 2009) and the rsf function in the package ResourceSelection (Lele et al. 2019). We randomly generated 15 points per rabbit location within each home range to sample resource availability and extracted covariates to selected points. We modeled RSFs as a function of proportion canopy cover at the rabbit locations and random point locations, canopy management (1 = managed, 0 = unmanaged), and invasive shrub treatment (1 = partial or total invasive treatment within plot, 0 = no invasive treatment), with species as strata. Because of computational limitations that prevented testing all subsets of a global model, we built 6 models containing different combinations of the above variables and interactions among them, representing hypotheses for resource selection. We performed model selection using an information-theoretic approach and Akaike's Information Criterion corrected for sample size (AIC_c; Burnham and Anderson 2002). We considered any model with a relative likelihood >0.125 to have support, and we based inferences on model-averaged predictions if the top model had a weight <90% (Burnham and Anderson 2002). We inferred a difference in predicted values for habitat selection between treatments if 95% prediction intervals overlapped by <25% (Cumming and Fidler 2005).

We modeled survival during the winter field season as a function of species, proportion of locations in a management plot in the previous 28 days, and average distance moved in the previous 7 days, using logistic exposure models (Shaffer 2004), including an interaction between species and both continuous variables. Although snow depth can influence cottontail survival (Cheeseman et al. 2021), across our 2 field seasons snowpack was minimal (average daily snow depth = 1.6 ± 3.8 cm [SD]); thus, there was little variability to model. Similar to our home range methods, we modeled individual survival separately by field season. We used the dredge function in the R package MuMIn (Barton 2020) to obtain a set of models with all combinations of the parameters in the global model. We used the same approach as in our resource selection analysis to perform model selection. When graphically depicting the influence of variables on survival, we predicted survival over 180 days (the approximate length of the leaf-off season) for all variables except distance, which we predicted to 7 days because long movements are ephemeral and rare, thus likely affect survival at small temporal scales.

RESULTS

We captured 54 cottontails (31 New England, 23 eastern, identified in the field and confirmed by DNA analysis) over 2 field seasons. For New England cottontails, we caught 3 juveniles and collared 28 adults. For eastern cottontails, we did not catch any juveniles and collared 22 adults. During the course of our study, we observed at least 1 New England cottontail location in 12 of 14 management plots. We never observed New England cottontails at 1 site, which accounted for the 2 unoccupied management plots. We confirmed New England cottontail use of newly managed areas as soon as the first trapping event (11 days post treatment). We observed at least 1 eastern cottontail location at 8 of the 14 management plots.

Our dataset for calculating CPUE included 31 New England cottontail and 6 eastern cottontail captures across 6,782 trap nights within 28 management and control plots. In managed plots, CPUE of New England cottontails (0.624 ± 0.189 [SE]) was greater than CPUE for eastern cottontails (0.055 ± 0.041, $P = 0.002$; Figure 2), but there was no difference in CPUE in control plots between New England cottontails (0.205 ± 0.095) and eastern cottontails (0.110 ± 0.061, $P = 0.371$). For New England cottontails, CPUE was greater in management plots than control plots ($P = 0.032$), but the difference for eastern cottontails was not significant ($P = 0.446$).

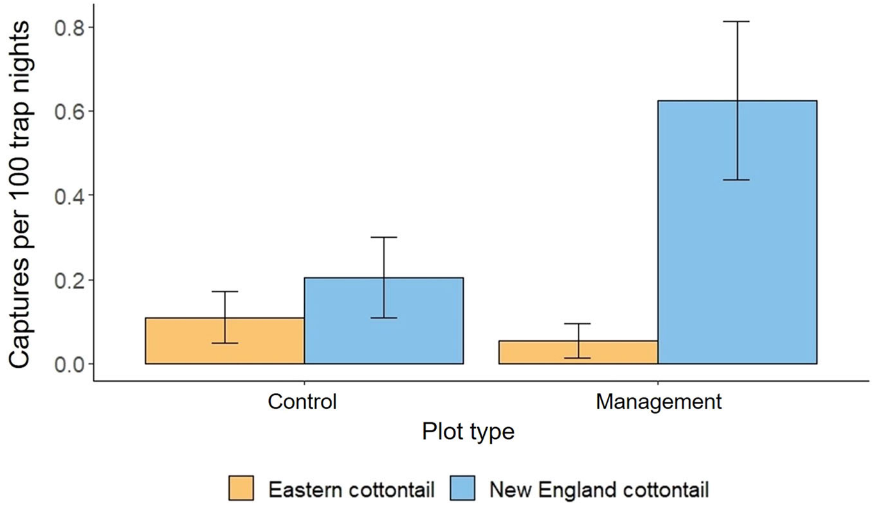

FIGURE 2 Predicted captures per 100 trap nights for eastern (orange) and New England (blue) cottontails in control and management plots in New York, USA, 2018–2020. Error bars represent standard errors.

We collared 50 adult rabbits (28 New England, 22 eastern) from November 2018 to March 2020 and obtained 2,279 locations from VHF and GPS collars. We calculated home ranges for 20 individual by field season combinations for New England cottontails (16 individuals), and 10 individual by field season combinations for eastern cottontail home ranges (10 individuals). Average home range and core area sizes for New England cottontails were 1.33 ± 0.16 (SE) ha and 0.35 ± 0.06 ha, respectively. For eastern cottontails, average home range and core area sizes were 1.43 ha ± 0.27 and 0.31 ha ± 0.06, respectively. The average patch size at our sites was 15.07 ha ± 2.28.

For New England cottontails, the median proportion of the home ranges and core areas within management was greater than the proportion of the patch containing management ($P = 0.013$; Table 1). For eastern cottontails, the median proportion of home ranges within managed areas was greater than that of management in habitat patches ($P = 0.017$; Table 1), but lower than the proportion of home ranges within managed areas observed for New England cottontails. The median proportion of eastern cottontail core areas in managed areas was 0, but the proportion within management did not differ from the proportion of the patch comprised of management ($P = 0.068$; Table 1).

Only 3 of 10 eastern cottontail core areas incorporated management, compared to 15 of 20 New England cottontail core areas. Seven of the 10 eastern cottontails were captured at a study site occupied by only eastern cottontails; New England cottontails no longer occurred at the site prior to the start of our study. For those 7 eastern cottontails, the average proportion of management in the home range (95% isopleth) was 0.17 ± 0.05 (SE), and only 1 included management in its core area.

We evaluated resource selection based on 951 locations of 20 New England cottontail individual × field season combinations paired with 14,265 available points, and 490 locations of 10 eastern cottontail individual × field season combinations paired with 7,350 available points. Of our 6 models, the top model had >90% of the weight. This model contained an interaction between species and management status, between species and proportion canopy closure, and between species and invasive vegetation treatment status (Table 2). New England cottontails selected for low canopy closure in unmanaged areas and high canopy closure in managed areas (Figure 3A). Where canopy closure was high (>75%), they selected for managed areas without invasive shrub treatment over unmanaged areas or managed areas with invasive shrub treatment (Figure 3A). For eastern cottontails, there was no evidence of an effect of canopy closure or treatment type on selection, although the lowest RSF value was for managed areas with no invasive shrub removal (Figure 3B).

TABLE 1 Multivariate medians of the proportion of New England and eastern cottontail 95% isopleth home ranges, 50% isopleth core areas, and habitat patches within management areas in New York, USA, 2018–2020.

Species	Area type	Median proportion of area type within management	Test statistic	P[a]
New England cottontail	Home range (95% isopleth)	0.38	−2.190	0.042
	Core area (50% isopleth)	0.50	−3.477	0.013
	Habitat patch	0.17		
Eastern cottontail	Home range (95% isopleth)	0.27	−3.025	0.017
	Core area (50% isopleth)	0.00	−1.627	0.068
	Habitat patch	0.14		

[a]P-value from comparing median proportion of home range or core area within management to median proportion of habitat patch comprised of management.

TABLE 2 Model structure and information-theoretic model selection criteria for New England and eastern cottontail resource selection functions in New York, USA, 2018–2020.

Model	K[a]	ΔAIC_c[b]	w_i[c]	Relative likelihood[d]	Deviance
No management (species)[e] + no management:canopy closure (species) + management:no invasive management (species) + management:canopy closure (species) + management:invasive management[i] (species)	10	0.00	0.996	1.000	18,958
No management (species) + management:no invasive management (species) + management:invasive management (species) + canopy closure (species)	8	11.68	0.003	0.003	18,972
No management (species) + management:no invasive management (species) + management:invasive management (species) + canopy closure	7	14.36	0.001	0.001	18,978
Canopy closure	1	30.74	0.000	0.000	19,006
No management (species) + management:no invasive management (species) + management:invasive management (species)	6	34.85	0.000	0.000	19,000
No management + management:no invasive management + management:invasive management	3	56.39	0.000	0.000	19,028

[a]The number of parameters in the model.

[b]The difference in the Akaike's Information Criterion corrected for small sample sizes (AIC_c) between a given model and the top model. The AIC_c of the top model was 18,977.09.

[c]Akaike weights, or the probability that the given model fits the data best, of the models tested.

[d]The likelihood ratio of the given model to the top model ($e^{-0.5\times\Delta AIC_c}$).

[e]Binary term of 1 = New England cottontail and 0 = eastern cottontail.

We monitored survival of 34 individual × field season combinations of New England cottontails (28 individuals) and 27 individual × field season combinations of eastern cottontails (23 individuals). We recorded 13 mortalities out of 1,218 observations for New England cottontails and 9 mortalities out of 1,005 observations for eastern cottontails. Mean predicted survival during the 180-day winter study period was 0.537 ± 0.085 (SE) for New

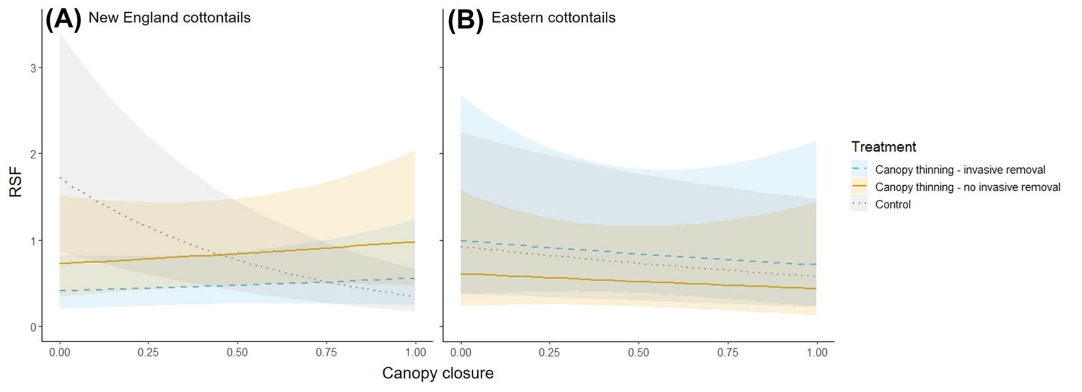

FIGURE 3 Resource selection functions (RSFs) of New England (A) and eastern (B) cottontails and proportion canopy closure in New York, USA, 2018–2020, where there was no management (gray), management with invasive shrub and canopy thinning treatment (blue), and management with only canopy thinning (orange). Shaded regions represent 95% prediction intervals.

TABLE 3 Model structure and information-theoretic model selection criteria for New England and eastern cottontail leaf-off season survival in New York, USA, 2018–2020.

Model	K[a]	ΔAIC_c[b]	w_i[c]	Relative Likelihood[d]	Deviance
Distance	2	0.000	0.298	1.000	218.125
Distance + management[e]	3	0.525	0.229	0.769	216.644
Distance + management × species[f]	5	1.523	0.139	0.467	213.626
Distance + species	3	1.953	0.112	0.377	218.072
Distance + management + species	4	2.526	0.084	0.283	216.637
Null	1	3.355	0.056	0.187	223.483
Management	2	4.700	0.029	0.095	222.824
Species	2	5.331	0.021	0.070	223.455
Management × species	4	5.446	0.020	0.066	219.557
Management + Species	3	6.702	0.011	0.035	222.821

[a]The number of parameters in the model.

[b]The difference in the Akaike's Information Criterion corrected for small sample sizes (AIC_c) between a given model and the top model. The AIC_c of the top model was 222.13.

[c]Akaike weights, or the probability that the given model fits the data best, of the models tested.

[d]The likelihood ratio of the given model to the top model: $\exp(-0.5 \times \Delta AIC_c)$.

[e]1 = management and 0 = no management.

[f]1 = New England cottontail and 0 = eastern cottontail.

England cottontails and 0.543 ± 0.088 for eastern cottontails. We found strong evidence that distance moved in a 7-day period affected survival; this variable was in all top models (Table 3). For both species of cottontail, weekly survival declined with mean distance moved in the previous 7 days (Figure 4). We only found weak evidence for a potential effect of proportion time spent in management over 28 days and species, which occurred in models with a lower deviance than the top model and a $\Delta AIC_c < 2$ (Arnold 2010). The model-averaged relationship with time spent in management was flat (Figure S2A, available in Supporting Information). The predictions of our global model, in

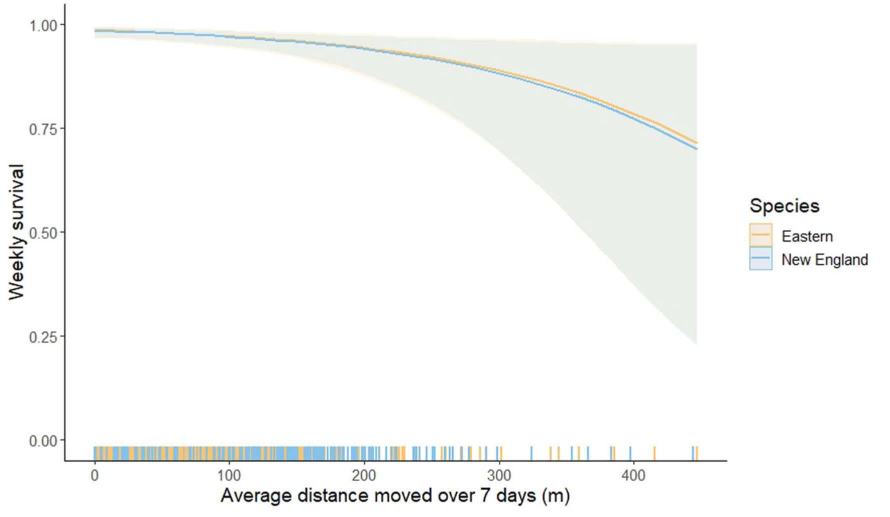

FIGURE 4 Model-averaged weekly probability of survival versus average distance moved over 7 days (m) for eastern (orange) and New England (blue) cottontails in New York, USA, 2018–2020. Probability of survival for both cottontail species was similar, resulting in overlapping regions. Observed values of averaged distance moved for individuals are plotted on the *x*-axis. Shaded regions represent 95% confidence intervals.

which survival of eastern cottontails but not New England cottontails was negatively related to proportion of time in management, suggest that this relationship can still be considered a remaining uncertainty worthy of further investigation with more study plots (Figure S2B).

DISCUSSION

Our results suggest that management strategies retaining higher canopy closure through selective thinning promoted selection by New England cottontails more than by eastern cottontails. In addition, these management strategies did not negatively influence survival of New England cottontails (or eastern cottontails). Both species used managed areas, but New England cottontails incorporated management into their core areas (50% isopleth), using it proportionally more than what was available on the landscape, while eastern cottontails did not. Even at a site solely occupied by eastern cottontails, only one individual included management in their core area, suggesting that eastern cottontail use of management is minimal even in areas that are not subject to competition from New England cottontails.

These results indicate thinning to 40–90% canopy closure and leaving the downed trees would benefit New England cottontails. Leaving fallen trees can help to create ground cover (Bull et al. 1997, Butts and McComb 2000) and retain understory by minimizing disturbance caused by removing trees and may help to reduce deer browse on shrubs and seedlings. We frequently observed both species of cottontails using downed trees and brush piles created from canopy thinning and invasive shrub removal as resting locations, suggesting that leaving felled trees and other coarse woody debris is providing cover. In New Hampshire, USA, New England cottontails chose poor quality forage resources during the leaf-off season to remain in cover, while eastern cottontails more readily foraged outside of cover during this time (Smith and Litvaitis 2000).

Although cover is important for protection from predators, forgoing forage can result in a greater loss of body mass and higher rates of predation for New England cottontails when compared to eastern cottontails (Smith and Litvaitis 2000). The downed crowns, however, might provide additional forage while shrub regeneration occurs in canopy gaps. We found no relationship between survival and time spent in management and thus no evidence that these management actions resulted in negative tradeoffs between cover and forage or otherwise had a detrimental impact on New England cottontail winter survival in the 2 years following cuts. Small sample sizes and the inclusion of only 2 years in our study may also have precluded the detection of trends.

Winter survival of cottontails in our study (New England = 0.537, eastern = 0.543) was similar to or higher than survival rates reported in other studies for New England and eastern cottontails (range = 0.05 – 0.69; Barbour and Litvaitis 1993, Boland and Litvaitis 2008, Weidman and Litvaitis 2011, Cheeseman et al. 2021). Snow has been associated with high mortality for cottontails (Trent and Rongstad 1974, Keith and Bloomer 1993, Brown and Litvaitis 1995), and previous research on New England cottontails in our study area indicated snow was a major factor affecting survival (Cheeseman et al. 2021). In our study, New England cottontail weekly probability of survival was 0.98 (95% prediction interval = 0.96–0.99), which was similar to weekly probability of survival under no snow conditions reported by Cheeseman et al. (2021), and suggests the high survival we observed may be due, at least in part, to low snowpack. Continued monitoring through more severe winters may provide further information on the value of our management plots for adult survival.

Where New England and eastern cottontail are sympatric, New England cottontails will select for higher canopy closure areas. Buffum et al. (2015) reported that where both species co-occurred, 79% of New England cottontail-occupied sites were within the 41–60% and 61–80% canopy closure classes, and New England cottontails were more likely to occupy sites with 61–80% tree canopy closure than eastern cottontails. Our results extend the above findings by implying that New England cottontails will be attracted to areas of high canopy closure as long as there is adequate ground cover, but eastern cottontails will not be. We have reduced uncertainty regarding habitat selection where the 2 species are sympatric and data favors the retroductive hypotheses of Cheeseman et al. (2018); our results may form the basis for adaptive management.

New England cottontails selected for the high stem density and ground cover of invasive shrubs in a prior study in New York (Cheeseman et al. 2018). Spraying and removing invasive shrubs reduces available cover in the short term and removes forage if invasive shrubs are a food source (Sweetman 1949). Lower cover and potentially forage in areas with invasive shrub treatment may explain why selection for these areas by cottontails was lower than areas where invasive shrubs were not treated. Further study should continue to evaluate the relationship between invasive removal and winter survival.

Management decisions regarding New England cottontails are made primarily by state and private landowners, based on guidelines that are under annual review by a centralized collaborative technical committee of state and federal biologists from across the species' range, with input from university researchers and other landowners. Thus, strategies are updated on a regular basis, and progress toward reducing uncertainties are evaluated, with new information and guidance, including research needs, then provided to landowners. Given the iterative nature of the decision-making and the continual need to update knowledge, we suggest that decision-makers implement an adaptive management framework for future New England cottontail conservation. Current coordination occurs primarily via standardized occupancy monitoring protocols and shared resources (e.g., funding opportunities and captive bred individuals) that are mediated via the technical committee. True adaptive management provides a framework for making decisions in the face of uncertainty (Holling 1978, Walters 1986), and there are few examples of the complete adaptive process in wildlife management. These examples emphasize identifying clear objectives for management, enlisting cost effective and statistically powerful monitoring and sampling, continuously learning from results and experiments, and ensuring information is accessible to continue the program (Gibbs et al. 1999, Armstrong et al. 2007, McCarthy and Possingham 2007). Our study, which turned observational inferences into experimental hypotheses, is an important step towards the adaptive management process for New England cottontails, and with our experiments being replicated in 1 other state involved in the cooperative conservation strategy, this provides an opportunity to consider how to implement adaptive management moving forward.

By testing retroductive hypotheses for New England cottontail habitat selection and survival where the species co-occurs with eastern cottontails via canopy thinning and invasive shrub treatments, we were able to find support for the predicted pattern of Cheeseman et al. (2018), which states that when habitat is occupied by both New England and eastern cottontails, New England cottontails will occupy higher canopy closure areas, while eastern cottontails occupy lower canopy closure areas. With our study as an example, we illustrate the need for implementing an adaptive management framework for New England cottontail conservation in addition to revising best management practices for the species. Current best management practices for New England cottontails suggest creating early-successional shrubland; however, this vegetation community is associated with low survival and density of New England cottontails and promotes occupancy by the invasive competitor. The revised best management practices tested in our study, where habitat is restored to mimic mid- to late-successional shrubland that retains higher canopy closure, promote use by New England cottontails over eastern cottontails and, at least, do not have a detrimental effect on survival relative to early-successional stages.

MANAGEMENT IMPLICATIONS

The results of our study suggest that creating habitat similar to mid- to late-successional shrublands (e.g., selective thinning, canopy gap phases) is an effective approach to management of New England cottontails where they co-occur with eastern cottontails. The effects of invasive plant removal on New England cottontail habitat selection and survival require further study. As such, invasive plants should be retained at sites that otherwise lack shrub cover, with removal only done experimentally. Leaving felled trees may help mitigate the loss of cover due to invasive removal, and was an integral part of our approach. Long-term monitoring in our study area, and the implementation of additional plots over time as succession changes the vegetation structure, will allow for the accumulation of evidence that can help with management, and is recommended to improve conservation of New England cottontails. We also recommend that adaptive management be formally introduced in New England cottontail conservation strategies going forward.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

Animal capture and handling procedures followed animal care and use guidelines of the American Society of Mammalogists (Sikes et al. 2016) and were approved by the State University of New York of Environmental Science and Forestry Institutional Animal Care and Use Committee (protocol 180601).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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