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Research Article

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Plant constituent predictors in the winter diet selection of the imperiled New England Cottontail (*Sylvilagus transitionalis*)

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Abstract

Herbivores are challenged when selecting a diet because many plants have limited nutritional value and some use defenses to avoid being eaten. Understanding diet selection of herbivores in most landscapes also involves choices between native versus nonnative plant species which, in turn, informs management actions to conserve the species. The New England Cottontail, *Sylvilagus transitionalis* (Bangs 1895)—a species on the decline—is the focus of a large conservation consortium. We conducted microhistological analyses of field collected fecal samples and field surveys of plant species available to determine winter diet of New England cottontails on Patience Island, Rhode Island. Energy density (total nitrogen, crude fat, energy, neutral detergent fiber, acid detergent fiber, ash, and total phenolics) was measured for each of the available plants. A used-available framework was used to determine the selection of each species identified in their feces and how this related to the measured nutritionally relevant constituents. We hypothesized that New England cottontails would select plant species with higher protein and energy values and select native versus nonnative plant species. Unexpectedly, New England cottontails did not select plants with higher protein or energy content but rather plants with higher phenolic and ash levels. In addition, New England cottontails strongly selected native plant species. Our results support previous research that New England cottontails are generalist herbivores, but that plant defenses and whether the plants are native play a role in diet selection.

Key words: ash, browse, energy, fat, fiber, New England Cottontail, nitrogen, Patience Island, phenolics, *Sylvilagus transitionalis*.

Herbivores have a host of obstacles to contend with when selecting a diet that will satisfy their nutritional requirements including plant defenses and consuming forages that contain limited amounts of required nutrients and are difficult to digest (Cunha and McDowell 2012; Rosenthal and Berenbaum 2012). Herbivores have evolved to extract energy and nutrients from foods that generally possess small amounts of these components, and on which nonherbivores cannot subsist (Foley and Cork 1992). Overcoming these obstacles has required some herbivores to adapt by developing varying degrees of forage selectivity and preferences (Belovsky 1978; Danell et al. 1987). Lagomorphs are one group that exhibit selective foraging (Turkowski 1975; Bryant 1981; Bryant et al. 1983; Reichardt et al. 1984; Tahvanainen et al. 1985; Sinclair et al. 1988; Crowell et al. 2018). Equipped with a unique digestive system that compliments their foraging strategy (Heisinger 1965), lagomorphs are monogastric, hindgut fermenters that ferment food in their cecum that is passed as cecal pellets, some of which are then re-ingested (Van Soest 1994; Hirakawa 2001). This process, referred to as coprophagy, allows lagomorphs to extract the maximum amount of nutrients out of forage that is difficult to digest or nutritionally poor (National Research Council 1977).

Studies on lagomorph nutritional ecology have suggested that the availability of quality forage is linked to population abundance (Sinclair et al. 1982; Keith 1987). The study of nutritional needs of wild herbivores shows that they are most limited by protein in available forages (White 1978). The few studies that exist pertaining to the nutrient requirements of cottontails indicate that protein and energy are limiting factors (Chapman et al. 1982; McNab 1988). Study of hares shows that they select for fat and energy in the plants that they consume (Schai-Braun et al. 2015). Thus, protein and energy content of vegetation may also dictate cottontail diet selection.

The main objective of our study was to determine the diet and nutritional quality of plants consumed by New England cottontails (*Sylvilagus transitionalis;* hereafter NEC) to support their conservation. The range of NEC includes portions of 6 states (Connecticut, Massachusetts, Maine, New Hampshire, New York, and Rhode Island) in the Northeastern United States, and their range has been reduced by ~86% since 1960 (Litvaitis et al. 2006). It is suspected that habitat loss resulting from forest maturation and habitat fragmentation may be the most imminent threat to NEC population viability (Litvaitis 1993; Litvaitis et al. 2006, 2008). The NEC was listed as a

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candidate species for protection under the Endangered Species Act from 2006 until 2015 (U.S. Fish and Wildlife Service 2015). Based on the success of the multiagency effort to restore NEC, a decision to not list was rendered by the United States Fish and Wildlife Service in 2015 (USFWS 2015). However, NEC is listed as vulnerable by the International Union for Conservation of Nature Redlist (Litvaitis and Lanier 2019), listed as state endangered in New Hampshire and Maine, and a Species of Greatest Conservation Need in multiple New England states (RI SGCN 2015).

One multiagency initiative to conserve NEC was the establishment of a captive breeding program and subsequently a breeding colony on Patience Island, an 85 ha island located within the upper Narragansett Bay in Portsmouth, Rhode Island (Fig. 1). In 2010, a captive breeding program was initiated at the Roger Williams Park Zoo in Providence, RI, which was subsequently expanded to include Queens Zoo in Corona, New York, in 2015 (Fuller and Tur 2012). The Roger Williams Park Zoo captive population included 47 wild caught founders from 2010 to 2014, mainly from Connecticut but also including animals from New Hampshire and Maine. In captivity, female NEC are paired with males during 3 periods that begin in April and end in August. On average, they have 2.5 litters per female and 4.2 offspring per litter (Litvaitis et al. 2018). Offspring

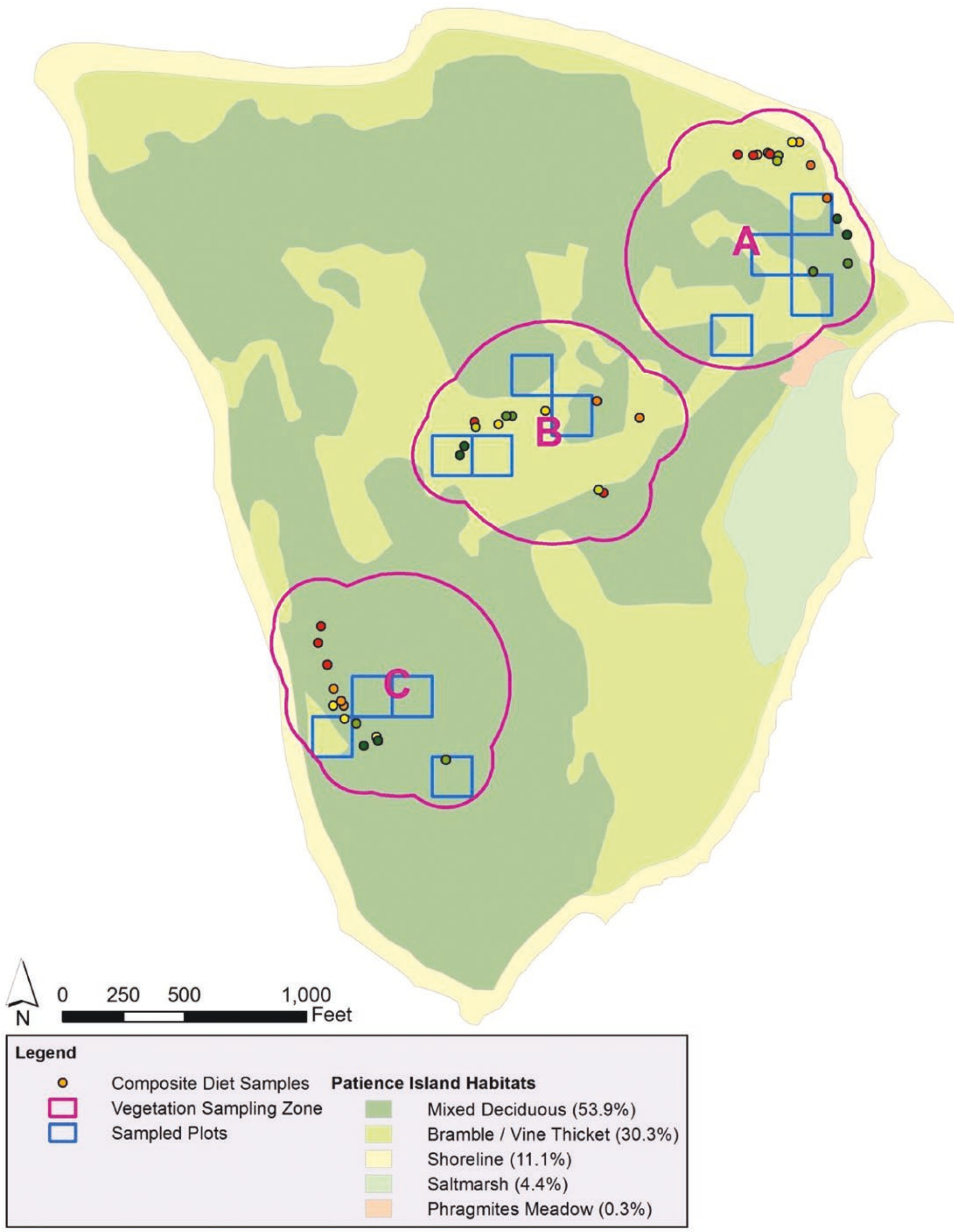

Fig. 1. Map showing the 3 vegetation sampling zones, sampled plots, and locations of New England Cottontail (*Sylvilagus transitionalis*) fecal diet samples collected on Patience Island, Rhode Island. Fecal samples were collected in March of 2015 and vegetation surveys were conducted within the blue sample plots in May and March of 2016 and 2017, respectively. Composite diet samples that are the same color represent fecal samples that were combined together for 1 diet analysis.

born early in the season can potentially breed the same year they are born and all juveniles have the potential to breed the following season. The initial goal of the captive population was to seed animals on Patience Island to establish a breeding colony on the island to repopulate the mainland. From 2012 to 2014, 50 mainly first-generation captive born NEC were released on Patience Island and their population size has been intensely monitored.

The current research on NEC ecology has not addressed whether the species exhibits a pattern of selective foraging that correlates to plant nutrition or plant defenses. If NEC exhibit selective foraging, this information will be useful for managers to ensure appropriate forages at reintroduction sites. Recently, the diet selection of NEC and the nonnative, invasive Eastern Cottontail, *S. floridanus* (Allen 1890) have been compared at a regional level and they both are dietary generalists that have similar winter diets (Carter et al. 2023). New England cottontails predominantly consume tree and shrub species in the winter depending upon which species are available in a particular area (Carter et al. 2023). Some plants preferred by NEC include species of *Betula*, *Corylus*, *Quercus*, *Salix*, *Sorbus*, *Spiraea*, and *Vaccinium* (Carter et al. 2023). However, a study of NEC diet on Cape Cod, MA, found only 1 species preferred in both studies (Etkind 2020; Carter et al. 2023). There has only been 1 other published study on NEC diet, but this study was conducted over 86 years ago (Dalke and Sime 1941). Interestingly, over 80% of the top plant species preferred were the same between Dalke and Sime (1941) and Carter et al. (2023). Understanding why NEC consistently select certain plant species can help inform management decisions for their conservation.

Our specific objectives included: (i) characterizing the winter diet of NEC on Patience Island; (ii) estimating the nutritional value (total nitrogen, crude fat, neutral detergent, and acid detergent fiber), energy, and total phenolics of available vegetation on Patience Island; and (iii) determining if any of the 7 plant constituent values can explain why certain plants are selected or avoided by NEC on Patience Island. By focusing on the winter season, the diets and available nutrition to NEC were examined during the most challenging foraging period for this herbivore (Smith et al. 1988; Hovey and Harestead 1992; Klein and Bay 1994). We predicted that Patience Island NEC diet selection is positively related to the amounts of protein and energy, the nutrient hypothesis (Sinclair and Smith 1984). We also predicted that NEC preferred native versus nonnative plant species.

Methods

Study site.

Patience Island has an elevation range 1 to 15 m, average temperature of 10.6 °C, annual precipitation of about 100 cm, and annual snow fall of about 50 cm (https://dem.ri.gov/climate/climate-overview-ri.php). Patience Island is almost entirely owned by the Rhode Island Department of Environmental Management (RIDEM) and is part of the National Estuarine Research Reserve System. As classified by Maynard (2013) in 2012, Patience Island is composed of 53% deciduous forest and 30% early successional shrubland. The remainder of the island is composed of a small salt marsh and shoreline. Leaf out typically occurs in April and fall senescence usually occurs in November. Other mammals residing on the island are: White-Tailed Deer, *Odocoileus virginianus* (von Zimmermann 1780); Raccoon, *Procyon lotor* (Linnaeus 1758); Coyote, *Canis latrans* Say in James (1823); American Mink, *Neovison vison* (Prentiss 1903); and North American River Otter, *Lontra canadensis* (von Schreber 1776) with animals immigrating from nearby Prudence Island, which is separated from Patience Island by a 200 m channel. Extensive surveys were conducted by RIDEM staff prior to NEC introductions to ensure the absence of eastern cottontails on the island.

Estimating diet of New England Cottontail.

The diet composition of NEC on Patience Island was conducted at the population level and began with analyzing fecal samples that were collected to estimate the population size. Pellet collections for diet analysis were conducted in 2 sampling events on 11 March 2015 and 24 March 2015 that each included 11 transects. Pellet samples were collected after a snow event to ensure the samples were recently produced. Patience Island was gridded into 11,375 m × 375 m squares to allow the entire island to be surveyed by ~7 personnel in 1 day. Two transects per each 14 ha square were randomly selected in the general north/south and east/west cardinal directions within a given square. The first survey included 11 vertical transects, while the second survey was on 11 horizontal transects. Surveyors walked the transects and collected fecal samples in sterile 15 ml tubes that contained silica beads as a preservative. Genetic analysis was conducted on samples for species confirmation using the methods described by Sullivan et al. (2019). Microsatellite marker analyses were used to identify individual NEC based on fecal samples collected the first sampling period to estimate a population size of 147 animals or a density of ~1.7 NEC per hectare. At this point in NEC colonization of Patience Island, they unlikely had a significant impact on the vegetation composition on the island and what was available for them to consume.

The 3 densest areas of pellets were identified along all transects with the point density tool in ArcGIS 10 (ESRI) and labeled as zones A, B, and C (Fig. 1). The 3 sampling zones were created to serve as strata for browse surveys and for conducting vegetation sampling. Within each of the sampling zones, pellets were selected for diet analysis in a stratified random design based upon the 2 habitat types within each of the zones. Stratifying by habitat ensured that a full representation of both habitat types was captured in the diet results. When choosing pellets to combine into a composite sample, pellets that were near each other (<1 m) and located within similar habitats (e.g., forest or shrubland) were combined. These guidelines were followed for 15 of the 18 composite samples, while the remaining 3 composites consisted of a combination of pellets that originated from both habitat types. The composite fecal samples (n = 18) consisted of 8 pellets that originated from a combination of 2 to 3 separate collection tubes with at least 2 and no more than 5 pellets from each tube. The goal was to combine enough pellet material from a given location into a composite sample to have a sufficient amount of fecal material to view the diet at a population level.

Pellets were dried in an oven at 50 °C for 24 h and sent to Washington State University (WSU) for microhistological diet analysis. To minimize errors associated with underreporting less frequent species in NEC diet, we chose 200 views of each composite for the diet analysis at WSU. This procedure analyzed the composite pellet sample by dividing material among 8 slides, with 25 views per slide to identify the epidermal fragments of ingested vegetation (Flinders and Hansen 1972). Plant fragments found in microhistological analysis were identified visually by WSU staff to the species level when possible and reported as a percent of diet composition. A list of species found by Maynard (2013) during previous vegetation surveys on Patience Island was sent to WSU to ensure that the reference collection for species was complete. Three species were not found in the collection at WSU and were collected from Patience Island, oven dried at 50 °C for 48 h, and shipped to WSU. It is important to note that the diet results reported were not corrected for differences in plant digestibility. However, due to the high lignin content of woody material, it is assumed that many of the species consumed during winter months are less digestible than species present during other seasons and therefore will be representative of species consumed (Van Soest 1967; Walski and Mautz 1977; Klein and Bay 1994).

Defining 50% core use areas and vegetation sampling zones.

Vegetation survey zones were established on Patience Island to determine the potential forage area available to an NEC within a given area. Boundaries for vegetation surveys were based upon the location data of NEC released on Patience Island. Nearly all founding animals released on the island were fitted with an Advanced Telemetry Systems (Insanti, MN) model 1555 very high frequency radio collar to track their movements and survival. Since March 2012, location data were collected for 65 individuals via triangulation, which was conducted opportunistically depending on accessibility to the island. Locations for individuals were identified using a 3 element Yagi antenna, an Advanced Telemetry Solutions model R-2000 receiver (Freq. 150.000 -151.999), and a compass. Bearings were collected for each individual at 3 base stations along the southeastern edge of Patience Island. Total data collection time was kept under 30 min to minimize error from movement (Saltz 1994). Bearings were then entered into the software Location of a Signal version 4.0.3.8 (Ecological Software Solutions LLC 2010), which uses the maximum likelihood estimator to produce a location estimate for each individual. A 50% contour interval (i.e., core use area) for the pooled population data was conducted using Kernel Density Estimates with least squares cross-validation (LSCV) with a Geospatial Modeling Environment (Worton 1989; Beyer et al. 2010). The LSCV method was chosen for the bandwidth estimation because it provides the best available estimate for home range for point shape distributions that exhibit a concave pattern (Downs and Horner 2008). To eliminate the effects of triangulation error on the pooled population of 50% core use area, we compared core use areas in a process that began with estimating the 50% core area of the population after location estimates associated with an ellipse error greater than 10 ha were excluded. Next, location estimates that were off the island and were associated with an error ellipse that was more than 50% of the diameter of the island were removed from the analysis. This resulted in a final population level 50% core use area of 6.09 ha originating from 292 location estimates from 65 individuals (Supplementary Data SD1).

To represent the potential vegetation available to a given NEC on Patience Island, the population level of 50% core use area was overlaid using ArcGIS 10 on the 3 densest areas of pellet collections previously identified. We assumed that an individual NEC would not forage in an area greater than 6 ha. To ensure that all diet samples were associated with an adequate distance of potential local foraging opportunities, we also surrounded each pellet location with a 1.1 ha boundary. This 1.1 ha boundary represented the average individual 50% core use area of NEC based on data from Kilpatrick and Goodie (2020). The 3 distinct zones (A, B, and C), which served as the location for diet sample collections and formed the boundaries for vegetation sampling, were created by merging the 6 ha core use area with the 1.1 ha core use areas placed around each fecal sample for each zone (Fig. 1). When portions of a vegetation sampling area overlaid the ocean, the area was moved laterally so that it was entirely over land and available to the animal for forage. In each zone, intensive vegetation sampling was conducted to determine the plant species browsed and vegetation available.

Intensive vegetation sampling plots and diet selection.

Upon establishing the 3 vegetation sampling zones (A, B, and C), a vegetation map created by Maynard (2013) was overlaid and total area of the 2 dominant habitat types (shrubland and forest) within each sampling zone was calculated using the clip function in ArcMap (Fig. 1). Sampling zone A (7.44 ha) contained an even mix of shrubland (48%) and forest (44%), sampling zone B (6.88 ha) was more shrubland (61%) than forest (39%), and sampling zone C (6.85 ha) was dominated by forest (93%) with little shrubland (4%) present. In addition to these 2 major habitat types, sampling zone A also contained 7% shoreline habitat and 0.5% *Phragmites* marsh and sampling zone C also contained 2% shoreline. The shoreline and *Phragmites* habitats were excluded from vegetation analysis based on evidence from the telemetry data that indicated NEC rarely used these habitats on Patience Island.

Each of the 3 vegetation sampling zones was gridded into 18 50 m × 50 m plots using ArcMap. Using a random numbers table generated by Microsoft Excel, 4 50 m × 50 m plots within each of the 3 sampling zones were selected for analysis. The 4 plots were chosen in a stratified random design based upon the approximate proportions of each habitat type within each vegetation sampling zone. Sampling zone A had 2 plots in shrubland and 2 in forest; sampling zone B had 3 plots in shrubland and 1 in forest; and sampling zone C had all 4 plots in forest (Fig. 1). The center of each 50 m × 50 m plot served as the center of the intensive vegetation survey. Two 50 m tapes were placed perpendicularly within each plot and oriented so that the center of each tape (the 25 m mark) intersected the center of the plot. One 50 m tape was oriented north–south and the other east–west. In each plot, 24 1 m² quadrats were randomly placed along the 50 m transects using a random numbers table with 12 alternating quadrats along each of the 2 transects.

Sampling for both browse and vegetation availability occurred in May 2016. In each 1 m² quadrat, all woody species that were ≤5 mm in diameter were considered available and the number of stems of each species was recorded. When evidence of browsing was observed, the species and number of browsed stems also was recorded to obtain an alternative measure of the plant species NEC were eating. All vegetation browsed and available up to a height of 1 m from the ground was recorded to account for the combination of snow depth in March 2015 and the height that NEC could reach while browsing. Previous studies have used 50 cm as the maximum browse height of snowshoe hares, *Lepus americanus* Erxleben, 1777 (Bider 1961; Wolff 1978). Species diversity of all plant species ≤5mm in diameter was calculated for each plot, quadrat, and vegetation sampling zone using the Shannon diversity index (Shannon 2001). The variance of species diversity using calculations for Shannon's evenness was monitored during data collection to ensure that each vegetation sampling area had received adequate sampling to produce accurate estimates of available NEC forage (Krebs 1999).

We determined NEC relative food selection using the Johnson's Rank Preference Index (hereafter Johnson's Rank) test proposed by Johnson (1980). Johnson's Rank was calculated for each vegetation zone using dietary data obtained from analyzing fecal samples as the used data and the availability rank were obtained from vegetation surveys as previously described. The ranks of diet data and vegetation data were ordered from highest rank starting at 1 and increasing incrementally. If 2 plant species had the same rank, then each was given the same rank number with 0.5 added. Johnson's Rank was estimated as usage minus availability and then ordered from highest to lowest selected. Johnson's Rank was chosen because the analysis is not affected by scarce resources in the diet (Krebs 1999) and this analysis allowed for the comparison of diet analyses on NEC and eastern cottontails from the mainland previously conducted by Etkind (2020) and Carter et al. (2023). Our sample design was at the population level, which is a Design I study after the typology of Manly et al. (1993).

Nutritional analysis of Patience Island vegetation.

To understand why certain forages are selected over others, we estimated 7 constituents from plant species found on Patience Island. In May 2016 and March 2017, plant samples for nutritional analysis were collected within each of the 3 zones and were analyzed per zone for comparison with the fecal diet results. We compared the plant constituent values for each season to see if their average values had overlapping standard errors. During March 2017, vegetation was collected in exclosures that were erected the previous year. To ensure that a wide variety of vegetation was sampled, vegetation also was collected from locations of previous quadrats or opportunistically within a zone to collect missing plant species. For each species encountered, at least 10 g of unbrowsed woody material <5 mm in diameter and <1 m high were collected when possible from each of the 3 zones for subsequent nutritional analysis. Samples collected for nutritional analysis were collected from portions of the plant between ground level and 1 m in height and between the terminal bud and 5 mm in stem diameter (Shafer 1963). Collected samples for nutrition were stored on ice in a cooler in the field, then stored in a commercial freezer, and finally in a −80 °C freezer until the material was analyzed. All samples were weighed with a Mettler-Toledo (Columbus, OH) scale. Vegetation samples were dried in an oven at 50 °C until 3 consistent weights were obtained. Samples were then ground in a Wiley Mill grinder with a #40 sieve.

We measured the total nitrogen, crude fat, energy, neutral detergent fiber, acid detergent fiber, ash, and total phenolics of collected plants. The sample size of each plant constituent varied due to the amount of material available for a particular measurement. Total nitrogen content of forage ($n = 167$) was determined by using a Carlo-Erba NA 1500 Series II Elemental Analyzer in combination with an isotope ratio Micromass Optima Spectrometer (CF-IRMS). For each zone, 3 replicates of each plant species collected were weighed to ~10 mg and placed into tin cups. Samples were sent to the Environmental Protection Agency's National Health and Environmental Effects Research Laboratory for nitrogen analysis. Crude protein was estimated by multiplying nitrogen by 5.6, which is the conversion recommended for plant tissues by Mariotti et al. (2008).

Extraction of fat from browse was performed for 165 samples. When possible, 3 replicates were analyzed for each species collected in each zone. Fat was extracted by the repeated rinsing of samples with petroleum ether in a Soxhlet extraction system for 6 h (Maynard et al. 1979). Samples were weighed to ~0.5 g and were corrected for moisture content.

We estimated the energy density for 168 samples using a bomb calorimeter (Model 1266, Parr Instruments, Moline Il; Gessaman 1987). When possible, depending on the amount of material available, 1 replicate per species per zone was analyzed. Samples were weighed to ~0.5 g and were formed into pellets by using a pellet press before placement into the calorimeter. Samples were combusted in pure oxygen at a pressure of 3,102.6 kPa and the calorimeter's chambers were cleaned with deionized water and wiped down between samples. Instrument calibration was verified every 20 samples and at the start and end of each day by combusting 2 1 g benzoic acid standards. Temperature rise for each sample along with Energy Equivalents from standards were recorded and used to estimate the energy content of samples.

We conducted a sequential analysis of neutral detergent fiber (NDF; $n = 167$) and acid detergent fiber (ADF; $n = 159$) as recommended for browse by Goering and Van Soest (1970) with modifications proffered by Undersander et al. (1993). To determine the amount of insoluble fiber in samples, 0.5 g of each sample was treated with NDF solution. Nondigestible (insoluble) fiber may aid in helping rabbits maintain a healthy digestive tract (National Research Council 1977). Acid detergent fiber (cellulose, lignin, and silica) impacts growth in the domestic rabbit with low levels of ADF leading to a lower growth rate (Hoover and Heitman 1972; National Research Council 1977). Ash was included in the analysis ($n = 167$) to measure the mineral content of forage dry matter (Nielsen and Ismail 2017). Samples were burned in a furnace for 6 h at 450 °C and the remaining mineral content was weighed. The amount of phenolics found in forages ($n = 168$) was determined following the methodology of Singleton and Rossi (1965). Unlike the other nutritional values measured, phenolics represent a postsecondary metabolite that is often used by plants as a defense against herbivores. We tested for equality of variance in the plant constituent values in R using the LeveneTest command in the *car* package (Fox and Weisberg 2018). Any variables that failed the test of equality of variance were log10 transformed and retested. We visually tested for the normality of the residuals by plotting the theoretical quantiles versus standard deviance of residuals using the *plot()* function in R.

Nutrition analyses did not include some plant species detected in the fecal diet because we were unable to find the plant on Patience Island. To determine if there was a relationship between nutritional components of forage and browse diet selection, we averaged the Johnson's Rank values for fecal diet among the zones to rank each plant species as either a high (1–6 rank), medium (7–8 rank), or low (11–16 rank) selected species. The plant constituent values for each of the 3 selection categories were averaged and compared, as well as the average values for native and nonnative plants. We used the *glm* package in R to test if any of the nutritional values explained the Johnson's Rank values as a binomial response variable, highly preferred as 0 (high and medium ranks combined) and least preferred as 1 (low rank). The independent variables included whether the plant was native (0) or nonnative (1), zone, season, and the plant constituent variables. We included zone and season to make sure our results did not vary by these variables, which were subsequently removed in further modeling because the variables were nonsignificant. We also modeled the plant constituent values for each season separately and tested for multicollinearity among the variables in our model using the *vif* command in the *car* R package.

Results

Estimating diet of New England Cottontail.

The 18 composite diet samples included 7 composite samples (2 from forested habitat and 5 from shrubland) from Zone A, 6 composites (3 in shrubland and 3 in mixed habitat) from zone B, and 5 composites (all from forest habitat) from zone C. Sixteen genera of plants were identified in the NEC diet based on fecal samples collected on Patience Island (Supplementary Data SD2). A relatively low percent of plant species was unknown stems in NEC fecal samples and the vast majority of plant material was from stems in each zone. The number of plant species in each of the 3 zones was 19, 15, and 17 for zones A, B, and C, respectively (Supplementary Data SD3). The percent of each plant species available in each of the 3 zones was relatively similar. The visual inspection of available browse showed that *Celastrus orbiculatus* was the most frequently encountered species in both zones A (29% of stems) and B (48% of stems). Whereas *Smilax rotundifolia* was the most frequently encountered species in zone C (79% of stems). Raw diet results based on the analysis of fecal samples showed that the 2 species representing the largest proportion of NEC diet were *Rubus* spp. (including blackberry, raspberry, and wineberry) and *V. dentatum* (Arrowwood Viburnum; Supplementary Data SD3). Despite comprising a relatively high proportion of NEC diet, these 2 species accounted for a relatively small proportion of the stems counted during habitat surveys in all 3 zones. *Rubus* spp. accounted for 15%, 5%, and 1% of stems surveys in zones A, B, and C, respectively; while *Rubus phoenicolasius* accounted for 1.1%, 0.69%, and 0.04% in the same zones (Supplementary Data SD2). *Viburnum* accounted for 3%, 7%, and 6% of stems surveyed in zones A, B, and C, respectively. Aside from *Rubus* spp., other highly selected species (top 5 selected in 2 of 3 zones) such as *Acer*, *Amelanchier* spp., *Parthenocissus quinquefolia*, *Rhus typhina*, and *Vaccinium* spp. each accounted for less than 4% of stems surveyed in each zone, and some were not detected in certain zones during surveys despite being present in NEC's diet.

Diet selection.

The results of Johnson's Rank for NEC diet based on fecal analyses was similar among the 3 zones (Table 1). In only 1 case was a plant species, *Juniperus virginiana*, ranked the highest and lowest in different zones. The top 4 species found in NEC fecal diet were *A. rubrum*, *P. quinquefolia*, *R. typhina*, and *Vaccinium* spp. *Rubus* spp. was the only taxon that was not in the highest selection category, but *Rubus* spp. was the highest ranked taxon in the medium selection category. The visual observation of stems browsed by NECs produced Johnson's Ranks that only matched the fecal samples-based Johnson's Ranks 57% of the time (Supplementary Data SD4). Five plant species were identified by visual inspection that did not appear in NEC fecal samples.

Results of Johnson's Rank for NEC fecal-based diet revealed a pattern of selection for native species. The vast majority (14 of 19) of plant species in NEC diet are native to New England (Table 1). For the averaged Johnson's Rank values, all of the species in the high selection category are native to New England, except for *Rubus* spp. which can have native and nonnative species (Supplementary Data SD5). On Patience Island, *Rubus* spp. primarily consists of native raspberry and blackberry species, as well as wineberry—a nonnative species that occurs infrequently on Patience Island. One of the 4 species in the middle selection category (*Berberis thunbergii*) is not native to New England. This nonnative species also had the highest total N content (1.5%, $n = 4$) of species listed in Supplementary Data SD5. Four of the 6 species in the lowest selection category are nonnative to New England.

Nutritional analysis of Patience Island vegetation.

The highest range in average values was estimated for phenolic levels, which ranged 35-fold from 207.30 uM (*S. rotundifolia*) to 7,189.57 uM (*Vitis labrusca*; Supplementary Data SD5). The next largest range of average values was for percent nitrogen, which ranged threefold from 0.54 (*V. labrusca*) to 1.50 (*B. thunbergii*), followed closely by percent crude fat that ranged 2-fold from 4.81 (*Rubus* spp.) to 10.69 (*R. typhina*). The average values for ash ranged from –0.0029 (*Lonicera morrowii*) to 0.0121 (*R. typhina*). The average energy values had a minimal range from 4.39 (*P. quinquefolia*) to 4.97 kcals/g (*Myrica*

Table 1. Johnson's rank (Johnson 1980) of New England Cottontail (*Sylvilagus transitionalis*) microhistological fecal diet collected March 2015 on Patience Island. Johnson's Ranks were estimated as usage rank minus available rank and then ordered numerically from higher to lower selection rank. Darker gray indicates higher selection. Categories for high, middle, and least selection were established by dividing the highest rank number for each zone by 3. Species abundances in each zone are listed for reference. Plants native to New England are marked with an *. Plants that have both native and nonnative species are marked with a+.

Species in Diet	Zone A		Zone B		Zone C	
	Johnson's Rank	% Stems Surveyed	Johnson's Rank	% Stems Surveyed	Johnson's Rank	% Stems Surveyed
*Acer rubrum**	2	0	2	0	10	2.3
Amelanchier sp.*	5.5	0	3	0	8	0.4
Berberis thunbergii	8	0.6	9	0.04	7	0
*Betula popufolia**	15	2	…	…	…	…
Celastrus orbiculatus	17	28.8	14	47.9	15	3.2
*Ilex verticillate**	13	0.6	…	…	…	…
*Juniperus virginiana**	11.5	0.3	…	…	5.5	0
Lonicera spp.	14	4.5	13	13.4	14	2.4
*Myrica pensylvanica**	6	1.3	5	0.7	6	1.2
*Parthenocissus quinquefolia**	5.5	3.6	6	1.4	3	0.4
*Prunus serotine**	9	0.2	…	…	13	0.9
*Rhus typhina**	4	0.1	7	0.1	1	0
Rosa multiflora	12	4.1	11	2.9	11	0.7
Rubus spp.+	7	14.9	4	5.2	5.5	1.4
*Smilax rotundifolia**	16	7.5	15	13.6	16	79.1
*Toxicodendron radicans**	11.5	0.3	12	1.3	12	0.8
Vaccinium spp*.	1	0	1	0	2	0.6
*Viburnum dentatum**	3	3.2	8	7.3	9	6.4
*Vitis labrusca**	10	28	10	6.1	4	0.2

pennsylvanica). The standard error for the average plant nutritional values overlapped the majority of times (36 of 67 comparisons) between the 2 plant collecting periods (May and March).

Average nutritional values for the 3 selection categories (high, medium, and low) based on Johnson's Rank all had overlapping standard error values except for the phenolic values (Table 2). Average phenolic values went in a descending order along with the descending selection category. Average ash values also showed higher values for the high and medium selection categories compared with the low selection category. Average plant constituent values for native and nonnative plants were mostly similar, except for phenolic values (Table 3).

The majority of plant constituents passed Levene's test for equal variances (Supplementary Data SD6). Both aNDF and phenolic had significant *P*-values, so the values were log transformed and then retested using Levene's test. The transformed phenolic values passed Levene's test, but the transformed aNDF values still failed the assumption of equal variances, so we removed these values from our modeling analyses. ADF had a missing value for 2 plant species (*Myrica pensylvanica* and *R. phoenicolasius*) so we used the average value for each species. In general, the plant constituent residual values conformed to a normal distribution (results not shown). For the most part, the Q-Q residuals plot followed a slope of 1. All of the Generalized Variance Inflation Factor values for the multicollinearity test were less than 2.2 (Supplementary Data SD6). The *glm* analysis of the binomial Johnson's Rank as the response variable with 9 independent variables showed a significant estimate for the intercept, native plant, protein, ADF, ash, and phenolics (Table 4). The zone and season variables were not significant and removed from further analyses. The *glm* analysis of 7 variables showed the same significant variables as previously stated. However, when the native variable was removed from the analysis, the protein variable was no longer significant.

To further ensure that our results did not depend upon the season the plant material was collected for nutritional analyses, we conducted our *glm* analysis separately for each season. Our *glm* analysis of the first season—collected in May—vegetation did not have any significant variables, but the model did not converge (Supplementary Data SD7). However, the analysis of the second season—collected in March—vegetation showed a similar result to our full data analysis with native, ash, and phenolic variables significant (Supplementary Data SD7).

Discussion

New England cottontails are the focus of a large-scale conservation effort. An integral component of the conservation program has been the establishment of a breeding colony on Patience Island. Understanding the feeding ecology of NEC on the island is important for ensuring that their nutritional requirements are met and their preferred food is available. Our 3 objectives were to characterize NEC winter diet on Patience Island, determine the nutritional content of the vegetation on the island, and determine if any of the measured nutritional values explained their selection. These objectives allowed us to test the nutrient and secondary chemical hypotheses (Sinclair and Smith 1984). The nutrient hypothesis predicts that lagomorphs will select their diet based on nutrient content such as crude protein and energy, while the secondary chemical hypothesis predicts that they will avoid defensive chemicals in plants, such as phenols or resins (Sinclair and Smith 1984). New England cottontails did not conform to either hypothesis and selected plants with high ash and phenolic values and strongly selected for native plants. Our study is the first to investigate why NEC selects certain plants in their winter diet. Managers will be able to use this information to support NEC conservation in the wild at mainland sites and help inform the appropriateness of additional islands as potential breeding colonies.

We assessed the winter diet of NEC on Patience Island by analyzing the content of their fecal samples using a microhistological approach to accomplish our first objective. We also quantified their winter diet by directly observing browse. However, the general preference rank matched only about half the time for both methods. The lack of congruence between the 2 methods could have been because the data were collected in the winter for the microhistological approach and in the spring for direct observation of browse. Ensuring that all browse in a given area is counted accurately can be difficult. To address this issue, we reduced our search areas to 1 m^2 quadrats, but it is possible that browsed twigs were missed because we did not have an estimate of our detection rate. To limit the impact of missing plant species, we used the Johnson's Rank method which is less sensitive to missing data. The microhistological analysis of fecal pellets represents what the given animal has eaten at a specific point in time, which could vary over a season. The method also can only identify plant material that is not completely digested by the animal. Our analyses were conducted on fecal samples collected in the winter when rabbits are eating more woody material, which increases the chance of detecting the plant material. In NEC diet, we detected nearly all plant species recorded by Maynard (2013) in a presurvey of Patience Island. The 2 species we did not detect in their diet (*Malus* spp. and *R. copallinum*) only had a 1% frequency in the plots surveyed and were not detected in a range-wide diet analysis of NEC (Maynard 2013; Carter et al. 2023).

Table 2. Average and standard error (SE) for 3 Johnson's Rank (Johnson 1980) selection categories based on the microhistological analysis of New England Cottontail (*Sylvilagus transitionalis*) diet.

Selection	% Crude Fat	SE	Energy (kcals/g)	SE	Protein	SE	aNDF % OM (g)	SE	ADF % OM (g)	SE	Phenolics (uM)	SE	% Ash	SE
High	7.39	0.84	4.60	0.03	4.55	0.27	75.33	1.29	58.11	0.94	1848.34	193.36	0.0073	0.001
Medium	6.9	0.66	4.70	0.07	4.44	0.49	81.26	1.17	60.83	0.93	1420.4	174.11	0.0079	0.001
Low	8.96	0.67	4.58	0.04	4.34	0.27	78.42	0.86	57.75	0.77	679.02	94.31	0.0023	0.001

Table 3. Average constituent values for native and nonnative plants on Patience Island, Rhode Island.

Category	% Crude Fat	SE	Energy (kcals/g)	SE	Protein	SE	aNDF % OM (g)	SE	ADF % OM (g)	SE	Phenolics (uM)	SE	% Ash	SE
Native	7.55	0.52	4.65	0.04	4.34	0.24	78.31	0.93	58.24	0.70	1514.01	136.02	0.01	0.00
Nonnative	8.11	0.76	4.55	0.03	4.59	0.33	77.92	0.91	59.90	0.67	930.96	130.03	0.00	0.00

Table 4. A modeling estimate summary using the *glm* package in R to test if any of the nutritional values explained Johnson's Rank (A–C) and plant status (D) as a binomial response variable.

A) Johnson_Rank ~ Native_binary + Zone + Season + Fat + Energy + Protein + ADF_Edited + Ash + Phenolic_log10, family = "binomial"

Variable	Estimate	Std_Error	z_value	Pr(>|z|)
(Intercept)	15.33026	6.68723	2.292	**0.02188**
Native	3.86633	0.8992	4.3	**1.71E-05**
Zone2	−0.87171	0.86356	−1.009	0.31276
Zone3	0.38126	0.82896	0.46	0.64557
Season2	0.47	0.83443	0.563	0.57326
Fat	0.0213	0.07823	0.272	0.78542
Energy	1.27808	1.11716	1.144	0.25261
Protein	−0.51177	0.22671	−2.257	**0.02399**
ADF_Edited	−0.22945	0.07498	−3.06	**0.00221**
Ash	174.88113	60.806	−2.876	**0.00403**
Phenolic_log10	−2.44533	0.81756	−2.991	**0.00278**

B) Johnson_Rank ~ Native_binary + Fat + Energy + Protein + ADF_Edited + Ash + Phenolic_log10, family = "binomial"

Variable	Estimate	Std_Error	z_value	Pr(>|z|)
(Intercept)	1.46E + 01	6.33E + 00	2.308	**0.02101**
Native	3.67E + 00	8.52E–01	4.305	**1.67E–05**
Fat	5.09E–03	7.72E–02	0.066	0.94749
Energy	1.09E + 00	9.29E–01	1.178	0.23896
Protein	−4.17E-01	1.92E–01	−2.174	**0.0297**
ADF_Edited	−2.21E-01	7.30E–02	−3.031	**0.00244**
Ash	−1.57E + 02	5.56E+01	−2.813	**0.00491**
Phenolic_log10	−2.13E + 00	7.82E–01	−2.724	**0.00644**

C) Johnson_Rank ~ Fat + Energy + Protein + ADF_Edited + Ash + Phenolic_log10, family = "binomial"

Variable	Estimate	Std_Error	z_value	Pr(>|z|)
(Intercept)	11.64408	5.74706	2.026	**0.04276**
Fat	0.04669	0.06063	0.77	0.4412
Energy	0.05147	0.98444	0.052	0.9583
Protein	−0.15656	0.14659	−1.068	0.2855
ADF_Edited	−0.09412	0.052	−1.81	0.07028
Ash	121.05945	46.03109	−2.63	**0.00854**
Phenolic_log10	−2.07529	0.71479	−2.903	**0.00369**

D) Native_binary ~ Fat + Energy + Protein + ADF_Edited + Ash + Phenolic_log10, family = "binomial"

Variable	Estimate	Std_Error	z_value	Pr(>|z|)
(Intercept)	7.23681	6.01199	1.204	0.2287
Fat	0.04634	0.05718	0.81	0.4177
Energy	−2.94055	1.35134	−2.176	**0.0296**
Protein	0.2143	0.12322	1.739	0.082
ADF_Edited	0.09922	0.05042	1.968	**0.0491**
Ash	−24.76708	35.00354	−0.708	0.4792
Phenolic_log10	−0.49519	0.485	−1.021	0.3072

We did not find many species consumed on both Patience Island and the range-wide analysis by Carter et al. (2023). Previous range-wide analyses of NEC fecal diet showed that they select *Quercus*, *Corylus*, *Betula*, *Sorbus*, *Salix*, *Vaccinium*, and *Spiraea* (Carter et al. 2023). The only plant species that was selected by NEC on both the mainland and Patience Island was *Vaccinium* spp. The *Vaccinium* spp. identified in the diet analyses was only at the genus level, but the visual inspection of browse on Patience Island identified the presence of Blueberry (*V. corymbosum*). The lack of other common species between mainland and Patience Island NEC diet is likely due to differences in plants available at the different sites. Carter et al. (2023) also found that both NEC and Eastern Cottontail diet varied by region.

The second and third objectives of our study were to determine the nutritional values of plants consumed by NEC on Patience Island and what plant constituent values relate to NEC winter diet selection. We hypothesized that NEC diet selection will be influenced by the amount of protein (in the form of nitrogen) and energy in the plants consumed. The average protein and energy values in plants categorized as high and medium selection were higher than those categorized as low selection, but the values had overlapping standard errors. Protein was only significant in our model when the native/nonnative status of each plant was included in the analysis. The effect of protein was as expected with a negative coefficient estimate. In a captive study of snowshoe hares, the level of protein in twigs was not related to their diet preference (Sinclair and Smith 1984). However, Sinclair and Smith (1984) found that the level of protein varied by size and age of the twigs, which could be important variables for diet selection that we were not able to measure.

The plant constituents that were significant in all 3 versions of our diet selection models were percent ash and phenolic levels. The coefficient estimates for both of these variables were negative meaning that as the ash and phenolic values increased, the selection value was more likely medium or high (a zero binomial value). The amount of ash and protein is correlated to plant digestibility in Moose (Belovsky 1981) and this also may be why NEC selected for plants with a high ash content in their winter diet. The ash values also represent the amount of minerals in the plant (Nielsen and Ismail 2017). New England Cottontail could be selected for certain minerals in the winter.

The largest range in plant constituent values was the phenolic levels. Previous studies have found that herbivores avoid vegetation with high phenolic content and select plants based on protein content (Bucyanayandi and Bergeron 1990). Specifically, it has been documented that hares will avoid advantageous shoots of heavily browsed vegetation if phenolic concentrations are high which renders the browse less palatable (Bryant 1981). Investigations of herbivore relationships with food quality show that low fiber and low phenolic concentrations of forages are primary driving factors of food choice (Chapin et al. 1985; Hjältén and Palo 1992; Shipley et al. 1998; Nordengren et al. 2003) and that within forage species, nitrogen is a secondary factor (Ball et al. 2000). Our results are contrary to previous lagomorph research on phenol intake. We found that plant species in the highest Johnson's Rank selection category had the highest phenolic values, while plants selected in the lowest category had the lowest phenolic values. New England Cottontail may have adapted a tolerance to high phenolic levels if this vegetation is not consumed by other herbivores, such as Eastern Cottontail or White-tailed Deer. However, comparative analyses of the diet of NEC and Eastern Cottontail show that they select similar plant species (Carter et al. 2023). New England Cottontail may be avoiding competition with White-tailed Deer, but their diet would need to be studied to confirm this hypothesis.

Other lagomorphs have adapted to tolerate high levels of phenolics in their diet. One well-studied species is the Pygmy Rabbit, *Sclerobunus idahoensis* (C.H. Merriam 1891), whose main diet consists of sagebrush (Green and Flinders 1980). Sagebrush contains a variety of plant secondary metabolites that deter herbivory. One type of postsecondary metabolite is phenol, but a Pygmy Rabbit study found no influence of phenolic level on their browse species selection (Ulappa et al. 2014). It can be energetically costly to herbivores to remove toxins, which has caused some herbivores to diversify their diets to reduce the amount of plant secondary metabolites consumed (Parikh et al. 2017). New England Cottontail have a generalist plant diet (Carter et al. 2023), which could be an additional example of an herbivore using this strategy to tolerate the consumption of phenol in the plants. Another possible explanation is that herbivores consume plants with more toxins in the winter when high-quality food is limited (Kontsiotis et al. 2015). To know if NEC only consume plants with high phenolic levels in the winter, their diet would need to be estimated in the summer when a greater variety of plant material is available. Alternatively, the vegetation could be responding to NEC herbivory and producing phenol in an effort to deter their consumption. Plant defense evolution occurs in response to European Rabbit, *Oryctolagus cuniculus* (Linnaeus 1758) herbivory, but this developed over a greater than 20 y period (Didiano et al. 2014). However, another study on European rabbits did not see a vegetation defense response (Turley et al. 2013). Thus, plant defensive production of phenol in response to NEC herbivory on Patience Island would require further investigation to confirm.

The second part of our hypothesis was that NEC will prefer native versus nonnative plant species. Not surprisingly, most highly ranked and medium-ranked species were native. Our modeling analysis showed a significant effect of categorizing the plants consumed as native or nonnative. The energy values for native plant species were higher than nonnative plant species with nonoverlapping standard errors and could explain why NEC prefer native plant species in the winter. The ADF values were similar with overlapping standard errors. Interestingly, the one nonnative species (Japanese Barberry) in the medium-ranked selection category had the highest N content, which could explain why this nonnative species was selected. Our analysis of native versus nonnative plant species is limited because the diet analyses were not always able to identify the plant material to species. *Rubus* presents a difficulty because the genus includes both native and nonnative species. We were only able to identify 2 *Rubus* taxa during our vegetation sampling: *R. phoenicolasius* (Wineberry) and *Rubus* spp. (all other *Rubus*). Therefore, it was not possible to determine the proportion of each of the 2 *Rubus* taxa in their fecal diet given the methods used to analyze diet samples. Because *R. phoenicolasius* accounted for a relatively small proportion of stems surveyed in each zone compared with *Rubus* spp., we assume that *Rubus* spp. represents other species. A range-wide analysis of NEC diet also found a strong selection for native plant species in their diet (Carter et al. 2023). Our results in conjunction with Carter et al. (2023) provide strong evidence that NEC select native vegetation in the winter.

To better understand NEC diet preference, captive experiments are needed to directly test their food preferences using cafeteria style studies (e.g., Shipley et al. 2006). The plant species in the various selection categories could be fed to captive NEC. Currently, there are 2 captive populations of NEC in zoos; experiments could be conducted in the nonbreeding period similar to previous research on pygmy rabbits. Experimentation with captive NEC also could determine their nutritional requirements by conducting digestion trials. The nutritional requirements for NEC to maintain weight are unknown. In closely related eastern cottontails, the daily energy requirement to maintain weight in captivity is 549.2 $kJ/kg^{0.75}/d$ (Shipley et al. 2006). The protein remaining in their fecal samples collected in the winter could then determine if NEC are likely to maintain weight in the winter, which could potentially provide an early indication that the population size may decline.

Browse surveys we conducted could be used as a comparison to the level of browse impact NEC are currently having on Patience Island. A baseline survey on vegetation was conducted by Maynard (2013) and could be repeated to see if the abundance of native plant species has decreased on the island. Additional NEC diet selection studies also could determine if NEC food selection has changed, that is, if the amount of native plant species available has been drastically reduced. To improve the food source for NEC on Patience Island, native species identified in their diet on the island and mainland could be planted by habitat managers. If NEC has to switch its diet to more nonnative species, it is unknown if that would have a negative impact on their health. The constituent values for native and nonnative plant species were similar, but there could be other components that we did not measure that are different between native and nonnative plant species and essential for NEC health. Nonnative species can provide other value such as cover (e.g., Japanese Barberry; Cheeseman et al. 2018), but preservation of native plant species should be the focus of managers to support NEC populations.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

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Author contributions

WCF (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Validation, Visualization, Writing—original draft), TJM (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing—original draft, Writing—review & editing), BCT (Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing—review & editing), TPH (Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing—review & editing), WAC (Formal analysis, Investigation, Methodology, Writing—review & editing), and SRM (Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing—review and editing)

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Conflict of interest

None declared.

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