Determinants of home range size of imperiled New England and introduced eastern cottontails

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In fragmented habitat, population persistence depends in part on patch quality and patch size relative to home range size. The imperiled New England cottontail (*Sylvilagus transitionalis* (Bangs, 1895)) is an obligate user of shrublands in the northeastern United States, a highly fragmented and declining ecosystem. New England cottontail conservation efforts have targeted habitat creation; however, efforts are hindered by a limited knowledge of seasonal space use and its relationship to habitat quality, which could help inform minimum patch size requirements and implications of competition with non-native eastern cottontails (*Sylvilagus floridanus* (J. A. Allen, 1890)). To address these uncertainties, we modeled home range areas for both species as a function of season, patch size, sex, and two indicators of forage and cover availability. Home range was generally inversely correlated with measures of forage and cover resources and the response differed by season and species and did not vary with patch size. Instead, inclusion of matrix habitat within home ranges increased with decreasing patch size, placing individuals within smaller patches at a high risk of mortality. These risks may be mitigated in patches > 7 ha, and absent in patches >20-25 ha where predicted inclusion of matrix is lower or absent.

Key Words: Early Successional Forest, Eastern Cottontail, Home Range, Japanese Barberry, Local Convex Hull, LoCoH, New England Cottontail, *Sylvilagus floridanus, Sylvilagus transitionalis,* Telemetry

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Introduction

Habitat fragmentation is one of the greatest current threats to biodiversity, leading to species extinction and shifts in community distribution, with disproportionately strong effects on habitat specialists, large-bodied animals, and species that cannot or do not readily adjust their home range sizes or locations (Ims et al. 1993; Andren 1994; Buchmann et al. 2013). Fragmentation may benefit edge specialists, as habitat heterogeneity is increased (Saïd and Servanty 2005). However, occupancy of smaller fragments can expose wildlife to predation and disease or may restrict foraging opportunities, leading to population decline (Wilcove et al. 1986). As a result, many species have a size threshold for patch persistence, which is related to the individual home range or territory area requirements that result from nonrandom space use in response to the distribution of resources (Börger et al. 2008). These home ranges and territories are affected by factors including density, spatial arrangement of patches, and habitat quality (Barbour and Litvaitis 1993; Chandler et al. 2009; reviewed in Pe'er et al. 2014), are sensitive to habitat loss and fragmentation (Hinam and St. Clair 2008), and their size is often correlated with measures of fitness such as reproductive success and survival (McLoughlin and Ferguson 2000; Hinam and St. Clair 2008). Therefore, an understanding of home range behavior can provide conservationists with useful information on resource distribution, quantity, and quality, and its import to population and habitat management has been demonstrated for species ranging from beetles in old growth forests (Tini et al. 2018) to elephants on savannas (de Beer and Aard 2008).

Within the northeastern United States, severe loss and fragmentation of successional shrublands has resulted in the decline of many associated wildlife species (Litvaitis 1993). Efforts to restore successional shrublands and connectivity among these shrublands are ongoing; however, as 55% of forested lands in this region are owned by private individuals (61% of which

are less than 3.6 ha; Butler and Ma 2011), habitat restoration is heavily reliant on management by many private individuals (Fuller and Tur 2012). Efforts to create shrubland on private lands have generally resulted in small patches averaging 1.3 ha (Buffum et al. 2011). As a result, patch size is expected to constrain patch quality for many successional species (Barbour and Litvaitis 1993; Chandler et al. 2009). This system thus provides an exceptional opportunity to examine the relationship between animal space use and habitat characteristics for species of conservation concern.

A focal species for early successional forest conservation is the shrubland obligate New England cottontail (*Sylvilagus transitionalis* (Bangs, 1895)). Habitat loss, degradation, fragmentation, and the introduction of eastern cottontails (*Sylvilagus floridanus* (Allen, 1890)) have contributed to an 86% contraction of the historic range of New England cottontails (Litvaitis et al. 2006), with recent research suggesting declines and range contractions are ongoing (Fenderson et al. 2014; Cheeseman 2017). Typical of a shrubland obligate, New England cottontails are reluctant to forgo dense understory cover, which provides both food and refuge (Barbour and Litvaitis 1993; Smith and Litvaitis 2000). Within patches of shrubland ≤ 2.5 ha, New England cottontails engage in atypical behavior for the species, foraging further from cover, and experience reduced winter survival when compared to patches ≥ 5 ha (Barbour and Litvaitis 1993). This observation, coupled with low abundance within these patches, indicates small patches may act as population sinks (Barbour and Litvaitis 1993); however a formal study of space use in relation to patch size has not been undertaken. Furthermore, although seasonal differences in environmental productivity and habitat availability often result in differences in space use (McLoughlin and Ferguson 2000), studies of New England cottontails and the conservation strategies developed from these studies have overwhelmingly focused on the

winter, when survival is presumed lowest (Barbour and Litvaitis 1993; Fuller and Tur 2012; Smith and Litvaitis 2000). Resource scarcity, such as the availability of cover or soft mast, during spring and summer combined with the onset of reproduction during this time are suspected to limit populations of other small mammals in seasonal environments (Forbes et al. 2014; Manjerovic et al. 2009). Conservation strategies for New England cottontail developed from examination of winter biology and habitat needs may overlook requirements necessary for summer survival or for spring and summer reproductive efforts (Chapman 1975; Chapman et al. 1980). Given that reproductive output is also a better indicator of population growth than adult survival in other short lived rabbits (Zeoli et al. 2008), consideration of the summer space needs of New England cottontails may be critical for developing strategies focused on population recovery.

Our goal was to quantify seasonal space needs of New England cottontails and a sympatric competing habitat generalist, the eastern cottontail, and to understand the role of patch quality in determining home range size. Because eastern cottontails exploit a larger range of shrubland successional stages than New England cottontails and do not suffer similar costs of venturing outside of shrubland patches (Smith and Litvaitis 2000), we hypothesized that home range area of New England cottontails would be constrained by shrubland patch size, whereas home range area of the generalist eastern cottontail would be independent of patch size. Home ranges of small-bodied habitat specialist mammals are also likely to respond strongly to particular habitat elements in patches within fragmented landscapes, compared to large-bodied mammals and generalists that perceive fragmented landscapes as homogeneous (Gehring and Swihart 2003). In particular, forage availability and quality frequently correlate inversely with home range area, such that animals in areas with sparse or poor quality resources often require a

larger area to meet their fundamental resource needs (Mcloughlin and Ferguson 2000). Density of understory vegetation is both a measure of cover and forage for cottontails and is considered a good indicator of habitat quality for both species (Barbour and Litvaitis 1993; Boyd and Henry 1991; Swihart and Yahner 1982). We thus hypothesized that the density of pooled palatable native understory stems, hereafter "palatable stems" would be inversely correlated with home range area of both cottontails. Cover can be more important than forage availability to prey species, such that they confine their home range to areas of high cover (Tufto et al. 1996; Getz et al. 2005). As winter is a survival limiting time for lagomorphs at northern latitudes and high elevations (Trent and Rongstad 1974; Keith and Bloomer 1993; Hartman and Barry 2010), we hypothesized that leaf-off home ranges would be smaller than leaf-on home ranges.

Invasive shrub species are also particularly pervasive in successional shrublands (Litvaitis et al. 2013). For New England cottontails these shrubs may provide a beneficial cover resource (Litvaitis et al. 2013; Warren et al. 2016; Cheeseman et al. 2018), but may also reduce the abundance and diversity of other plant species (Silander and Klepeis 1999; Yurkonis et al. 2005), which could have detrimental impacts on the quality or availability of forage resources. As invasives could thus alter space use if additional areas are sought for foraging, we separately considered the impact of the most common invasive shrub in our study area, Japanese barberry (*Berberis thunbergii* DC.) on home range area. As eastern cottontails were not found to select for Japanese barberry, but New England cottontails were found to select for this resource (Cheeseman et al. 2018), we hypothesized that home range area would be inversely correlated with the density of Japanese barberry for both cottontail species, but that this relationship would be weaker for the generalist eastern cottontail. We also hypothesized that as a measure of forage and cover, the density of native stems would have a greater effect on home range area than

invasive Japanese barberry. Finally, as sex differences in home range size have been reported in eastern cottontails, with larger male home ranges generally attributed to mate searching, we also considered sex within our models (Trent and Rongstad 1974; Bond et al. 2001).

Understanding the response of species to small patches is critical, given the severity of global habitat fragmentation. This study improves our understanding of how habitat obligate species respond to a fragmented and degraded landscape. This study also fills an existing knowledge gap concerning seasonal space use and the impacts of a common invasive shrub on New England and eastern cottontails, and will help to inform conservation efforts and habitat design. Without such information, limited conservation funding may be applied toward creation of population sinks or inadvertently shift competitive interactions in favor of eastern cottontails.

Materials and Methods

Study Area — We studied cottontail home ranges at 15 shrubland patches within Putnam and Dutchess Counties, New York, where New England and eastern cottontails were sympatric (Fig. 1). Patches consisted of a mosaic of early- to mid-successional stages, native shrub dominated ericaceous shrubland, and/or forested shrublands. Patches were 0.2 - 22 ha, although median patch size was 2.7 ha. Early- and mid-successional forests in the region were primarily the result of agricultural abandonment, and thus were frequently rectangular in shape reflecting field boundaries. Common species included Japanese barberry, multiflora rose (*Rosa multiflora* Thunb.), Oriental bittersweet (*Celastrus orbiculatus* Thunb.), blueberry (*Vaccinium* spp. L.), and *Rubus* spp. L. (Table 1).

Data Collection and Analysis — We captured New England cottontails and eastern cottontails from December 2013 until May 2016 using single door box traps baited with apple (Barbour and Litvaitis 1993) and affixed a 24-g VHF radiotransmitter with a zip-tie closure

collar to adult rabbits over 800 g (Advanced Telemetry Systems, Isanti, Minnesota) (Litvaitis et al. 1991). As New England and eastern cottontails are similar in appearance, we obtained a 3 x 3-mm ear biopsy to genetically confirm species and analyzed samples as in Ryan et al. (2016), which incorporated previous methods described by Litvaitis and Litvaitis (1996), Litvaitis et al. (1997), and Kovach et al. (2003).

We located each individual 2 - 3 times weekly during 2 diel periods, active (2 hours before sunset to 2 hours before sunrise) and resting (2 hours after sunrise to 2 hours before sunset) until mortality of the individual (Bond et al. 2002). Once weekly we located and obtained coordinates of the individual while it was resting using a GPS unit (Garmin 72H GPS, Garmin, Olathe, Kansas). Remaining locations were obtained via triangulations during the active period following protocols by Cheeseman (2017). We assessed triangulation error for each observer by placing collars at 40 known locations within sites and having the blind observer triangulate the collar locations. We used Location of a Signal 4.0 software (LOAS™ 2010) to estimate triangulation locations from azimuths. All work was conducted following guidelines set by the American Society of Mammalogists on use of wild mammals in research (Sikes et al. 2016) and with approval of the SUNY-ESF IACUC, protocols #120801 and #151002.

We defined 2 seasons pooled across years based on availability of resources to New England cottontails and eastern cottontails in the northeast United States; leaf-on season (May – October) and leaf-off season (November – April; Cheeseman et al. 2018). As patch boundaries within the study area frequently abutted hard boundaries such as road and field edges, we calculated home range area using the adaptive Local Convex Hull method (*a*-LoCoH), which outperforms other methods when home ranges abut such boundaries without including unused areas within the utilization distribution and is robust to the selection of the kernel parameter

(Getz et al. 2007; Lichti and Swihart 2011). For every individual and season-year combination with ≥ 20 locations we estimated 95% isopleth home range boundaries with an a = 475 based on the maximum distance between locations but excluding dispersal movements (Getz et al. 2007). Home range area was calculated using package adehabitatHR (Calenge 2006) in program R v. 3.2.3 (R Core Team 2015).

We delineated shrubland patches in ArcMap GIS 10.4.1 (ESRI, Redlands, CA) based on visual interpretation of aerial imagery and ground surveys of vegetation structure. Patch boundaries were defined by features such as roads, mowed fields, or water bodies or by lack of dense understory vegetation (Barbour and Litvaitis 1993). Cottontail home ranges were typically centered within a single patch; if multiple patches were included within the home range area, use was centered within a single patch. We therefore assigned home ranges to patches based on the focal patch of use for each individual and calculated patch area for all shrubland patches in ArcGIS. We assessed stem density for all woody plant species at a height of 0.5 m within 1- x 10-m plots during the leaf-off season. Plots were spaced across a 50-m grid covering all areas of observed cottontail use. Vegetation data were rasterized in ArcGIS and resampled to 10-m resolution using bilinear interpolation (Bonnot et al. 2009; Stabach et al. 2009). We assessed stem densities of the most common invasive shrub, Japanese barberry, and combined native stems deemed palatable to New England cottontails (Pringle 1960; Cheeseman et al. 2018).

We modeled home range size using a generalized linear model with a Gaussian distribution for the residuals. Because home range area must be > 0, we used a log link function for the predicted values (Lindsey and Jones 1998). We developed 13 candidate models representing our hypotheses including a null model and 12 combinations of sex, species, season, patch area, and mean stem density of Japanese barberry and palatable native shrubs and saplings.

To avoid pseudoreplication due to including home ranges of the same individual in both seasons, the variable "season" was included in all models except the intercept-only null. We fit models using maximum likelihood estimation with an iteratively-reweighted least squares algorithm in the "glm" function of R. To reduce the risk of overfitting models, the number of parameters in the global model did not exceed 10% of the sample size (i.e. 12 parameters; Fieberg and Johnson 2015). We examined heteroscedasticity, normality, and collinearity[2] for the global model and found no evidence for overfitting and or violation of model assumptions. We performed model selection using an information theoretic approach and Akaike Information Criterion adjusted for small sample size (AIC_c) (Burnham and Anderson 2002). We considered models with a relative likelihood of <0.125 to have some support and made inferences based on model-averaged predicted values averaged across all models (Arnold 2010; Burnham and Anderson 2002, Cade 2015). We inferred a difference between levels of a covariate where model-averaged prediction intervals overlapped by less than 25% (Cumming and Finch 2005). To determine if the area used outside patch boundaries was related to patch size, we *post-hoc* modeled the home range area and the proportion of the home range external to the boundaries of each patch as a function of patch area and season, including patch identity as a random effect. Models were run using a mixed-effect generalized linear model with a Gaussian distribution for the residuals and a log-link function in the 'glmer' package in R.

Results

We estimated 55 seasonal home ranges for 36 eastern cottontails and 67 home ranges for 41 New England cottontails. Median triangulation error was 27 m, and the GPS accuracy of homing locations was 5 m. Mean stem density within shrubland patches was 37 811 ± 46 415 SD stems / ha.

[2] Supplementary materials table S 1

The top three models for factors impacting home range size accounted for 97% of model weight (Table 2). The top model included sex, season, Japanese barberry stems, and palatable stems and its interaction with season. The second-ranked model contained the same variables with the addition of species and its interaction with Japanese barberry. The third-ranked model was identical to the second but for the addition of the patch area and the interaction between Japanese barberry and season. Species and the interaction between Japanese barberry and species had some support based on their inclusion in the second model and a corresponding reduction in deviance (Arnold 2010). The addition of patch area and the interaction between Japanese barberry and season in the third model were uninformative based on their minimal effect on deviance (Table 2; Arnold 2010). The ΔAIC_c for the null model was 21.95 providing evidence for the explanatory ability of the top model (Table 2).

The confidence limits on the regression parameters for sex (coded as "Male"), season (coded as "Leaf-off"), Japanese barberry stem density, and palatable stem density did not contain zero (Table 3). Home range size was greater for males than females and greater in the leaf-on season than leaf-off season for both New England and eastern cottontails (Table 4). The home range size of both cottontail species was inversely correlated with palatable stem density in the leaf-on season (Fig. 2), such that home range area at high stem densities in the leaf-on season was not different from the leaf-off season. Home range size was inversely correlated with Japanese barberry stem density in both seasons (Fig. 3). There was some indication that Japanese barberry density had a greater effect on home range size of New England cottontails than eastern cottontails; however this result was inconclusive, as the interaction between species and Japanese barberry was lacking from the top model and the lower confidence limit of the regression parameter 'species × barberry' in the second-best model was 0 (Table 3). Home ranges of both

species were independent of palatable native stems in the leaf-off season. The degree of overlap in 95% prediction intervals between the prediction lines for Japanese barberry and palatable native stems indicated that during the leaf-on season, the influence of palatable native stems on home range area of eastern cottontails was greater than that of Japanese barberry (Fig. 4). However, this effect was not apparent during the leaf-on season or for New England cottontails, although we lacked the sample size to reliably assess home range area at high palatable native stem densities.

Patch size did not influence home range size (Table 2). Instead, the area of a home range outside of patch boundaries was negatively correlated with patch size in the leaf-on season (β = -0.393 ± 0.125 SE, $P < 0.001$) and leaf-off season (β = -0.393 ± 0.125 SE, $P = 0.002$) with predicted home range area external to patch boundaries approaching 0 in patches greater than 20 ha[3]. The proportion on the home range external to patch boundaries was also negatively correlated with patch size (β = -0.119 ± 0.034, $P < 0.001$), and predicted proportion of home range outside the patch approached 0% in patches greater than 25 ha; however, this relationship did not vary by season (β = -0.019 ± 0.122, $P = 0.875$; Fig. 5). Furthermore, when home ranges were centered in small patches of shrubland, home range boundaries often exceeded patch boundaries (Fig. 6a) and came into contact with patch edges (Fig. 6b) when compared to larger patches of shrubland where home ranges primarily fell within delineated patch boundaries (Fig. 6c).

Discussion

We demonstrated that the space use of an imperiled habitat obligate in a highly fragmented ecosystem depends on food and cover-related resources, but not on patch size. New England and

[3] Supplementary materials Fig. S 1

eastern cottontails are likely to be exposed to shrubland patch edges and matrix in small shrublands as fragmentation increases, because they have similar home range sizes and do not appear to adjust their home range sizes based on patch size. Rather, home range size was more sensitive to the shrub densities within the patches, an indicator of patch quality. Cottontail home ranges responded similarly between species to the covariates we assessed, with some suggestion that the response to Japanese barberry varied by species. These results support previous research suggesting the two species may compete over shrubland resources (Probert and Litvaitis 1996; Cheeseman et al. 2018).

As cottontail home ranges were not constrained to shrubland boundaries, New England cottontails may be required to engage in risky foraging behavior away from cover to meet resource needs within these patches. This trend is consistent with conclusions from Barbour and Litvaitis (1993) and Villafuerte et al. (1997) that New England cottontails residing in patches ≤ 2.5 ha during winter consume lower quality browse, forage further from cover, were more nutrient limited, and experience lower survival than New England cottontails in larger patches. However, although cover also may affect survival of the more generalist eastern cottontail (Trent and Rongstad 1974), foraging outside cover is not as costly for this species as for New England cottontails (Smith and Litvaitis 2000). We demonstrate increased inclusion of low-cover matrix within the home range of cottontails in smaller patches. These findings suggest that lower survival rates observed in other studies of New England cottontails residing in small patches may result in part from an inability to restrict the space used to meet their resource requirements to areas of low predation risk (Villafuerte et al. 1997; Smith and Litvaitis 2000). As a result, small patches may confer disproportionate survival costs to New England cottontails which can exploit

less habitat than eastern cottontails without incurring increased risk of predation (Smith and Litvaitis 2000).

An inverse correlation between home range size and vegetation density is commonly attributed to a reluctance to leave areas of high cover or abundant forage in other species (McLoughlin and Ferguson 2000). Increased cover in conjunction with smaller home ranges may also limit exposure to predators, thereby increasing individual survival (McLoughlin and Ferguson 2000). As hypothesized, the density of native palatable shrubs that likely provide both forage and cover to New England and eastern cottontails was inversely correlated with home range area of both species, suggesting they may be able to meet their resource requirements with smaller patches if patches contain a high density of palatable native shrubs. Japanese barberry also formed a dense understory and likely provided good cover for New England cottontails; however, its value as a food plant to New England cottontails is uncertain. In New York, New England cottontails selected for Japanese barberry out of proportion to its availability during the leaf-off season only when eastern cottontails were prevalent; however, eastern cottontails did not select for Japanese barberry (Cheeseman et al. 2018). Similarly, we demonstrate cottontail home ranges are inversely correlated with Japanese barberry density, and there is some suggestion that the effect is greater for New England cottontails than eastern cottontails. As a result, removal of dominant invasive shrubs may have disproportionately negative impacts on habitat quality for New England cottontails, and the negative impacts of such removal may be exacerbated in small patches. As native palatable plants were not observed at the high densities observed for Japanese barberry in this study, our ability to make inferences at high densities of native palatable stems was limited. However, we note the density of palatable native forage may have had a stronger influence than Japanese barberry on home range area, suggesting patches dominated by native

palatable shrubs and saplings are of higher quality than invasive dominated areas, as might be the case if the latter provides high quality cover but forage lacking. Examination of the value of high densities of native palatable plants along with invasive plants to New England cottontail should be a focus of future research.

High predation pressure results in an inverse correlation between protective cover and home range size of vole species (*Microtus* Schrank, 1798; Getz et al. 2005) roe deer (*Capreolus capreolus* (Linnaeus, 1758); Tufto et al. 1996), and has been suggested to explain variation in eastern cottontail home ranges (Bond et al. 2001). Lagomorph survival is lowest during the leaf-off season in northern regions or high elevations (Trent and Rongstad 1974; Keith and Bloomer 1993; Hartman and Barry 2010). A strong reluctance to forego cover has been described for New England cottontail during the leaf-off season, where individuals will forage on poor quality resources within cover and lose body mass rather than forage on high quality resources outside of cover (Smith and Litvaitis 2000). This reluctance to forgo cover could explain the seasonal difference in home range size observed here. Seasonal shifts in selection to incorporate resources provided by young shrubland and field edges, which have graminoids and forbs that may provide low cover during the leaf-off season but adequate cover during the leaf-on season, are apparent in New England cottontails and to a lesser degree, eastern cottontails (Cheeseman et al. 2018). The combination of relaxed predation pressures and the availability of seasonal graminoids and forbs during the leaf-on season likely facilitates leaf-on season home range expansion into areas that may have unsuitable cover during the leaf-off season. Sex-specific differences in home range sizes, such as those observed for male cottontails, are often attributed to mate searching (McLoughlin and Ferguson 2000; van Beest et al. 2011) which is likely the case here.

We present evidence that patch size does not constrain movements of New England and eastern cottontails, and that these individuals enter poor quality matrix in small patches. This finding implies that small shrubland patches confer disproportionately negative survival costs to New England cottontail, as survival is reduced for New England cottontails but not eastern cottontails when they forage in area of low cover (Smith and Litvaitis 2000). We observed a sharp increase the home range area and proportion external to patch boundaries within patches less than 7 ha; for patches exceeding 20 -25 ha, the area and proportion of home range outside patch boundaries approached 0. This suggests the minimum patch area should exceed 7 ha to satisfy most individual space needs; however, predation risk to New England cottontails may be minimized in patches greater than 20 ha. Many managed shrublands are smaller than 7 ha (Buffum et al. 2011) and may not be of sufficient size for New England cottontails to meet individual resource needs; the patch area necessary to sustain entire populations are likely greater. Increasing shrub density within small patches could allow cottontails to meet their space needs. Nonetheless, most shrubland creation projects on private lands in the northeastern United States are of insufficient size to support New England cottontails. Future management efforts should work toward creation of larger patches which may require cooperation among multiple private landowners.

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Figure Captions

Fig. 1. Locations of 15 study sites used for assessing home range of sympatric New England (*Sylvilagus transitionalis*) and eastern cottontails (*Sylvilagus floridanus*) in the lower Hudson Valley, New York, USA 2013 – 2016.

Fig. 2. Model-averaged predictions of 95% home range area by sex for leaf-off (gray) and leaf-on (black) New England cottontails (*Sylvilagus transitionalis*) vs. palatable stem density in New York, 2013-2016. Observed values of palatable stems per 10 m^2 are plotted along the x-axis. 95% prediction intervals are shown. Predictions for eastern cottontails (*Sylvilagus floridanus*; not shown) were nearly identical to those for New England cottontails.

Fig. 3. Model-averaged predictions of 95% home range area by sex for leaf-off (gray) and leaf-on (black) New England (*Sylvilagus transitionalis*) and eastern cottontails (*Sylvilagus floridanus*) vs. Japanese barberry stem density in New York, 2013-2016. Observed values of barberry stems per 10 m^2 are plotted along the x-axis. 95% prediction intervals are shown.

Fig 4. Model-averaged predictions of 95% home range area across values of palatable stems (black) when Japanese barberry stems were held at 0 and for Japanese barberry (gray) stems where palatable stems were held at 0. Values for male New England (*Sylvilagus transitionalis*) and eastern cottontails (*Sylvilagus floridanus*) in the leaf-on season, New York, 2013-2016 are presented. Response by female cottontails (not shown) was similar with a lower y-intercept reflecting the additive sex difference in home range area. Observed values of palatable and barberry stems per 10 m^2 are plotted along the x-axis. 95% prediction intervals are shown.

Fig 5. Predicted proportion of home range external to patch boundaries vs. patch area (ha) and 95% prediction intervals for pooled New England (*Sylvilagus transitionalis*) and eastern cottontails (*Sylvilagus floridanus*) in New York, 2013-2016. Average proportion of home range external to patch is shown for leaf-on (white dots) and leaf-off seasons (black dots).

Fig. 6. Example 95% leaf-on home ranges (black) of female New England cottontails (*Sylvilagus transitionalis*) in Putnam County, New York estimated using adaptive-local convex hull methods. Home range centers fall within a) a small 1.3-ha patch (b) a small 1.4-ha patch, and c) a large 5.3-ha patch of shrubland.

Table 1. List of the most commonly encountered woody plant species within shrublands occupied by New England cottontails (*Sylvilagus transitionalis*) in New York, 2013-2016.

Species	Status	Plots[a]	Stems[b]
Japanese Barberry (*Berberis thunbergii*)	Invasive	14.0%	36.0%
Multiflora rose (*Rosa multiflora*)	Invasive	12.7%	17.3%
Oriental Bittersweet (*Celastrus orbiculatus*)	Invasive	9.5%	12.9%
Blueberry (*Vaccinium* spp.)	Native	6.9%	4.9%
Rubus spp.	Native / Invasive	7.6%	3.7%

[a]Percent of plots where species was observed
[b]Percent of total stem composition by species

Table 2. Models, parameter count, and information-theoretic criteria model selection results for 95% home range areas of New England (*Sylvilagus transitionalis*) and eastern cottontails (*Sylvilagus floridanus*) in New York based on vegetation variables, season, sex, and species, 2013-2016 (n = 122 home ranges of 77 individuals).

Model	K[a]	Relative likelihood[b]	ΔAIC_c[c]	w_i[d]	Deviance	Pseudo R^2[e]
Sex + season + barberry + palatable + season * palatable	7	1.000	0.00	0.499	49.804	0.236
Sex + season + species + barberry + palatable + species * barberry + season * palatable	9	0.827	0.378	0.413	48.100	0.262
Sex + season + species + barberry + palatable + patch area + species * barberry + season * barberry + season * palatable	11	0.116	4.308	0.058	47.761	0.267
Sex + season + palatable + season * palatable	6	0.027	7.207	0.014	53.819	0.174
Sex + season + palatable + patch area + season * palatable	7	0.012	8.900	0.006	53.573	0.178
Sex + season + barberry + patch size + season * barberry	7	0.011	8.955	0.006	53.597	0.178
Sex + season + species + season * species	6	0.01	9.299	0.005	54.75	0.160
Season + barberry + palatable + season * barberry	6	0	16.138	0	57.907	0.112
Season + species + barberry + palatable + patch area + season *	8	0	18.424	0	56.845	0.128

palatable						
Season	3	0	18.489	0	56.845	0.045
Season + species + barberry + season * barberry	6	0	18.531	0	59.054	0.094
Season + barberry + patch area + season * barberry	6	0	20.048	0	59.793	0.083
Null	2	0	21.95	0	65.1841	0.000

[a] K = number of parameters in the model

[b] Relative Likelihood = exp (-0.5*ΔAIC_c), the likelihood ratio of the given model to the top model

[c] ΔAIC_c is the difference in the AIC_c (AIC corrected for small sample sizes) between a given model and the top model. The AIC_c of the top model was 307.53

[d] w_i = AIC_c weights, or the probability that the given model fits the data best, of the models tested

[e] Pseudo R^2 calculated using the Cox-Snell method (Cox & Snell 1989)

Table 3. Top models of 95% home range size of New England (*Sylvilagus transitionalis*) and eastern cottontails (*Sylvilagus floridanus*) in New York, 2013-2016, including estimates of coefficients, standard error, and 95% confidence limits (n = 122 home ranges of 77 individuals).

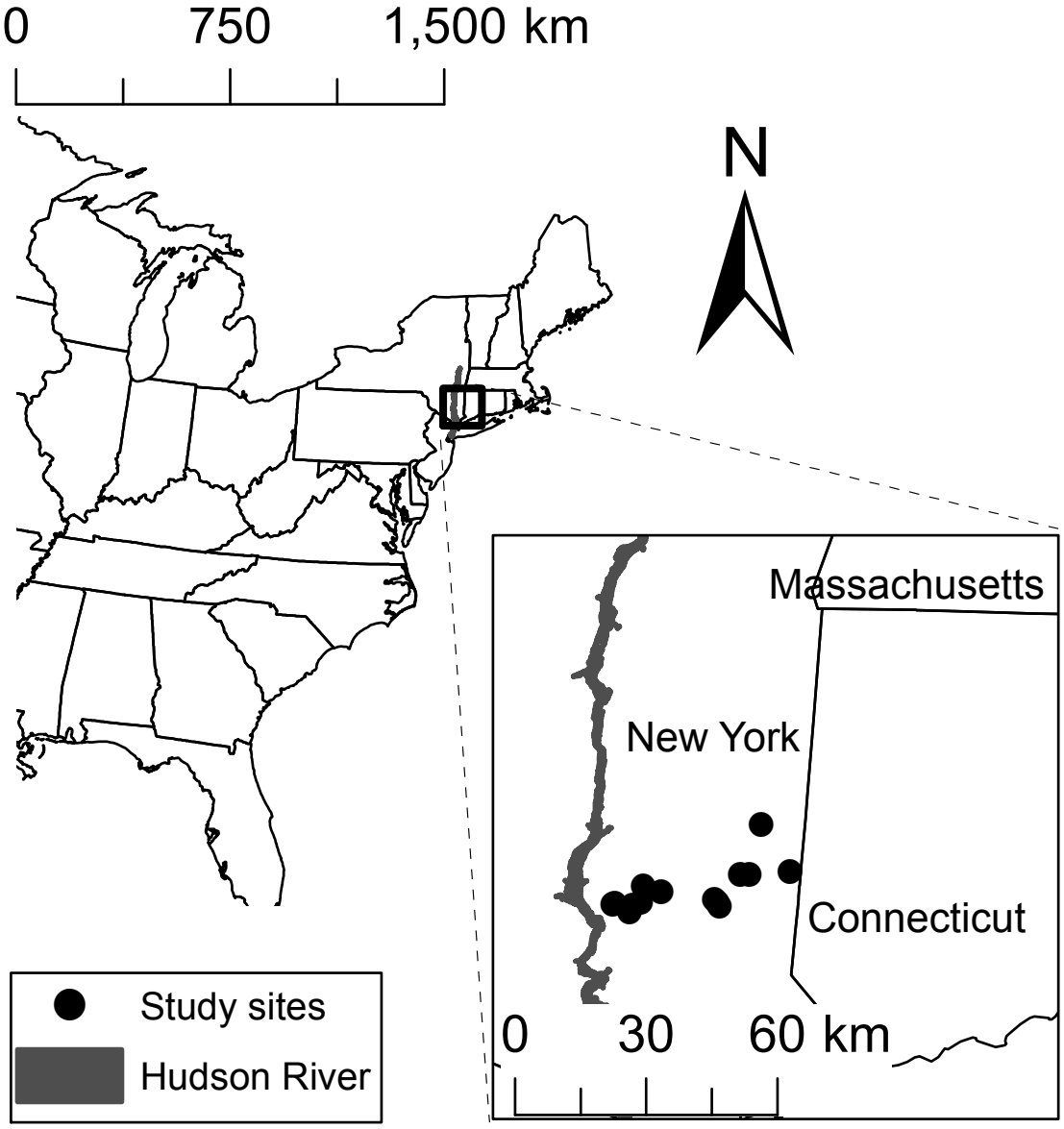
Model[a]	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI
Sex + season + barberry + palatable + season × palatable	Intercept (female, leaf-on)	0.440	0.117	0.210	0.670
	Males	0.418	0.101	0.220	0.616
	Leaf-off	-0.447	0.132	-0.706	-0.189
	Barberry	-0.007	0.003	-0.013	-0.002
	Palatable	-0.042	0.019	-0.079	-0.006
	Season × palatable	0.032	0.022	-0.010	0.075
Sex + season + species + barberry + palatable + species × barberry + season × palatable	Intercept (female New England cottontail leaf-on)	0.542	0.124	0.299	0.785
	Males	0.442	0.100	0.245	0.638
	Leaf-off	-0.509	0.134	-0.772	-0.246
	Eastern cottontail	-0.205	0.123	-0.445	0.036

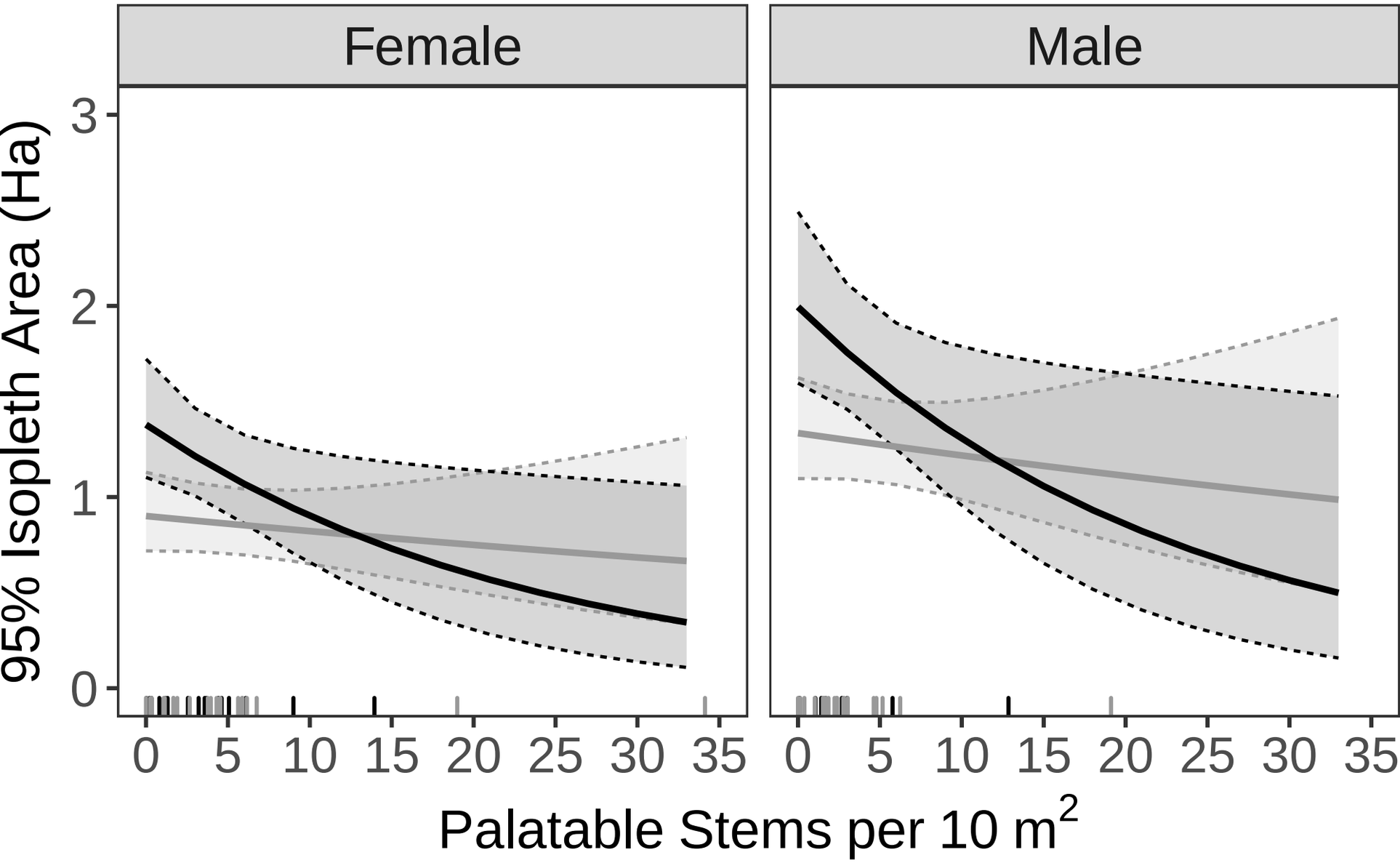
Barberry	-0.012	0.004	-0.020	-0.004
Palatable	-0.044	0.019	-0.081	-0.007
Species × barberry	0.011	0.006	0.000	0.022
Season × palatable	0.035	0.022	-0.008	0.078

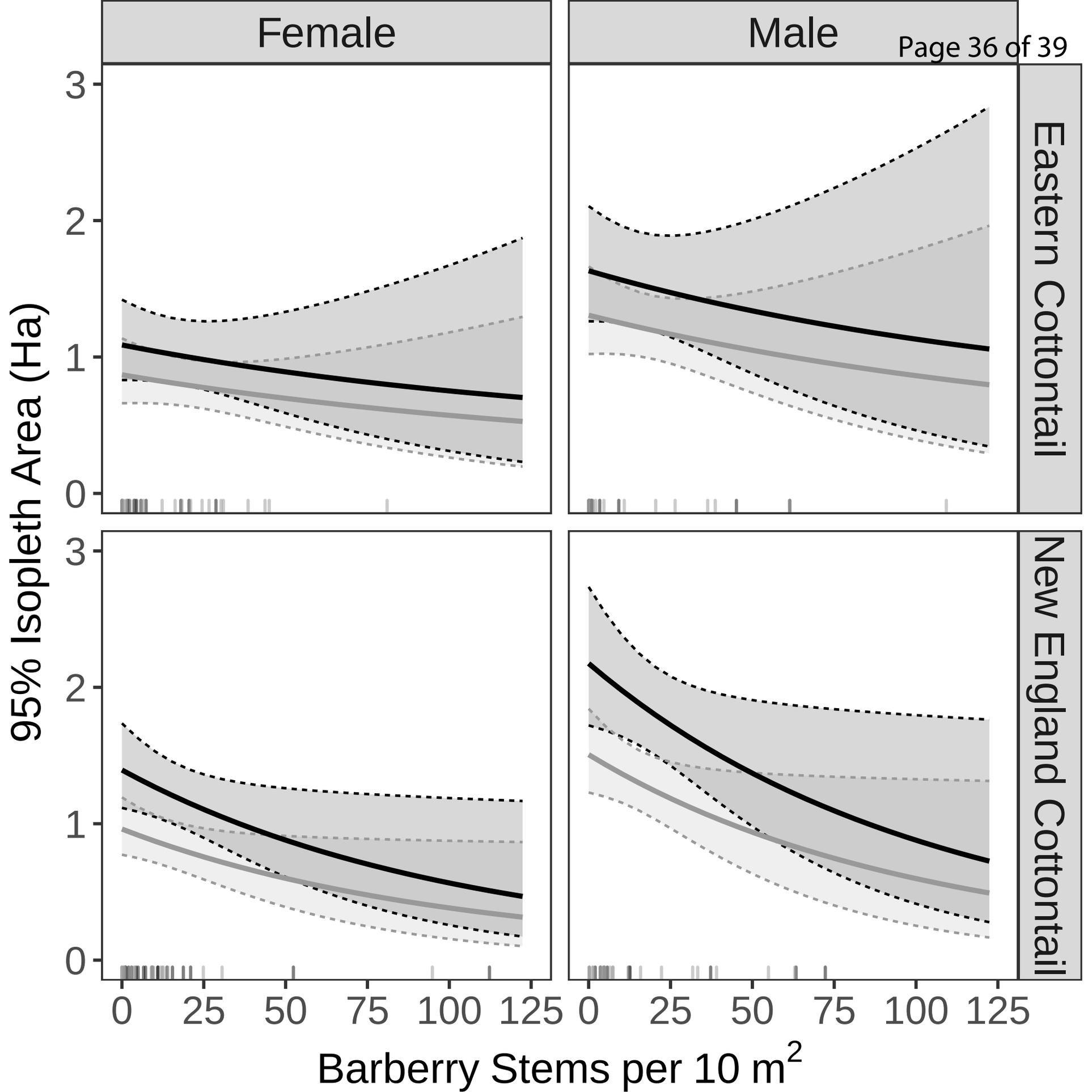
[a] For brevity only results from models with $AIC_c \leq 2.0$ are shown.

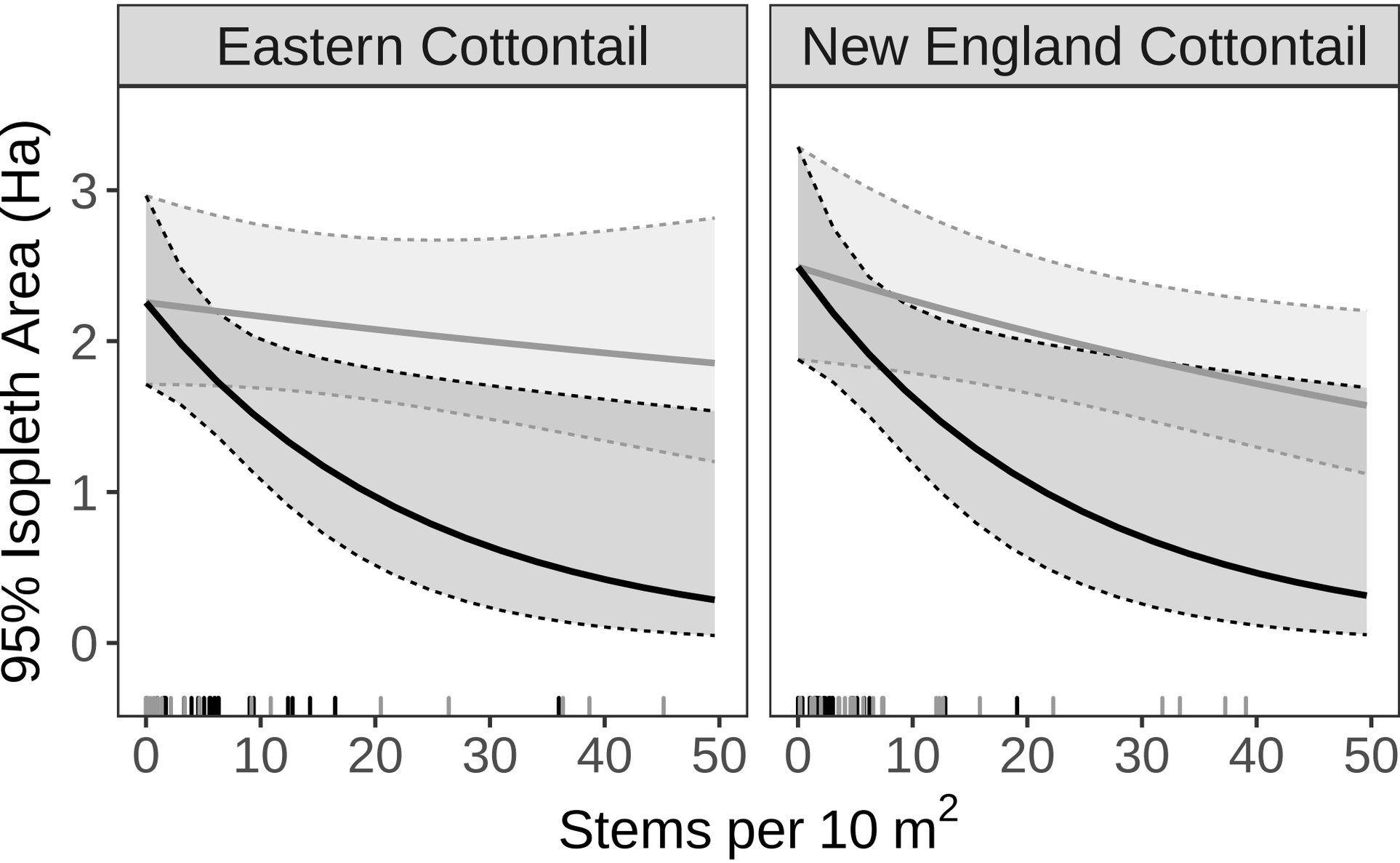
Table 4. Model-averaged mean 95% home range size (ha) for New England (NEC, *Sylvilagus transitionalis*) and eastern cottontails (EC, *Sylvilagus floridanus*) in New York, 2013-2016, when patch area, Japanese barberry and palatable stem densities are held at group (season, species, and sex) means (n = 122 home ranges of 77 individuals).

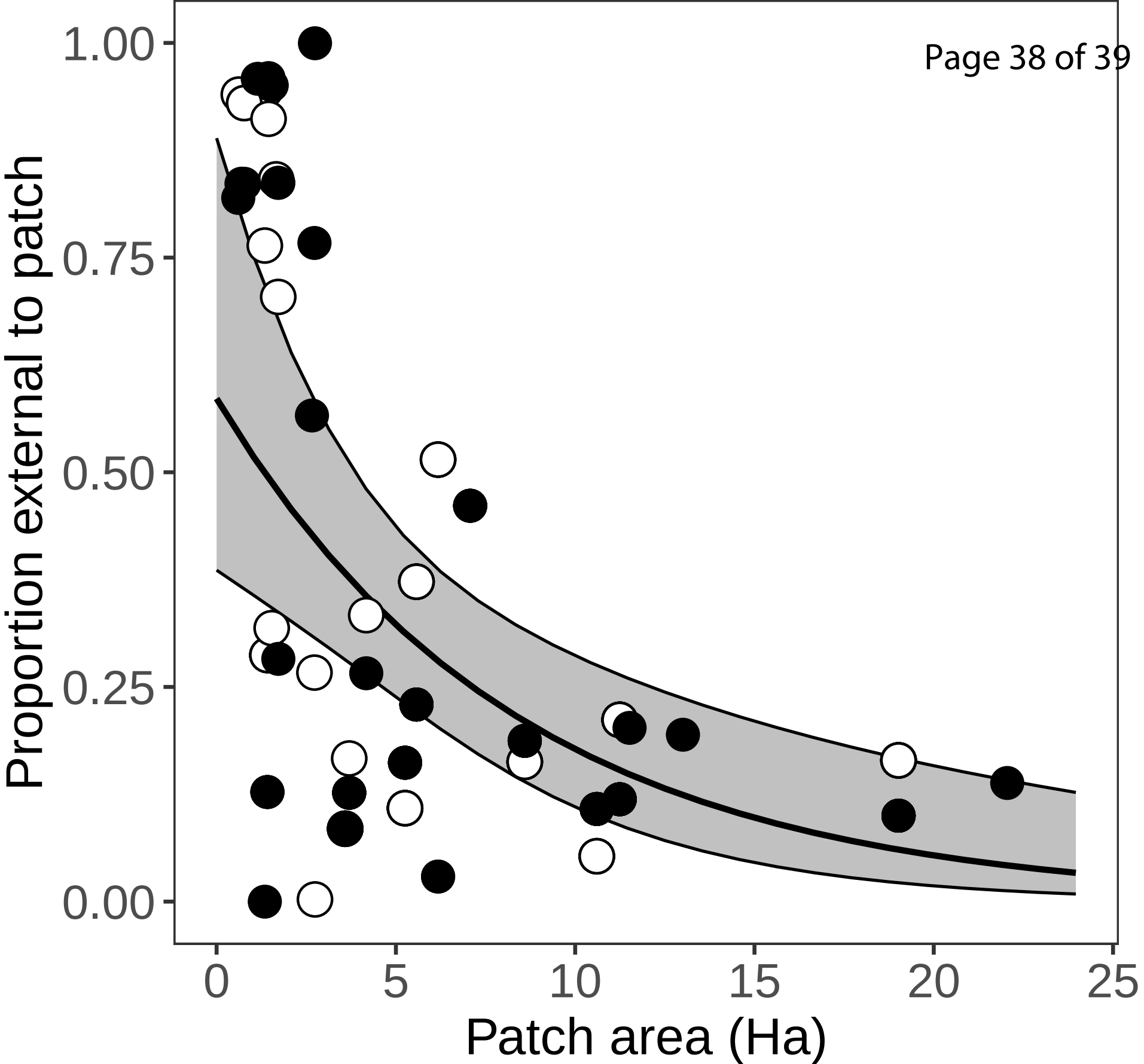
Season	Species	Sex	Area	SE	Lower 95% CI	Upper 95% CI
Leaf-off	NEC	M	1.295	0.112	1.093	1.534
		F	0.856	0.087	0.702	1.046
	EC	M	1.189	0.118	0.979	1.444
		F	0.795	0.087	0.641	0.986
Leaf-on	NEC	M	1.742	0.165	1.448	2.097
		F	1.186	0.114	0.982	1.431
	EC	M	1.532	0.175	1.224	1.917
		F	1.048	0.126	0.827	1.328

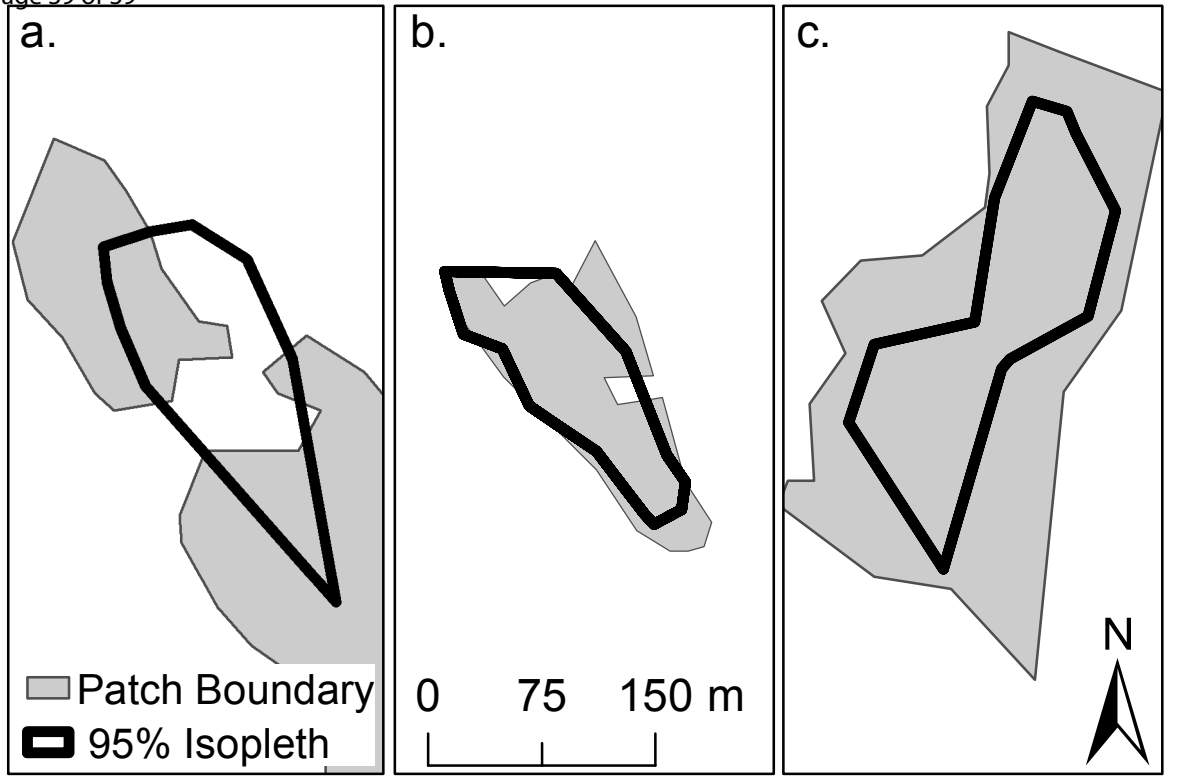

0
750
1,500 km
N
Massachusetts
New York
Connecticut
0
30
60 km
Study sites
Hudson River


Female
Male
95% Isopleth Area (Ha)
0
1
2
3
0
5
10
15
20
25
30
35
Palatable Stems per 10 m2


Female
Male
Eastern Cottontail
New England Cottontail
95% Isopleth Area (Ha)
0
1
2
3
0
25
50
75
100
125
Barberry Stems per 10 m^2


Eastern Cottontail
New England Cottontail
95% Isopleth Area (Ha)
3
2
1
0
0
10
20
30
40
50
Stems per 10 m2


1.00
0.75
0.50
0.25
0.00
Proportion external to patch
0
5
10
15
20
25
Patch area (Ha)


a.
b.
c.
Patch Boundary
95% Isopleth
0
75
150 m
N