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Spatial and Temporal Use of Early Successional Habitat Patches by a Community of Mammals in the Northeastern United States

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Spatial and Temporal use of Early Successional Habitat Patches by a Community of Mammals in the Northeastern United States

Kelly Marie O'Connor

B.S., University of Connecticut, 2013

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Master of Science Thesis

Spatial and Temporal Use of Early Successional Habitat Patches by a Community
of Mammals in the Northeastern United States

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Introduction

Human development is a global driver of landscape modification and homogenization. In particular, increased anthropogenic land-use often minimizes or removes patterns of disturbance from the landscape that historically maintained a diversity of habitats across multiple stages of succession. Loss of habitat heterogeneity and fragmentation of critical habitats may affect wildlife at both the scale of individual species and of species assemblages (Fischer and Lindenmayer 2007).

In the northeastern United States, the removal of natural disturbance process, including wind events caused by Atlantic hurricanes and spread of wildfires following lightning strikes, as well as diminished presence of beaver activity, have led to homogeneity in forest successional structure (Lorimer 2001). The loss of early successional forest habitat from the northeastern landscape has been well noted, especially regarding obligate residents of young-growth forest and on broader species assemblages that utilize these habitats to fulfill resource requirements (Litvaitis 2001). Recognizing the need to re-introduce habitat heterogeneity and a diversity of forest successional stages to the landscape of the northeast in order to fulfill the needs of a broad range of species, state and federal wildlife agencies have set goals for creating early-successional forest habitat on both public and privately owned lands (Oehler 2003).

Understanding patterns of behavior and habitat use occurring within patches of early successional forest helps us better understand the utility of these habitats for native fauna communities. Many members of mammal communities native to the northeastern US are either obligate or facultative users of young-forest habitat (Litvaitis 2001). Patterns of mammal behavior and resource use within young-forest habitat may be difficult to observe given the cryptic nature of most mammal species, and the sheer density of early successional vegetation. I choose to tackle these challenges by focusing on fine-scale resource selection of two closely related species while also broadening the focus to the mammalian community co-occurring within habitat patches.

The New England Cottontail (*Sylvilagus transitionalis*) (NEC) has become an umbrella species for young forest management in the northeastern US. Assessments of habitat quality at the patch level have thus far relied on a single metric, stem density per acre, a metric that may be informative for prioritizing habitat management at a broad scale, but less telling regarding the structural aspects of early-successional vegetation that NEC find desirable within a habitat patch. A better understanding of the structural components of early successional vegetation that NEC select for may better inform habitat management actions within occupied patches.

Patterns of daily activity may be shaped by major disturbances in an ecosystem, seasonal shifts in abundances of resources, or habitat preferences. Concentrated periods of activity within a specific habitat type may demonstrate this habitat as a source of desirable resources that cannot be obtained elsewhere on the landscape. Conversely, similar levels of activity spread across many habitat types would be indicative of a habitat generalist. While telemetry based studies of activity may be limited to few individuals of one species, camera trap photographs can be used to quantify activity patterns in broader species assemblages. Patterns of activity within early successional forest habitat may demonstrate the value of this habitat type to a broad suite of mammal species.

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Winter selection of cover habitat and survival of sympatric New England and Eastern Cottontail

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Abstract:

The New England cottontail (*Sylvilagus transitionalis*) (NEC) is a native species in decline while the range and abundance of a closely related species, the Eastern cottontail (*Sylvilagus floridanus*) (EC), is increasing. Data on habitat use of both species occurs largely at the patch or landscape level. Dynamics of habitat selection at a within-patch scale when the two species both occupy the same area are less well documented. Additionally, most estimates of NEC vital rates come from northern populations, where EC and NEC do not occur sympatrically. We homed to cottontails and quantified daytime cover habitat in a used-available framework and used conditional logistic regression to assess support for hypotheses of drivers of habitat use. Additionally, we monitored winter survival of 48 cottontails (35 EC, 13 NEC) across three sites and two years in southeastern Connecticut, and estimated survival using logistic exposure methods to explore whether survival probabilities differed among the two cottontail species. EC used a more diverse range of plant species as daytime cover. NEC and EC both selected daytime cover that maximized concealment from predators, but selected for different structural attributes of cover. Site-wide presence of snow cover and vegetative leaf cover did not impact the strength or direction of selection within our top-ranked models. Species was not a significant predictor of survival probability, and was ranked low among our candidate survival models. Female rabbits experiences a 20% lower probability of survival than males during the winter monitoring period, with an estimated cumulative survival rate of 50%. Competitive differences between two highly similar species like the NEC and EC are likely to be subtle, and should be explored at multiple spatial and temporal scales to maximize our understanding of both sympatric and allopatric cottontail populations.

Introduction

Habitat specialists are particularly vulnerable to global change, as they are less flexible than habitat generalists in their use of changed or degraded resources (Warren et al. 2001, Jiguet et al. 2007, Rowe et al. 2011, Varner and Dearing 2014). Closely-related competitors may show slight differences in life history traits that allow one species to be more successful than the other over a period of time (Jiguet et al, 2007). The New England cottontail (*Sylvilagus transitionalis*) (NEC) is a young forest obligate species endemic to the Northeastern United States. The NEC range has decline 86 percent since the 1960's (Litvaitis et al. 2006). NEC are now segregated to five remnant populations that are highly isolated and vulnerable to extirpation (Litvaitis et al. 2006, Fenderson et al. 2011). Land use patterns of the current New England landscape are vastly different from those in the early 20th century. Urbanization and exurban land use patterns in the late 20th and early 21st century have caused increased fragmentation of historic wildlife habitat and a dampening of the natural processes that traditionally maintained young forests across the landscape (Hansen et al. 2013). As a result, old fields and young forest stands, i.e. NEC habitat, now account for the smallest portion of forest lands in the northeast (Litvaitis 2001).

The introduction of the non-native Eastern cottontail (*Sylvilagus floridanus*) (EC) is also thought to be a factor in the decline of the NEC. EC's are capable of foraging at greater distances from cover, and are able to detect potential predators from greater distances (Smith and Litvaitis 2000). These characteristics enable EC to persist in less dense habitat and more heavily fragmented habitat than is preferred by the NEC. Young forest patches that are too early or too late in succession for NEC may still be useable habitat for EC, as they provide enough cover for the EC but are not dense enough for NEC to achieve adequate survival. Macrohabitat use of the NEC is generally well understood. New England Cottontails are an area sensitive species, requiring relatively large patches of unfragmented habitat to maintain adequate survival rates for persistence (Villafuerte et al 1997). Assessments of habitat quality at the patch level have thus far relied on a single metric, stem density per acre. Available cover has been quantified as density of woody stems per acre when assessing patch characteristics associated with NEC

and snowshoe hare (*Lepus americanus*) (Litvaitis et al. 2003). Microhabitat use was explored in northern NEC populations and concluded that NEC use areas of high stem density within occupied patches (Barbour and Litvaitis 1993). Microhabitat for NEC is designated by only one aspect of vegetative structure, and excludes comparative use of their defined microhabitats by sympatric species. While important for characterizing the probability of patch occupancy, stem density alone may not reflect all aspects of cover structure that lead to the use of that cover by NEC. A better understanding of the structural components of early successional vegetation that NEC select for may better inform habitat management actions within occupied patches.

Winter is often identified as a period of particularly high cottontail mortality, because resources are most limited at this time (Hodges et al. 2006, Davis and DeNardo 2009, Weidman and Litvaitis 2011). Survival estimates for NEC are largely sourced from the northern extent of the species' range where sympatry between NEC and other lagamorphs occurs less frequently (Barbour and Litvaitis 1993). Our goal was to quantify differences in habitat use and vital rates between sympatric EC and NEC that may better inform our understanding of the role of EC in the decline of NEC. Our objectives were to quantify patterns of daytime cover selection at a small, within-patch scale for both species of cottontail, and to estimate daily and cumulative survival probabilities during the winter in sympatric EC and NEC. We sought to explain if cover selection was being driven by cottontails seeking refuge from foraging predators, or by cottontails seeking to limit their exposure to harsh winter conditions. Furthermore, we aimed to address whether cottontails were selecting for structural characteristics of cover that provided maximum concealment from avian predators (i.e. vertical structure), or from terrestrial predators (i.e. horizontal structure at ground level). In our modelling of survival probabilities, we sought to determine whether harsh abiotic conditions on specific days within a winter result in elevated probability of mortality.

Methods

Study Sites

We collected data at one site in year one and three additional sites in year two. We chose public properties with confirmed records of NEC within the previous 10 years and properties located within focus areas designated by the regional New England Cottontail Conservation Management Plan (Fuller and Tur, 2012). In both years, we trapped on a parcel of privately owned land in Stonington, CT, referred to as the Nichols property (Nichols). This site consists of approximately 40 acres of young forest/shrub habitat that was at one time farmland. The site directly abuts 60 acres of farmland currently grazed by cattle. Cattle are not excluded by a fence from available early successional habitat. Game trails can be found throughout dense areas of vegetation. The site is dominated by woody shrub species with a heavy invasive component. Dominant species include multiflora rose (*Rosa multiflora*), autumn olive (*Elaeagnus umbellatae*), Japanese barberry (*Berberis thunbergii*), and eastern red cedar (*Juniperis virginiana*). A major interstate (I-95) runs along the southern extent of the property, and a golf course abuts the property to the north. Pachaug State Forest encompasses approximately 24,000 acres. We focused trapping on 60 acres off Wyassup Road in North Stonington, CT. Active timber harvest on Pachaug State Forest directly adjacent to our site is ongoing to create early successional habitat as part of the regional New England Cottontail Conservation Management Plan. Invasive species control occurs at this site regularly. Bluff Point State Park and Coastal Reserve is 800 acres of hardwood forest and coastal shrubland near Groton, CT. We focused trapping within 10-20 acres with known NEC records. The trapped site is dominated by thick vine growth and other woody shrub species. The most prevalent plant species in areas that were trapped include greenbrier (*Smilax spp.*), multiflora rose, autumn olive, and honeysuckle (*Lonicera spp.*). The rest of the park is largely mature upland hardwood forest, and is a peninsula bounded by the Long Island Sound and Route 1. James Spignesi Wildlife Management Area is a 469 acre WMA in Scotland, CT maintained as a mix of upland hardwood forest, open field, and early successional habitat. Trapping was focused throughout 18 acres of young forest habitat, which is

maintained through Connecticut's Young Forest Initiative. Invasive species removal has also occurred within young forest habitat on this site.

Capture Methods

During year one, we checked 216 Havahart 1-door box traps (B1079, 32" x 10" x 12", Woodstream Corp., Lititz PA) during the early morning from 3 October through 25 November 2013. We assigned captured cottontails an ID number and fitted cottontails with numbered metal ear tags in both ears (Size 898 2.75, National Band & Tag Co., Newport KY). We obtained GPS coordinates for any traps where cottontails were captured. We checked traps daily and baited with apple slices. We closed traps only in cases on inclement weather. Live-trapping for cottontails during year two occurred continuously from 1 October 2014 through 1 March 2014. Trapping at Nichols followed procedures in year 1 and occurred from 1 October through 1 November. Our goal in year 2 was a total of 10 cottontails, five of each species, collared at each of four sites. We stipulated that the first rabbit collared at a site be an NEC. Once an NEC was collared, we then collared the next EC captured. When cottontails were recaptured, we recorded their ear tag number and GPS location. We recorded all instances of bycatch (other small mammals, birds, and reptiles), and immediately released these individuals. Trapping began simultaneously at the Pachaug field site on 6 October 2014. We distributed arrays of 10 Tomahawk live traps (Model 106, 26"x9"x9" single-door, Tomahawk Live Trap LLC, Hazelhurst WI) at randomly generated points distributed across dense vegetation where cottontail activity was most likely to occur. We made trap cluster placement dynamic, such that after five days of no captures within a cluster, we generated a new random point within appropriate cover, and relocated the cluster. We spent a minimum of one month at a given site, with traps active every day of the week, excluding closures for inclement weather. After Pachaug, we relocated traps to Bluff Point (start date 9 November 2014), and finally to Spignesi (start date 9 January 2015).

For every captured rabbit, we recorded mass, ear length, hind foot length, gender and assigned species ID in the field based on pelage characteristics of individual cottontails. We obtained a small tissue

sample via a notch or ear punch in the right ear from each rabbit for later genetic confirmation of species ID. The Molecular Ecology Lab at the University of New Hampshire conducted all genetic analyses. DNA extracted from tissue samples was amplified at 16 microsatellite markers using multiplexed PCR to identify the species of captured individuals (Fenderson et al. 2011). We fitted cottontails with radio-collars (M1500 series transmitter, Advanced Telemetry Systems, Inc., Minnesota) equipped with 8-hour mortality sensors. In year 2, we used collars of the same make and model, except that transmitters were equipped with a four-hour mortality signal and a Precise Event Timer (PET) that began counting, in half hour increments, the time since the mortality signal on a collar was activated. The collar emitted this time data encoded in a pattern of binary beeps which we decrypted to produce an estimate of the date and time of individual mortality. All procedure were approved by Institutional Animal Care Committee in protocol A13-061.

Microhabitat Use

We quantified within-patch (hereafter referred to as “microhabitat”) daytime cover use by EC and NEC by directly homing to live cottontails and collecting data relating to choice of day-time refuge locations. We divided the winter field season into distinct sampling periods based on a combination of leaf and snow cover, so that cottontails were located repeatedly in: A) late fall (leaf-off, no snow), B) winter (leaf-off, snow cover present), and C) early spring (leaf-on, no snow) to represent the range of conditions that an individual might experience while selecting areas of refuge during the overwintering period. We collected microhabitat data using matched case-control design, which accounts for changing microhabitat conditions by pairing used and unused points (Cooper and Millspaugh 1999, Buskirk and Millspaugh 2006). Each paired used and available, unused point formed an individual strata, and thus the unit of analysis. Used points were assigned based on where collared cottontails were visually confirmed to location prior to flushing from cover. If a cottontail flushed before we obtained a visual, we could not confirm the used point and thus did not collect microhabitat data that day. We paired each used point with a single available, unused point defined as a point 15m from the used point in a random direction.

We navigated to these unused points immediately following collection of microhabitat data at used location and thus all data for each strata was collected within one hour. We selected the order in which we relocated cottontails at random each day, such that we located individuals at different times throughout the day over the course of the field season.

We collected data on 14 variables at each used and used point, including the presence or absence of snow cover and leaf cover, the type of cover object used, the species of cover object used if vegetation, the presence or absence of canopy cover, aerial concealment, maximum height of cover object (PVC pole marked in alternating 5cm bands), tally of coarse woody debris (CWD, woody stems >10cm), tally of fine woody debris (FWD, woody stems ≤ 10 cm), terrestrial concealment, air temperature 2m above the cover location, air temperature at ground level within cover (make and model pocket thermometer), wind speed 2m above cover using a handheld wind speed meter, and wind speed at ground level within cover (Table 2). We took concealment measures using a 30 cm x 30 cm board gridded with 3 cm x 3 cm squares. For aerial concealment, we placed the board in cover at the used point so gridded cells faced skyward. We used a camera mounted to the top of a 2m pole to take a photograph of the board through cover, and counted the number of grid cells that were $\geq 50\%$ visible. We subtracted this from a possible total of 100 for an estimate of percent aerial concealment (Camp et al. 2012, 2013). For terrestrial concealment, we placed the profile board within cover at the point of relocation, this time with grid cells faced outwards. Standing 1m away, we repeated the process of counting visible grid cells. We repeated this measurement at each of the four cardinal directions. After each value was subtracted from 100, we averaged concealment values across the four directions, producing an average percentage of terrestrial concealment for each point. We subtracted measurements of wind speed and air temperature at ground level from their counterpart at 2m height to create variables representing differences in environmental conditions outside of cover and within cover.

Microhabitat Analyses

We used Fisher's exact test to test the null of independence of two categorical variables. We repeated for comparisons of rabbit species versus cover object type and cover object species, snow cover presence/absence and cover object type and species, and leaf cover presence/absence and cover object type and species at used locations only. We also used this procedure to test for independence of cover object type and cover object species at used and randomly available locations. P-values for Fisher's tests were computed via Monte Carlo simulations with 2,000 replicates. We evaluated correlation among variables using the *corr.test* function in the *psych* package for R (Revelle 2015).

We used an information-theoretic approach to develop *a priori* candidate model sets that influenced our selection of measured microhabitat variables. We developed three sub-global models to test whether rabbit locations were based on features that offered cover from avian predators, features that offered cover from terrestrial predators, or features that minimized exposure to abiotic conditions associated with winter weather in our region (Table 2). We split sub-global models into sets of *a priori* candidate models featuring combinations of variables included in each sub-global model. We used conditional logistic regression to compare the microhabitat conditions stratified by paired used and available points. In using this model structure, we assume that used points are rare within the habitat, and paired points were unused by cottontails because we would have found cottontails at these locations while collecting microhabitat data given how close in time our visits to the two locations were (Keating and Cherry, 2004). We analyzed global, sub-global, and candidate models within a hypothesis group using the *clogit* function within the *Survival* package in R (Therneau 2015). We ranked our models and selected the best approximating model using the change in Akaike Information Criterion (ΔAIC) and Akaike weights (ω) using the *AICcmodavg* package in R (Mazerolle 2015). We performed the process of model ranking for NEC and EC data separately, to assess whether support for habitat selection models differed between the two species. We calculated model-averaged parameter estimates for the competing models (i.e., those within 2.1 AICc), as these competing models were from the same biological hypotheses in all cases. We then assessed the significance of an added interaction term between our reported model-averaged

parameters (i.e., those contained within competing models of habitat selection) and a binary variable for site-wide snow cover and leaf cover (i.e., leaf on or leaf off trees throughout the site). In this post-hoc analysis, we removed stratification terms and thus used logistic, rather than conditional-logistic regression to determine if habitat selection differed when snow cover was present or before/after leaf-out in the spring.

Survival Monitoring

During year 1, we relocated cottontails daily via triangulation from 4 October 2013 to 3 December 2013 and every three days from 4 December 2013 through 1 May 2014. During year 2, we relocated cottontails via triangulation once per week from their date of capture to their date of mortality or until the completion of the winter field season on 1 May 2015. After May, we reduced relocation frequency to once every other week, and continued relocations through the summer. When mortality signals were detected, we homed to individual cottontails for collar retrieval. Additionally, we recorded the emitted PET code for later decryption.

We used a handheld Yagi antenna and portable receiver for all radio telemetry (model R410 receiver, Advanced Telemetry Systems, Inc., Minnesota). If we detected a mortality signal, we located the collar via homing and assigned a cause of mortality to the individual rabbit where possible. We differentiated mortalities by major predator groups, categorizing mortality events as either avian or mammalian depending on visual characteristics of the carcass upon retrieval. We assigned avian cause of death if injuries included small puncture wounds (as one would expect from the impact of talons on the body, or from the beak of a raptor). We assigned predation events as mammalian if the carcass had significant damage. Where possible, we subset mammalian predation events into feline predation or canine predation. We classified mortality events as feline if the rabbit's pelt was separated from the carcass, and if an apparent effort was made to hide or cache the carcass. In canine predation events, we expected to observe no apparent effort to separate pelt from carcass, as well as no effort to cache the

carcass remains. When carcass was too degraded or had potentially been fed on by multiple predators, we left the classification of mortality as unknown.

Logistic Exposure Models of Survival

We used an information theoretic approach to evaluate support for proposed competing hypotheses regarding overwinter survival of cottontails. We created *a priori* hypotheses of factors we thought might contribute to elevated probabilities of mortality over the course of the winter, represented by one of three abiotic variables. We used average minimum temperatures endured within the interval to represent extreme cold events that might leave less fit individuals vulnerable to mortality. We used average maximum temperatures endured within the interval to represent warm winter days that might cause cottontails to forage more actively, thus exposing them to elevated predation risks. We used average wind speeds in meters per second within the interval to represent conditions that might best facilitate scent dispersal, causing cottontails in cover to be more easily found by foraging olfactory predators.

For each site, we measured patch size using ArcGIS and aerial satellite imagery. We monitored monthly levels of activity for three common mammalian predators of cottontails, coyote (*Canis latrans*), bobcat (*Lynx rufus*) and red fox (*vulpes vulpes*) using data collected from camera traps maintained at each site for the duration of the study. We collected data related to abiotic conditions from NOAA's National Climatic Data Center Climate Data Online.

We performed all survival analyses in SAS 9.4 (SAS Institute, 2014). Survival data was grouped in three-day intervals for rabbits captured in 2013, and one-day intervals for rabbits captured in 2014. Within each three day interval, an individual could be either alive, dead, or read as a right censored observation. Interval one in both years began on October 1. Individuals that were still alive on May 1 of the spring following their capture were censored in the analysis. We modelled daily and continuous rates of survival within the study period using PROC GLM in SAS 9.4 to construct logistic-exposure survival functions. This form of generalized linear models was introduced by Shaffer (2004) as an alternative to commonly used logistic regression functions to model nest success among birds. Logistic-exposure

models allow us to determine the influence of various factors on mortality, and allows for the inclusion of both constant and time-varying covariates. This model functions similarly to the logistic-regression model, and is composed of a binomial response distribution, the s-shaped logistic predictor function

$$s(x) = \frac{e^{\beta_0 + \beta_1 x}}{1 + e^{\beta_0 + \beta_1 x}}$$

and the link function

$$g(\theta) = \left[\frac{\theta^{\frac{1}{t}}}{1 - \theta^{\frac{1}{t}}} \right]$$

This link function allows us to account for the probability of surviving an interval depending on the length of the interval (Shaffer 2004). This model structure also allows the length of intervals to vary for different individuals, allowing us to incorporate survival data of the highest possible resolution for rabbits from each year.

Results

Trapping Effort

In year one, we captured 58 cottontails in 11,448 trap nights. Of these captured individuals, we collared 30 EC and 6 NEC after 11,448. In year two, we captured 14 cottontails (8 EC, 5 NEC) after 3,064 trap-nights at Nichols. Of these captures, we collared five EC and five NEC. We captured 14 EC and two NEC after 4,320 trap-nights at Bluff Point, and three EC and one NEC at Spignesi after 3,000 trap-nights at Spignesi. We collared one EC and one individual believed to be a NEC at Bluff Point. Later genetic analysis of collected tissue samples revealed our collared NEC to actually be an EC, thus we collared two EC at Bluff Point. We collared one NEC and one EC at Spignesi, in accordance with our protocol for maintaining a balanced sample of both species. We captured two EC after 1,280 trap nights at Pachaug, but collared no cottontails at this site, because no NEC were captured.

Use of Microhabitats

We used 40 readings across 20 cottontails to form the 40 strata used in subsequent microhabitat analyses (Table 1). We detected a lack of independence between cottontail species and used cover object species ($p = 0.03$), as well as a lack of independence between cover object species and whether a location was used or randomly available ($p = 0.0004$ for both comparisons) (Figure 1). We did not detect a lack of independence between cover object type and cottontail species, cover object type or species and snow presence/absence, or cover object type or species and leaf cover presence/absence (Table 2).

We removed measures of CWD from our candidate models, because used cottontail points and paired available locations did not contain any coarse woody debris (Table 3). The top ranking model for EC microhabitat selection fell under our terrestrial predation hypothesis group. This model contained a single parameter for terrestrial concealment (Table 4). The top ranking model for habitat selection in NEC fell under our avian predator hypothesis group, and contained a single parameter for the presence (1) or absence (0) of canopy cover (Table 4). Odds ratios from model-averaged estimates of these parameters indicated negative selection for canopy cover by NEC, and positive selection for terrestrial concealment by EC (Table 7). Candidate models that fell under our refuge from environmental conditions hypothesis consistently received the lowest ω values in the model ranking process (Table 4). The post-hoc analyses that included interaction terms with site-wide variables were not significant, indicating that habitat selection did not differ when snow cover was present or absent, or before or after leaf-out in the spring.

Logistic Exposure Models of Survival

We fit and ranked a set of candidate single-term models, exploring the effects of species, gender, mass at capture, and time (both as a linear and a quadratic effect), as well the abiotic variables featured in our *a priori* hypotheses of elevated mortality risk. Our top ranked model of survival probability included terms for a quadratic effect of time and an effect of gender (Table 8). The lowest daily probability of survival for males and females occurred at days 127 and 128, respectively, corresponding to early February

(Figure 2). Cumulative probability of survival from 1 October through 1 May as indicated by our parameter estimates was 0.70 for males and 0.50 for females (Table 9, Figure 3).

Discussion

New England cottontail occur sympatrically with the introduced eastern cottontail throughout the southern extent of the NEC range. Physiological traits of the Eastern cottontail lend support to the idea that EC are able to colonize lower-quality habitat while being overall less vulnerable to predation (Smith and Litvaitis 2000). We found that subtle differences in within-patch cover selection existed between the species, with NEC selecting for vertical and EC selecting for horizontal aspects of cover (Table 4). Our top ranked model of survival probability included quadratic effects of time, and an effect of gender, with female cottontails experiencing a 20 percent lower probability of surviving through the winter to 1 May than males (Table 8, Figure 3). Notably, both species favored concealment from predators over shelter from exposure to abiotic conditions (Table 4). Survival models featuring abiotic climate variables such as temperature or wind speed received minimal support in both our study of microhabitat selection and survival probability, leading us to conclude that these factors are not major drivers in overwintering ecology of cottontails in our study area.

New England Cottontail are an area-sensitive, obligate resident species of early-successional forest and shrubland habitat (Barbour and Litvaitis 1993, Litvaitis et al. 2003). Quantification of NEC habitat selection has largely been limited to the landscape or between-patch level, and is largely quantified by stem density. EC in our study used a broader diversity of species of vegetation as daytime cover objects than sympatric NEC within the same habitat patch (Figure 1). Species of vegetation used as cover objects by EC ranged from densely-growing multiflora rose (*Rosa multiflora*), to relatively sparse vegetative cover provided by fern growth in forest understory or grassy areas of open fields. While NEC also used dense vegetative growth for cover, we did not observe as great a diversity in the use of plant species by NEC (Figure 1). We provide evidence that, even at the microhabitat scale, EC use a wider variety of cover than NEC. Additionally, those species of vegetation used as cover by NEC were used less

frequently, or not at all, by sympatric EC (Figure 1), suggesting some partitioning of resources between the two species.

Patterns of habitat selection at a within-patch level may be more informative than those at the between-patch or landscape level when making patch-by-patch decisions for vegetation management. The majority of support in our models of NEC habitat selection fell within our hypothesis group of refuge from avian predators being the governing driver of habitat selection (Table 4). Odds-ratios for the two parameters contained within this hypothesis, canopy cover and aerial concealment, suggest negative selection for points where tree canopy is present overhead, and positive selection for points with increasingly high percentages of aerial concealment (Table 7). We highlight the need to study habitat use in NEC and EC at multiple spatial scales by pointing out that our top-ranked model of NEC cover selection is in direct contrast to the findings of Buffum *et. al* (2015). These authors found canopy cover to be a significant predictor of NEC patch occupancy, with NEC being more likely to occupy patches with greater percentages of overstory tree cover, and EC being more likely to occupy patches with less overstory tree cover (Buffum et al. 2015). Conversely, our results suggest that retention of seed trees within clear cuts may reduce desirable cover habitat within NEC-occupied patches. Lone-standing trees that provide canopy cover may also be optimal perches for foraging raptors, leaving cottontails in surrounding shrubby growth potentially vulnerable to predation, hence our observed trend in selection towards high levels of what we termed aerial concealment (Janes 1985). Where canopy cover is present, understory growth of the density required by cottontails may be limited (Litvaitis 2001). Detections of NEC in patches with > 50% canopy cover may also result from NEC being forced to occupy patches of marginal quality as they are excluded from more suitable habitat that is sympatrically occupied by EC. The majority of support in our models of EC habitat selection fell within our hypothesis that refuge from terrestrial predators was the driving force behind selection of cover. This hypothesis contained parameters for fine woody debris (FWD), maximum height of cover, and terrestrial concealment (Table 3). Odds-ratios from model-averaged parameter estimates suggest positive selection for locations of increasing

terrestrial concealment, positive to neutral selection for cover maximum height, and negative to neutral selection for FWD (Table 7). We conclude that not all dense vegetation is equally suitable habitat for NEC and that managers should consider both the vertical and horizontal structure of the cover objects provided for cottontails.

Our top ranked logistic exposure survival model indicated effects of gender on winter survival probabilities, with females experiencing a marked decrease in both daily and cumulative probabilities of survival when compared to males (Figure 2, 3). Estimates of winter cottontail survival are highly variable, with high estimates ranging from 70-84% in EC provided supplement cover and food, and low estimates often falling around 30% (Barbour and Litvaitis 1993, Weidman and Litvaitis 2011). Our estimate of cumulative probability of survival from October to May of 10.6% is comparatively low, but contributes to the theory that winter is a period of considerable mortality in cottontails. Estimates of survival collected within a short time frame can provide us with a snapshot of patterns of cottontail survival at a given place and time, but are likely subject to high variability. We were unable to detect differences in survival among the two species, but acknowledge that our sample size of NEC is small. Given the flexibility of our chosen logistic exposure models in handling mortality data collected over exposure intervals of varying lengths, cottontail survival data from multiple studies done at either a small spatial or temporal scales could be integrated to increase our power to detect effects of relevant covariates on survival probabilities.

Winter is suggested to be a period of particularly high cottontail mortality due to shortages in adequate food resources (Weidman and Litvaitis 2011). We detected a trend of decreasing daily survival probability from the start of our study in October through approximately early March (Figure 2), after which point daily survival probability increased through the end of our study period in May. If supplemental feeding is being discussed as a strategy for boosting cottontail survival, managers may consider timing their introduction of supplemental food resources when daily survival probabilities are at their lowest. Additionally, yearly patterns of daily survival probability may have some utility in informing

the timing of the release of captive-bred individuals into the wild. Our data suggests that captive-reared individuals be released following spring-time leaf out, otherwise resource availability in the early spring may be fairly limited.

Most management effort in conserving the NEC is focused on habitat alteration, improvement, and management, and current recommendation regarding desired habitat condition are likely to create suitable habitat for both NEC and EC. Literature focused on interactive dynamics between EC and NEC frequently theorize that EC have greater dispersal capabilities than NEC, and thus are able to colonize available habitat more rapidly and at greater distances than NEC. We note that timing, average distance, and age at which dispersal occurs in either species are either scarce or absent from current literature. Population genetic structure has revealed minimal connectivity between five relatively isolated NEC populations, and has increased our understanding of how linear features on the landscape such as road and utility corridors may act as both barriers and facilitators of cottontail dispersal (Fenderson et al. 2011, 2014). Prior to quantifying natal dispersal in pygmy rabbits (*Brachylagus idahoensis*), the assumption was that small body size and specific habitat requirements of the species would limit dispersal to very small distances (Estes-Zumpf and Rachlow 2009). However, radio-collared juveniles were observed making multi-kilometer dispersal movement (Estes-Zumpf and Rachlow 2009). Over two years of monitoring, three of our 38 radio-collared EC made movements off of the Nichols site property. Distances travelled by these individuals were approximately 2.85 km, 1.48 km, and 0.60 km. The former two individuals remained on air for 4 weeks and 6 weeks, respectively. Mortality for both individuals was due to predation. The latter individual is still alive (Oct 2015) and has remained in the same location following the initial dispersal event. Additional documented movements outside of habitat patches of capture are needed to understand dispersal from patches and colonization rates of newly created habitat patches.

Differences in life history traits and vital rates that would support the occurrence of competition between two similar species like the New England and Eastern are likely to be subtle, and require data on

key vital rates compared between both sympatric and allopatric populations. Studies of mortality at small spatial and temporal scales are likely influenced by the high variability in the survival of r-selected prey species, but may be integrated across space and time to be more informative. EC and NEC exhibit traits of habitat generalists and specialists (respectively) at both large and small spatial scales, a fact which should be considered when making decisions for habitat management. We found that cottontails are assessing the structure of cover habitat both vertically and horizontally, and cottontail species differ in the types of plants used for cover. We suggest that these assessments of cover may be useful when designing best management practices for patches undergoing management to create or maintain young forest habitat. Current best management practices encourage first and foremost the planting of native shrubs, which we suggest may provide adequate vertical cover but limited horizontal cover at ground level. Openings between areas of shrub growth may also be sufficient to allow predator access to otherwise densely vegetated habitat. Structures comprised of fine woody debris (here termed twig piles), provide adequate vertical and horizontal cover, and limit gaps available for foraging predators.

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Table 1. Summary of cottontails relocated in the 2014 field season and the number of strata (i.e., used and unused locations) where microhabitat measurements were collected.

ID	Species	Site	Contributed Strata
150.591	EC	Nichols	2
151.253	NEC	Nichols	1
151.383	NEC	Nichols	1
164.122	NEC	Spignesi	1
164.183	EC	Nichols	2
164.304	NEC	Nichols	3
164.325	NEC	Nichols	1
164.383	NEC	Nichols	1
164.424	EC	Nichols	3
164.584	EC	Nichols	1
164.624	NEC	Nichols	3
164.665	EC	Spignesi	1
164.681	EC	Bluff Point	1
164.723	EC	Nichols	1
150.343	EC	Nichols	3
150.481	EC	Nichols	3
150.591	EC	Nichols	1
151.253	NEC	Nichols	4
151.343	EC	Nichols	4
151.383	NEC	Nichols	3
			40

Table 2. P-values from Fisher's test for independence of two categorical values for comparisons of cover object type and species, and rabbit species, presence/absence of snow cover, and presence/absence of leaf cover. Significant relationships ($p < 0.05$) are in bold.

	Cottontail Species	Snow Cover	Leaf Cover
Cover Object Type	0.09	0.37	0.67
Cover Object Species	0.03	0.19	0.12

Table 3. 14 *a priori* models of cottontail habitat selection for daytime cover. Models were developed based on three sub-global hypotheses of factors driving within-site overwinter habitat selection by cottontails, including concealment from avian predators (i.e., avian pred. sub-global), concealment from terrestrial predators (i.e., terrestrial pred. sub-global), and refuge from harsh environmental conditions (i.e., abiotic exposure sub-global).

Model Name	Variables
Avian Pred. Sub-Global	canopy + aerial concealment
Avian Pred. 1	canopy
Avian Pred. 2	aerial concealment
Terrestrial Pred. Sub-Global	cover max. height + FWD + terrestrial concealment
Terrestrial Pred. 1	cover max. height
Terrestrial Pred. 2	FWD
Terrestrial Pred. 3	terrestrial concealment
Terrestrial Pred. 4	cover max. height + FWD
Terrestrial Pred. 5	cover max. height + terrestrial concealment
Terrestrial Pred. 6	FWD + terrestrial concealment
Abiotic Exposure Sub-Global	diff. airtemp + diff. windspeed
Abiotic Exposure 1	diff. airtemp
Abiotic Exposure 2	diff. windspeed
Global	canopy + aerial concealment + cover max. height + FWD + terrestrial concealment + diff. airtemp + diff. windspeed

Table 4. Ranking of conditional logistic regression models based on $\Delta AICc$ and ω to test alternative hypotheses of cottontail selection of overwinter daytime cover locations. Model ranking occurred separately for the two cottontail species.

NEC				
Model	K	AICc	$\Delta AICc$	ω
Avian Pred. 1	1	7.07	0	0.54
Avian Pred. Sub-Global	2	8.44	1.37	0.27
Terrestrial Pred. 3	1	10.78	3.71	0.09
Terrestrial Pred. 5	2	12.75	5.68	0.03
Terrestrial Pred. 2	1	13.33	6.26	0.02
Terrestrial Pred. Sub-Global	3	14.05	6.98	0.02
Terrestrial Pred. 4	2	15.45	8.38	0.01
Terrestrial Pred. 1	1	15.64	8.57	0.01
Avian Pred. 2	1	16.1	9.03	0.01
Global	7	18.15	11.08	0
Abiotic Exposure 1	1	24.12	17.05	0
Abiotic Exposure Sub-Global	2	26.36	19.29	0
Abiotic Exposure 2	1	26.98	19.91	0
EC				
Terrestrial Pred. 3	1	10.19	0.00	0.46
Terrestrial Pred. 5	2	10.77	0.58	0.35
Terrestrial Pred. Sub-Global	3	12.25	2.06	0.17
Avian Pred. Sub-Global	7	17.11	6.92	0.01
Global	2	20.37	10.18	0.00
Avian Pred. 1	1	20.68	10.49	0.00
Terrestrial Pred. 1	1	22.07	11.88	0.00
Terrestrial Pred. 4	2	23.84	13.65	0.00
Terrestrial Pred. 2	1	24.21	14.02	0.00
Avian Pred. 2	1	30.24	20.05	0.00
Abiotic Exposure 2	1	30.76	20.57	0.00
Abiotic Exposure 1	1	31.38	21.19	0.00
Abiotic Exposure Sub-Global	2	32.40	22.21	0.00

Table 5. Parameter estimates for single-variable logistic models featuring terms contained within competing models of NEC and EC habitat selection. We tested for significant interactions with conditions that occurred at the site level. Snow represents the presence, or alternatively the absence, of site-wide snow cover. Leaf represents data collected in either the leaf-on or leaf-off period of the study season.

Variable	Coeff.	SE	Z	P-value
Canopy	-2.11	0.59	-3.60	0.003
Snow	-0.64	0.76	-0.84	0.40
Canopy x Snow	1.60	1.17	1.36	0.17
Canopy	-1.70	0.80	-2.13	0.03
Leaf	-0.58	1.22	-0.47	0.64
Canopy x Leaf	-0.2	1.64	-0.001	0.99
Aerial Concealment	0.05	0.01	4.42	0.00001
Snow	-2.01	3.11	-0.64	0.52
Aerial Concealment x Snow	0.03	0.04	0.70	0.48
Aerial Concealment	0.08	2.0	-2.32	0.02
Leaf	2.34	2.14	1.10	0.27
Aerial Concealment x Leaf	-0.04	0.03	-1.43	0.15
Terrestrial Concealment	0.05	0.02	3.34	0.0008
Snow	-0.001	2.56	0.00	0.99
Terrestrial Concealment x Snow	0.03	0.04	0.68	0.50
Terrestrial Concealment	0.10	0.03	2.85	0.004
Leaf	-2.66	3.60	-0.74	0.46
Terrestrial Concealment x Leaf	-0.01	0.05	-0.28	0.78
Maximum Height	1.75	0.49	3.58	0.0003
Snow	-3.41	3.57	-0.01	0.99
Maximum Height x Snow	1.73	1.78	0.01	0.99
Maximum Height	0.02	0.01	2.82	0.004
Leaf	-0.20	0.96	-0.21	0.84
Maximum Height x Leaf	0.01	0.01	0.55	0.58
FWD	0.11	0.03	3.40	0.001
Snow	-0.01	0.91	-0.02	0.99
FWD x Snow	-0.02	0.06	-0.27	0.79
FWD	0.10	0.04	2.30	0.02
Leaf	-0.16	0.75	-0.21	0.84
FWD x Leaf	0.02	0.06	0.27	0.79

Table 6. Model-averaged parameter estimates for all parameters contained within competing models for New England and Eastern Cottontail habitat selection.

NEC				
Variable	Coeff.	SE	CI	Odds Ratio
Canopy	-2.36	2.82	(-7.9, 3.17)	0.09
Aerial Concealment	0.05	0.03	(0, 0.11)	1.05
EC				
T. Concealment	0.33	0.25	(-0.16, 0.82)	1.39
FWD	-0.08	0.11	(-0.29, 0.13)	0.92
Max. Height	0.08	0.09	(-0.1, 0.25)	1.08

Table 7. Ranking of logistic exposure models based on $\Delta AICc$ and ω to test alternative hypotheses of cottontail survival/mortality.

Model	k	AICc	$\Delta AICc$	ω
Time + Time ² + Gender	4	268.68	0.00	0.64
Time + Time ² + Mass	4	271.15	2.48	0.19
Global	10	272.45	3.77	0.10
Time + Time ² + Interval Avg. Windspeed	4	274.20	5.52	0.04
Time + Time ²	3	277.53	8.85	0.01
Time + Time ² + Interval Avg. Min. Temp.	4	277.59	8.91	0.01
Time + Time ² + Interval Avg. Max. Temp.	4	278.12	9.44	0.01
Time + Time ² + Year	4	278.57	9.89	0.00
Time + Time ² + Species	4	279.12	10.44	0.00
Time	2	285.37	16.69	0.00
Null Model	1	292.17	23.49	0.00

Table 8. Parameter estimates for the top ranked model in our survival analyses, with parameters for time, time², and gender.

Variable	Estimate	SE	Wald X ²	P-value	95% Confidence Interval	
					Lower	Upper
Intercept	9.83	1.68	34.29	<0.001	7.05	13.71
Time	-0.08	0.03	7.8	0.005	-0.14	-0.03
Time ²	0.0003	0.001	6.19	0.01	0.001	0.005
Gender (Male)	0.6232	0.39	2.48	0.11	-0.15	1.42

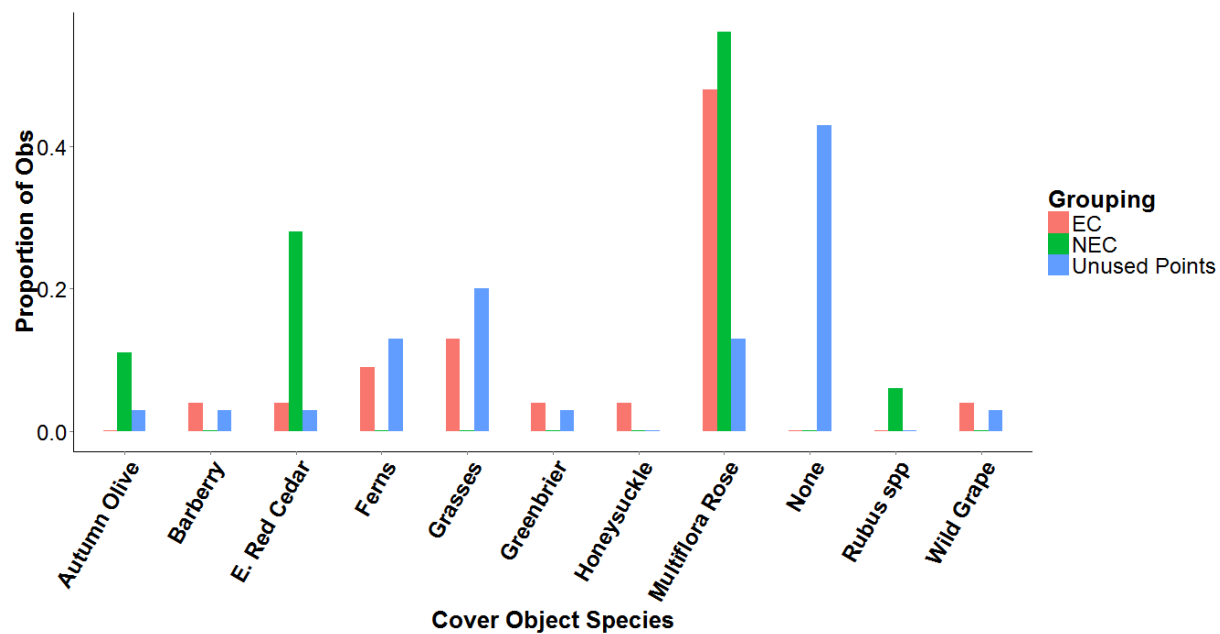


Figure 1. Proportion of observations for use of cover object species, grouped by available locations, known EC locations, and known NEC locations.

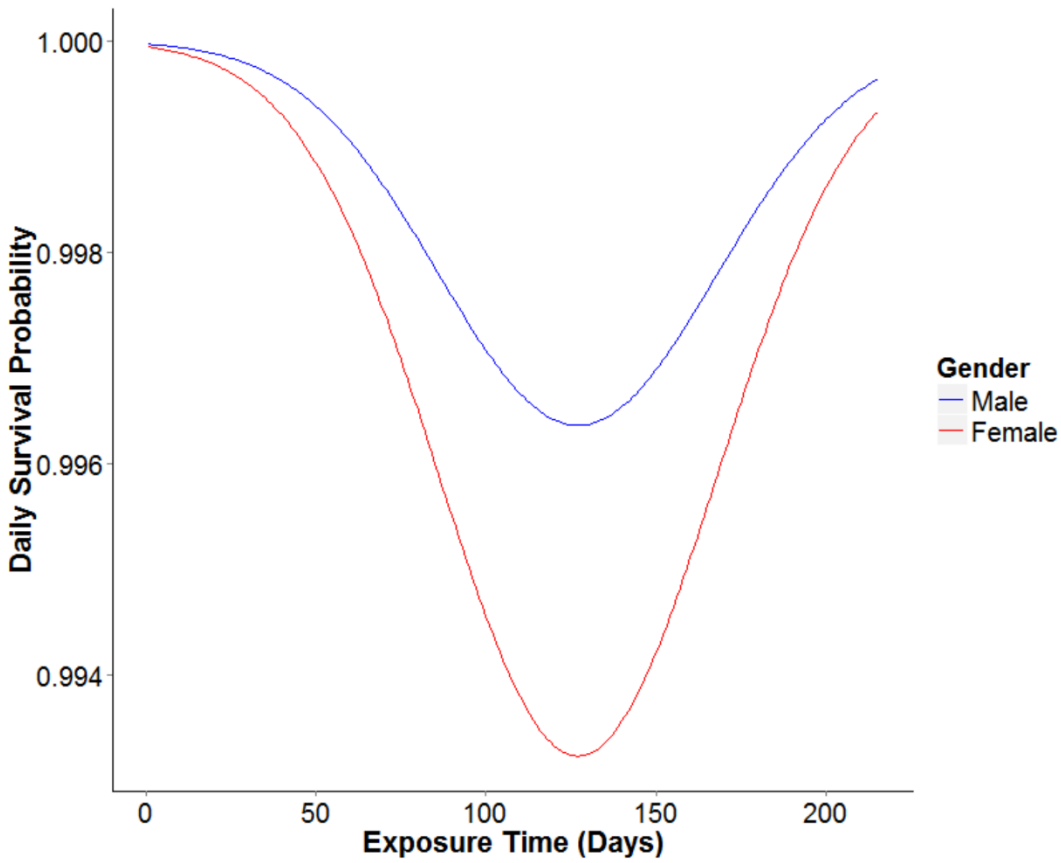


Figure 2. Daily probabilities of male and female cottontail survival using parameter estimates from our top ranked model with terms for time, time², and gender, where day 0 is 1 October. The curve is terminated at day 212, or 1 May, to depict daily survival probabilities during the winter.

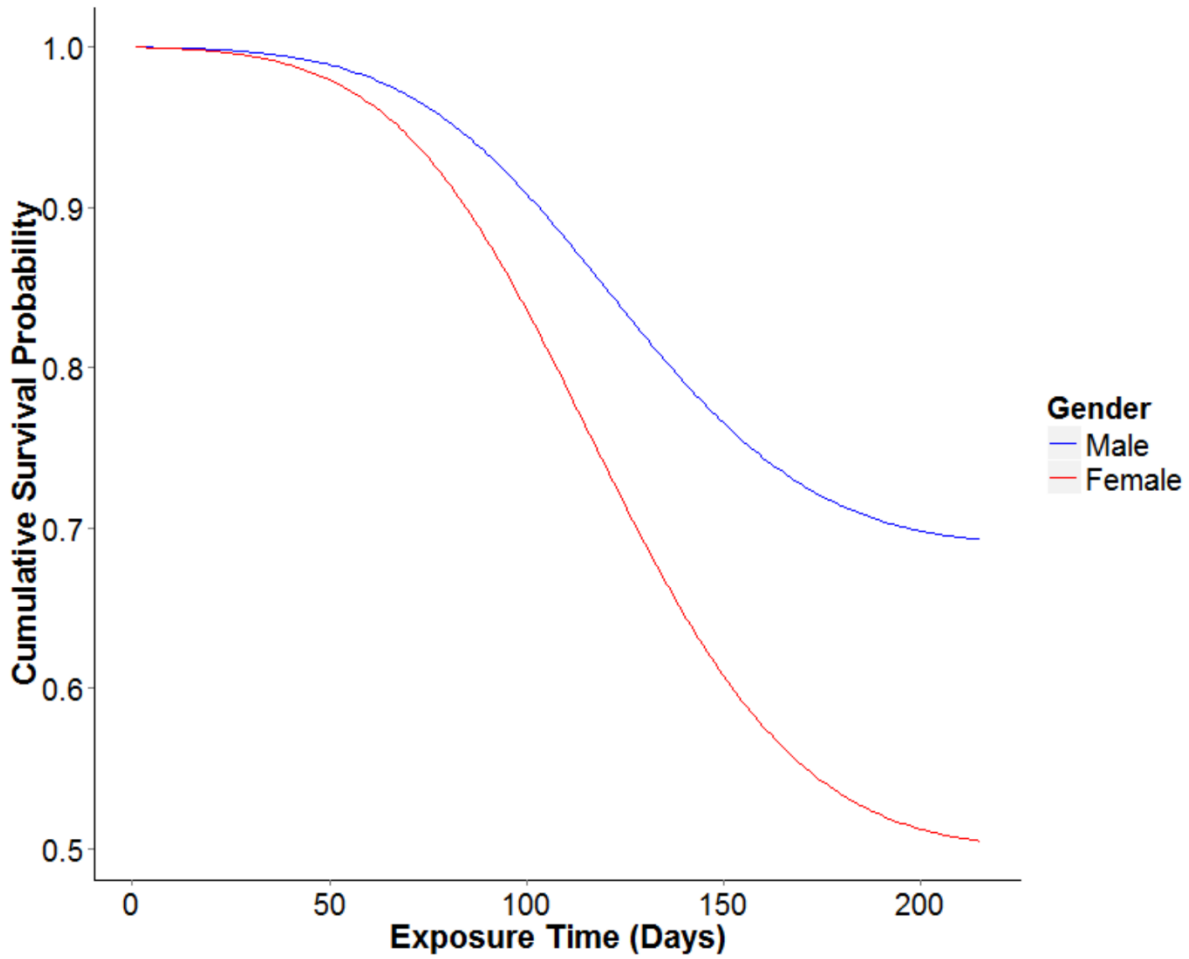


Figure 3. Cumulative probabilities of male and female cottontail survival using parameter estimates from our top ranked model with terms for time, time², and gender, where day 0 is 1 October. The curve is terminated at day 212, or 1 May, to depict daily survival probabilities during the winter.

Daily activity levels of wildlife in patches of early successional and mature forest habitat in eastern Connecticut

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Abstract:

Combining our knowledge of how wildlife behave across space and time broadens our understanding of patterns of resource use. Patterns of activity may be shaped by major disturbances in an ecosystem, seasonal shifts in abundances of resources, or habitat preferences. Camera trap photographs can be used to quantify activity patterns in wildlife. Our study, based in southern New England, focused on changes in activity patterns of common mammal species based on habitat type, specifically early successional (ES) and mature hardwood (MH) forest patches. Our goals were to quantify how daily activity patterns of mammals common to southern New England differed between our focal habitat types, and to quantify how activity patterns changed seasonally over the course of the year. For species with sufficient observations, activity patterns did not differ significantly between adjacent ES and MH habitat patches. Daily cottontail (*Sylvilagus* spp.) activity was greatest in the fall and winter, but we did not detect shifts in daily levels of activity among seasons for all other species. With sufficient data, these methods could be expanded to address questions of how activity patterns may change when compared across an interaction of seasons and habitats, as well as how patterns of activity change in the context of the broader surrounding landscape.

Introduction

In managing and conserving wildlife populations, much of our effort is often directed at answering where an animal or a group of animals are located on the landscape as expressed through the quantification of home range, movement, and space-use (Kernohan et al. 1998, Blundell et al. 2001, Matthiopoulos 2003). By connecting space-use to available resources, we attempt to better understand species presence and movement across a larger landscape (Johnson 1980, Arthur et al. 1996, Boyce and McDonald 1999, Lele et al. 2013). Species occurrence and utilization of resources at a temporal scale should be considered equally necessary in understanding how best to manage wildlife populations. Furthermore, the amount and distribution of time an individual or species spends active in its surrounding environment is an important metric critical to understanding physiology (Schmidt-Nielsen 1997), foraging ecology and energy expenditure (Kronfeld-Schor and Dayan 2003), and exposure to risk (Skelly 1994). Changes in patterns of activity may result as a response to major disturbances in an ecosystem, shifts in abundances of prey or predator species, or human alterations of habitats.

Seasonal shifts in activity levels of mammals in temperate environments are often dictated by resource availability and demands placed on individuals by changing environmental conditions. Annual changes in temperature and availability of daylight may alter overall activity levels, or may shift peaks in daily activity, particularly in grazing species whose foraging patterns follow the 24 hour clock (Sparrowe and Springer 1970, Green and Bear 1990, Street et al. 2015). Prey species may have to compromise between maximizing foraging time and minimizing exposure to predators (Lee et al. 2010). Seasonal scarcity in prey or access to prey may similarly affect predator activity patterns (Koehler and Hornocker 1991, Messier et al. 1992). Peaks in daily activity may occur in habitat types that provide access to key resources. (Collins et al. 1978, Street et al. 2015). Where animals choose to spend more time, or where peaks in animal activity occur, help to further support our knowledge of resource use and habitat preference. Activity patterns may also interact with changes in habitat, changes in community composition, and anthropogenic disturbances.

While daily patterns in wildlife activity are often tied to sunlight, many species exhibit plasticity in activity levels resulting from shifts in overall community dynamics. The introduction of predators where they were previously absent can have meaningful impacts on patterns of activity in their prey. The removal of pressures imposed by predators or humans in a system may also alter patterns of diel activity (Loe et al. 2007). Increased use of wildlife habitat by humans has the potential to be a prominent driver in shifts in wildlife activity, and often leads to increased nocturnal activity to reduce interactions with humans. Studies of bobcat (*Lynx rufus*), coyote (*Canis latrans*), mountain lion (*Felis concolor*), and black bear (*Ursus americanus*) around the U.S. have noted increasingly nocturnal behavior in areas coinciding with heavy use by humans (Van Dyke et al. 1986, Bridges et al. 2004, George and Crooks 2006, Wang et al. 2015). While these scenarios occur in areas of moderate human activity, particularly extreme examples of wildlife modifying their activity patterns to avoid interactions with humans have been observed in major urban centers (McClennen et al. 2001, Tigas et al. 2002, Riley et al. 2003, Ditchkoff et al. 2006). Opposite shifts in activity patterns may occur following the removal of human pressures from a system, as was observed in coyote in Colorado, where activity increased during daylight hours following the end of a period of intense human persecution (Kitchen et al. 2011). Where humans and wildlife co-occur, knowledge about overlap in diel activity may help to inform how to manage potential instances of conflict between the two.

Researchers seeking to quantify activity patterns have historically focused on the ecology of a single species. Using radio-transmitter collars to quantify activity patterns limits researchers to only a handful of individuals (Gervasi et al. 2006, Kays et al. 2011). Researchers may also quantify activity via direct observation, in which case sample size and diversity of species studied is still limited (Parker et al. 2014). Coyote, bobcat, raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), and cottontails (*Sylvilagus* spp.) make up a group of small and medium-sized mammals that occur sympatrically throughout their respective ranges. We are therefore able to study patterns of activity in all of the above species simultaneously, giving us greater

insight into activity patterns within this group of species as a whole (Lesmeister et al. 2015). Our goal for this study was to use camera trap data to explore patterns of activity in mammal species common to southern New England. We sought to estimate daily activity levels for mammals readily detected with wildlife cameras. Given that humans and human development is omnipresent across the Connecticut landscape, we were particularly interested in quantifying daytime activity to determine if mammals limit daytime activity even within the natural areas we sampled. We also sought to quantify changes in mammalian activity levels between early successional (ES) and mature hardwood forest (MH) habitats, and to quantify changes in mammalian activity levels among seasons. We predicted that seasonal activity patterns of herbivores (e.g., deer, squirrel, cottontails) would be increased in fall and winter compared to spring and summer, as these time periods may require increased foraging effort, either to prepare for harsh winter conditions or to compensate for the limited food resources present in the winter. Conversely, we predicted that carnivores (e.g., bobcat) that are active year round would have similar activity levels among seasons. Although many of the species that we expected to detect can be considered generalist species, we predicted that activity in early successional habitat patches would be elevated when compared to mature hardwood patches, as ES habitats represent areas of plentiful food resources that may also offer herbivores increased cover to forage longer into daylight hours.

Methods

Study Sites

We deployed wildlife cameras across four sites that were simultaneously being live-trapped as part of an ongoing study on overwintering mortality in cottontails (*Sylvilagus spp.*) (Figure 1). All four sites were located in southeastern CT, and fall within the boundaries of focal areas identified in the regional New England Cottontail Conservation Plan. All four sites also contained a mixture of young forest/shrubland habitat, and mature upland forest habitat. Details on our four study sites are as follows:

Nichols Property (Nichols): This site is privately owned land in Stonington, CT. This site consists of approximately 40 acres of young forest/shrub habitat that directly abutted 60 acres of farmland used for

the grazing of cattle. The ES habitat is regeneration from what was previously also farmland. Remnant game trails can be found throughout dense areas of vegetation, but extensive vegetative cover largely excludes cattle from the study area. The site is bounded by a major interstate (I-95), and also abuts a neighboring land trust, which contains the mature hardwood that we sampled and open fields managed for grassland bird species.

Pachaug State Forest (Pachaug): While the entirety of Pachaug State Forest accounts for approximately 24,000 acres of land in eastern Connecticut (CT), cameras were deployed on 60 acres of state forest property in North Stonington CT off of Wyassup Road. Management for the creation of early successional habitat is ongoing on and around this property as part of the regional New England Cottontail Conservation Management Plan. Invasive species control has occurred in this area in the past. This site is bounded by relatively continuous forest cover.

Bluff Point State Park (Bluff Point): Bluff Point is approximately 800 acres in total, and is located in Groton, CT. Much of these 800 acres is scattered mature hardwood trees with areas of dense understory growth. The outer edge of the park is largely tidal shrubland habitat. The park supports heavy recreational use, except in areas isolated via dense vegetation in early successional growth.

James Spignesi Wildlife Management Area (Spignesi): Spignesi is a 469 acre wildlife management area in Scotland, CT maintained as a mix of upland hardwood forest, open field, and early successional habitat. Vegetation regenerating from previous timber harvests also receives invasive plant control, thus limiting the presence of common invasive shrubs such as Japanese barberry and multiflora rose.

Field Methods

We deployed a total of 40 wildlife cameras (Trophy Cam HD Essential, Bushnell, Kansas) across our four study sites from November 2014 through November 2015 (Figure 1). All cameras took three photos upon activation, with a latency period of one minute before the next set of photos was taken. We set 10 cameras per site, divided between two study areas. For each site, we defined the study area a 1 ha square within each of the two targeted habitat types using ArcMap 10.1 (Esri, California), and thus we set five cameras

in early successional forest/shrub habitat, and five cameras in mature hardwood forest. We generated 5 sets of random coordinates to guide camera placement. We navigated to these coordinates in the field, and placed cameras at knee height, faced so they were not obstructed by large objects or dense vegetation. We visited cameras once a month to exchange data cards and batteries.

Data Structure and Quantification of Activity Patterns

We quantified latency to initial detection (LTD) as the number of trap-nights before a species was first detected at a camera trap (Gompper et al. 2006). We calculated this metric by pooling data across all cameras at all sites where a species was detected. We organized data collected from each camera into observations. Observations began when a camera was triggered by an individual or group of individuals, and ended when a new individual or group of individuals triggered the camera. We mandated that at least 30 minutes had to pass between two sets of photographs before a set of photos was considered a new observation to ensure our observations were sufficiently independent from one another (i.e. one individual was not counted as multiple observations). Our protocol was the same protocol for ensuring independence of camera detections followed in previous camera-trapping studies (Kelly 2003, Silver et al. 2004, Kelly and Holub 2008, Wang et al. 2015). We applied this stipulation across all observations from cameras within each five-camera habitat array at each site, given that the distance between cameras within an array was easily traversable within a 30-minute window for the mammals we expected to detect. Each observation contained the following information: 1) Date and time of observation, 2) species observed (more than one species could be contained within a single observation, 3) quantity of individuals of a species observed, 4) temperature at the time the observation was recorded (temperature was collected by our cameras), and 5) number of images contained within the observation.

We used both the *activity* and the *overlap* packages in R to fit kernel density functions to time series data collected for each species (Ridout and Linkie 2009, Rowcliffe et al. 2014). Prior to analyses, we converted all 24-hour time data into radial time, following the steps outlined in the Activity reference manual (Rowcliffe 2015). We used the *activity* package to fit kernel density functions and estimate

overall daily activity for detected species across all sites and within all habitats. We followed guidelines for the inclusion of at least 30 observations per individual (or in our case, per species) for fitting univariate kernel density estimates, and did not fit activity estimates for species that fell below this observation threshold (Vokoun 2003). Pooling observations across sites, we then divided species observations by habitat type (either ES or MH), and produced estimates of daily activity for each species within one of two habitat types. We achieved seasonal estimates of species activity by pooling observations across habitats and sites, then splitting these observations into three-month long seasonal intervals (i.e., spring, summer, fall, and winter). We tested for statistical differences in daily activity estimates using the *compareAct* function provided by the *activity* package. The Institutional of Animal Care and Use Committee exempted this research from further review (E15-003).

Estimation of Detection Probability

We fit simple single-species models of occupancy to our detection/non-detection data to achieve estimates of detection probability that could be compared to observed latency to detection. We broke the year-long sampling period into week-long survey periods, within which a species could be either detected or undetected at each of our four sites. We ran occupancy models with probability of occupancy and detection as fixed terms using the *unmarked* package for R.

Results

Number of independent observations per camera ranged from 15-501 (Table 1). We recorded a total of 4,661 individual observations from November 2014-November 2015 (Table 2). We detected 16 species over the course of the study. Sixty-three point five percent of observations occurred in early successional/young forest habitat. 29% of observations occurred in spring (March-May), 19% in summer (June-August), 20% in fall (September-November), and 32% in winter (December-February). White-tailed deer (*Odocoileus virginianus*) was the first species detected, with an average LTD of only 2.8 days (Table 2). Domestic cat took the longest to detect of any observed species, with zero detections in the first eight months of the study. Detection probabilities ranged from 0.06 for fisher to 0.98 for deer (Table 2).

We fit daily activity estimates for seven mammal species that are common across the northeastern US: White-tailed deer, Eastern gray squirrel (*Sciurus carolinensis*), raccoon, cottontail, Virginia opossum, coyote, and bobcat. Gray squirrel had the lowest overall activity estimate with approximately 33% (± 0.02) of the day spent active and bobcat had the highest activity estimate with approximately 67% (± 0.10) of the day spent active (Figure 2).

Of the seven species listed above, we fit activity estimates in ES and MH habitat for squirrel, deer, raccoon, and coyote. Activity estimates did not differ significantly between habitat types for any of the four species where we fit this comparison (Table 3). We tested for seasonal differences in activity among deer, coyote, squirrel, raccoon, and cottontail. With the exception of cottontails, which were significantly more active in fall and winter than in spring and summer, we detected no seasonal differences in daily activity estimates among any of our five tested species (Table 4).

Discussion

Mammals generally showed more minimal shifts in seasonal activity patterns than we expected. For all observed species, we had greater numbers of detections in early successional habitat patches compared to mature forest patches. We detected no significant differences in daily activity levels in species utilizing both ES and MH habitat patches. Seasonal differences in overall daily activity estimates were absent for all species tested across all seasons, except for the comparison of winter and fall activity next to summer and spring cottontail activity. Activity patterns (i.e., where peaks in daily activity occurred) remained relatively similar for all species across all seasons. Activity levels within a day varied species, with squirrel being the least active and bobcat being the most active within a day. We discuss our findings in relation to prior knowledge of behavior and activity in our focal species, and discuss implications of these findings in regards to seasonal and habitat-driven activity patterns.

Seasonal Differences in Activity

Our estimates of daily activity in cottontails was greater in fall and winter (the two seasons were not significantly different from one another), than the estimates for spring and summer activity (Table 4).

This peak in activity later in the year may represent increased foraging effort in a time of food scarcity. European hares (*Oryctolagus cuniculus*) exhibited the most daytime activity in January, as well as the greatest peak in nighttime activity during the winter months (Villafuerte et al. 1993). Roadside activity of Eastern cottontails (*Sylvilagus floridanus*) surveyed from a vehicle was twice as intense during the winter months than during the summer (Lord 1961). Cottontails were the only species that followed our prediction of elevated winter activity as a potential response to limited food resources. As is typical of known cottontail behavior, we observed peaks in activity corresponding to dawn and dusk (Figure 4). In addition, we observed a prolonged period of activity through the nighttime hours. We observed little to no daytime activity in cottontails during winter months, suggesting that these patterns are not a result of cottontails limiting activity during periods of extremely low temperatures that might be associated with nighttime and early morning hours. Our only observed occurrences of daytime activity in cottontails occurred in the summer months, which we suggest may be due to the dense visual obstruction provided by vegetative cover during these months, allowing cottontails to forage during daylight hours with fewer chances of encountering foraging predators.

We were surprised to detect no seasonal differences in levels or patterns of activity for any other species (Table 4, Figure 4). White-tailed deer are known to reduce metabolic rates and overall activity levels as a response to cold temperatures and decreased availability of food resources during the winter (Moen 1978, Beier and McCullough 1990). Conversely, a study of South Dakota white-tailed deer reported high rates of movement in the winter, attributed to elevated hunting pressures (Sparrowe and Springer 1970). White-tailed deer in our study were neither more nor less active among seasons, suggesting that the climate in our study region may be mild enough that winter temperatures and food availability are not limiting factors in daily activity levels. We experienced temperatures below freezing and snow accumulation throughout the 2014–2015 season, but given our proximity to the Long Island Sound our winters are overall milder than those experiences at more northerly latitudes. A pattern of no

differences in activity levels from season to season held true for coyote, raccoon, and Eastern gray squirrel.

Finally, biologically significant phenomena may not be accurately represented in our statistical tests of significance (Johnson 1999). For example, when examining our estimates of seasonal activity levels across multiple species of wildlife, small differences in percentage of a day spent active may have significant implications on the state and health of habitats being inhabited by these species. White-tailed deer exist at high abundances throughout New England, and have the potential to alter the structure and health of forest ecosystems through prolonged browse pressure (Rooney and Waller 2003, Côté et al. 2004). Although not marked as statistically significant, white-tailed deer in our study areas were highly active during spring months. This elevated time of deer activity may correspond to increased browse pressure in the spring, a time when vegetation is just beginning to grow. Similarly, coyote in our study areas were most active during the winter months. Coyote spending more time actively foraging may translate to elevated risks of predation among focal prey populations.

Observed Differences between Early Successional and Mature Hardwood Habitats

Virtually all of our observed species were detected more frequently in ES patches than in MH patches. As one would expect, cottontail, which are obligates of early successional habitats (Barbour and Litvaitis 1993, Brown 1995, Litvaitis 2001, Litvaitis et al. 2003, 2006), were detected exclusively at cameras placed in ES patches of forest. Other than cottontails, the majority of our detected species are considered to be habitat generalists, leading us to expect equal detections between the two focal habitat types. Despite more numerous observations in ES habitat across all species, we detected no differences in daily activity estimates between ES and MH habitats for four species (Table 3, Figure 3). The dense cover provided by early successional habitats did not result in any species spending a significantly greater time active in these habitats. Cottontails, the most obvious choice for a habitat specialist among our detected species, was virtually never detected in mature forest habitat, making this comparison redundant.

Success in Species Detection

Low camera-trap success is typically reported for large mammalian carnivores with the ability to travel large distances in a day, and fast-moving, small-bodied animals (Kelly and Holub 2008). We experienced similarly low detection of Virginia opossum and red fox to Kelly and Holub (2008), but did not experience their reported low detections of cottontails and coyote. Previous studies estimate approximately 1,000 camera-trap nights to ensure that a species is or is not present in an area (Carbone et al. 2001). With 11,600 total trap nights, we are therefore confident that we detected the presence of most species in the region. Virtually all of our failed identifications, termed “unknowns”, occurred when image quality was poor, or the species was moving too rapidly to see clearly. Most importantly, within one year of sampling, we achieved detections of the majority of those mammal species that we would expect to occur in this region within our focal habitats. We did not detect Red Squirrel (*Tamiasciurus hudsonicus*), which we attribute to this species’ association with coniferous forest stands, which were either very limited or completely absent from our study sites (Haughland and Larsen 2004). Moose (*Alces alces*) and American black bear occur in Connecticut, but are primarily found in the northwestern corner of the state (Wattles and DeStefano 2011, Evans et al. 2014). Gray fox were not observed within the study period, although our study area is within their species range. All of our red fox observations occurred around dawn or dusk, allowing us to obtain color images from which we could use coat color and markings to prevent the mis-identification of Gray Foxes as Red Foxes. Baited camera traps, which are used frequently to increase detections of mammalian carnivores, may have improved our ability to detect species such as fisher, bobcat, fox, skunk, and Virginia opossum. We chose not to bait cameras to avoid potential biases that can occur when additional food source caused nearby individuals to shift activity patterns (Rowcliffe et al. 2014) and to prevent the possibility that bait would attract an individual from one study area into the paired study area within a site.

Surprisingly, perhaps most notably lacking in our data was the presence of domestic cats. Free-ranging domestic cats (*Felis catus*) have been introduced to natural systems globally, and have become a serious issue in conservation due to their impacts as predators of reptiles, birds, and small mammals (Loss

et al. 2013). In a survey of protected and urban areas in the southeastern U.S., the presence of coyote seemed to be limiting the colonization of protected areas by free-roaming cats (Kays et al. 2015). Land use in southern New England is largely urban, suburban, or exurban, and lacks the large rural or protected areas that are present in the southeastern US (Brown et al. 2005, Hansen et al. 2013). Similarly, domestic cats were detected at only one site being monitored by camera traps in the Midwestern US, the only site where coyote were not reported to be present (Cove et al. 2012). The extremely low frequency of cat observations prevents us from drawing any conclusions regarding overlaps or dissimilarities in coyote and cat activity patterns, however, with only one domestic cat observed over the course of the survey, we suggest that predator activity is substantial enough in our small patches of forests to exclude populations of free-ranging cats.

When placing cameras, we made a conscious effort to avoid biasing placement towards apparent game trails in both habitat types, assuming this placement may have an impact on our estimates if animals used trails non-randomly across a 24 hour period (Rowcliffe et al. 2014). We also maintained cameras low to the ground throughout the season to avoid the potential of missing small-bodied animals that might pass under a camera set higher up a tree. Greater detections in ES patches may be the result of dense vegetation directing animal movement or making movement more predictable (Heilbrun et al. 2006). We had initial concerns that detections in ES patches would be low, given the potential for obstruction by characteristically dense vegetation. However, we had little difficulty distinguishing and detecting species moving through dense vegetation, even in the spring and summer when leaf cover was particularly dense in these patches. This NOUN was true even for small rodents and passerine birds, which were detected throughout all seasons.

Daily Levels of Activity

Our study represents the first quantified estimate of daily activity for many of our detected species in over a decade in our region, with the added benefits of greatly increased sample sizes and monitoring throughout all seasons. Where published estimates are available, we see at least some similarities between

our estimates and those derived from telemetry-based studies or direct observations. One reported estimate for eastern gray squirrel falls slightly below our own estimate at 23.1–25.9% of the day spent active, but was derived from urban squirrel populations, and may reflect the influence of human activity on foraging behavior in wildlife (Parker et al. 2014). References of activity patterns in raccoon, another species we observed frequently, refer mainly to the time of day where activity occurs, namely sunset to sunrise (Glueck et al. 1988, Ladine 1997). Our estimate of daily coyote activity corresponds well to estimates of coyote activity on Cape Cod, MA, relatively close to our own study sites (Way et al. 2004). Way et al. (2004) report their focal individuals spending from 48–56% of the day active, compared to our estimate range of 38–67%. A telemetry study of bobcat activity in California reported focal animals spending from 30–50% of the day active with limited daytime activity, falling within our estimate range of 37–72% (Tigas et al. 2002). Estimates of activity for coyote and bobcat were notably lower than our own in a camera-trap study of a similar design in California (23.16% and 31.83%, respectively) (George and Crooks 2006). The study was conducted in areas used for human recreation, and may reflect changes in patterns of wildlife activity when humans are frequently present.

Much of southern New England can be considered neither highly urbanized, nor truly rural, but is rather an intermediate of the two. Much of Connecticut is classified as exurban, where housing and development is intermixed with forest cover (Theobald 2010). As such, we note that although none of our study sites could be considered isolated from human influence, we did not observe patterns of activity in multiple wildlife species that we might expect from wildlife exhibiting human avoidance behaviors, namely a tendency towards mostly nocturnal activity (Ditchkoff et al. 2006). Both coyote and bobcat, two common mammalian predators in our study area, were detected fairly readily during daylight hours, with bobcat spending up to 72% of the day actively moving about the landscape (Table 2, Figure 2). Three of our four study sites lacked well-established human trail systems and our 1 ha study sites were placed away from any trails known to contain high human activity.

Management Implications

Creation of early successional habitat in New England is limited due to private ownership of small parcel sizes. Our results support the notion that early successional habitats are a valuable component of the landscape, because a wide variety of mammalian species occur in patches of early successional habitats throughout the year. Our results also indicate the domestic cats are not a conservation concern on these sites.

Our methods and study design could be applicable in many other management contexts. Estimates of daily human activity on a site by site basis may be a useful metric for managers wishing to understand potential interactions between wildlife and humans in a landscape that is neither rural nor urban. Targeted seasonally, these techniques could readily be applied to understanding how hunting pressure affects temporal trends in wildlife resource use. Researchers might ask when peak use of human food resources occurs by nuisance wildlife, and in doing so better predict and manage human-wildlife conflicts. With sufficient observations, activity levels could be quantified at the site level for all detected species. The effects of surrounding landscape cover on activity levels would be more broadly informative.

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Table 1. Total number of observations by site and by camera, pooled across all detected species.

Site	Camera ID									
	ES1	ES2	ES3	ES4	ES5	MH1	MH2	MH3	MH4	MH5
Bluff Point	193	79	463	373	234	175	71	94	89	62
Nichols	127	501	110	161	260	49	151	150	108	148
Pachaug	107	46	70	82	56	128	71	43	33	40
Spignesi	168	142	121	63	15	57	93	73	156	60

Table 2. Latency to detection, probability of detection, number of observations by species both overall and subset by early successional (ES) and mature hardwood (MH) habitat patches, and activity estimates for species with ≥ 30 observations (overall and subset by habitat type).

Species	Latency to detection (Days)	Probability of detection	n, Activity estimate (overall)	n (ES)	n (MH)
Bobcat (<i>Lynx rufus</i>)	26.5	0.17	47, 0.67	42	5
Cottontail (<i>Sylvilagus</i> spp.)	9.5	0.44	442, 0.47	442	0
Coyote (<i>Canis latrans</i>)	17.5	0.45	195, 0.56	116	79
Domestic Cat (<i>Felis catus</i>)	214	.	2, -	0	2
Eastern Gray Squirrel (<i>Sciurus carolinensis</i>)	9	0.58	542, 0.33	412	130
Eastern Striped Skunk (<i>Mephitis mephitis</i>)	182	.	14, -	10	4
Fisher (<i>Martes pennanti</i>)	30.6	0.06	11, -	6	5
Human (<i>Homo sapiens</i>)	18	.	93, 0.38	50	43
Long-Tailed Weasel (<i>Mustela frenata</i>)	95.5	.	4, -	2	2
Virginia Opossum (<i>Didelphis virginiana</i>)	20.5	0.11	56, 0.42	37	19
Raccoon (<i>Procyon lotor</i>)	21	0.5	503, 0.37	371	132
Red Fox (<i>Vulpes vulpes</i>)	59	0.09	18, -	9	9
White-tailed Deer (<i>Odocoileus virginianus</i>)	2.75	0.98	2734, 0.59	1470	1264

Table 3. Comparisons of activity estimates between early successional (ES) and mature hardwood (MH) habitat for species with at least 20 recorded observations in both habitat types.

Species	n(ES)	Activity Estimate (ES)	97.5% CI (ES)	n(MH)	Activity Estimate (MH)	97.5% CI (MH)	Difference (ES v MH)	W	p-value
Coyote (<i>Canis latrans</i>)	116	0.55	(0.38, 0.63)	79	0.58	(0.39, 0.69)	-0.03	0.08	0.77
Eastern Gray Squirrel (<i>Sciurus carolinensis</i>)	412	0.34	(0.29, 0.38)	130	0.30	(0.24, 0.38)	0.04	0.81	0.38
Raccoon (<i>Procyon lotor</i>)	371	0.36	(0.30, 0.41)	132	0.42	(0.30, 0.44)	-0.05	1.81	0.18
White-Tailed Deer (<i>Odocoileus virginianus</i>)	1470	0.65	(0.57, 0.70)	1264	0.56	(0.48, 0.65)	0.09	2.73	0.09

Table 4. Seasonal estimates of daily activity and p-values from tests for significant differences between seasons for : A) Cottontail (*Sylvilagus* spp.), B) Coyote (*Canis latrans*), C) Raccoon (*Procyon lotor*), D) Eastern Gray Squirrel (*Sciurus carolinensis*), and E) White-tailed Deer (*Odocoileus virginianus*). P-values <0.05 are marked in bold.

A. Cottontail	Spring	Summer	Fall	Winter
Spring (0.33 ± 0.04)	.	0.69	0.001	0.02
Summer (0.37 ± 0.08)	0.69	.	0.07	0.26
Fall (0.54 ± 0.05)	0.001	0.07	.	0.36
Winter (0.48 ± 0.05)	0.02	0.26	0.36	.
B. Coyote	Spring	Summer	Fall	Winter
Spring (0.46 ± 0.07)	.	0.88	0.94	0.63
Summer (0.47 ± 0.09)	0.88	.	0.95	0.61
Fall (0.46 ± 0.08)	0.94	0.95	.	0.56
Winter (0.54 ± 0.1)	0.63	0.61	0.56	.
C. Raccoon	Spring	Summer	Fall	Winter
Spring (0.36 ± 0.03)	.	0.56	0.40	0.47
Summer (0.31 ± 0.04)	0.56	.	0.24	0.8
Fall (0.41 ± 0.05)	0.40	0.24	.	0.19
Winter (0.31 ± 0.05)	0.47	0.8	0.19	.
D. Eastern Gray Squirrel	Spring	Summer	Fall	Winter
Spring (0.30 ± 0.03)	.	0.53	0.85	0.22
Summer (0.33 ± 0.05)	0.53	.	0.67	0.80
Fall (0.31 ± 0.04)	0.85	0.67	.	0.38
Winter (0.35 ± 0.03)	0.22	0.80	0.38	.
E. White-tailed Deer	Spring	Summer	Fall	Winter
Spring (0.63 ± 0.05)	.	0.57	0.89	0.2
Summer (0.59 ± 0.04)	0.57	.	0.65	0.46
Fall (0.62 ± 0.05)	0.89	0.65	.	0.27
Winter (0.55 ± 0.04)	0.2	0.46	0.27	.

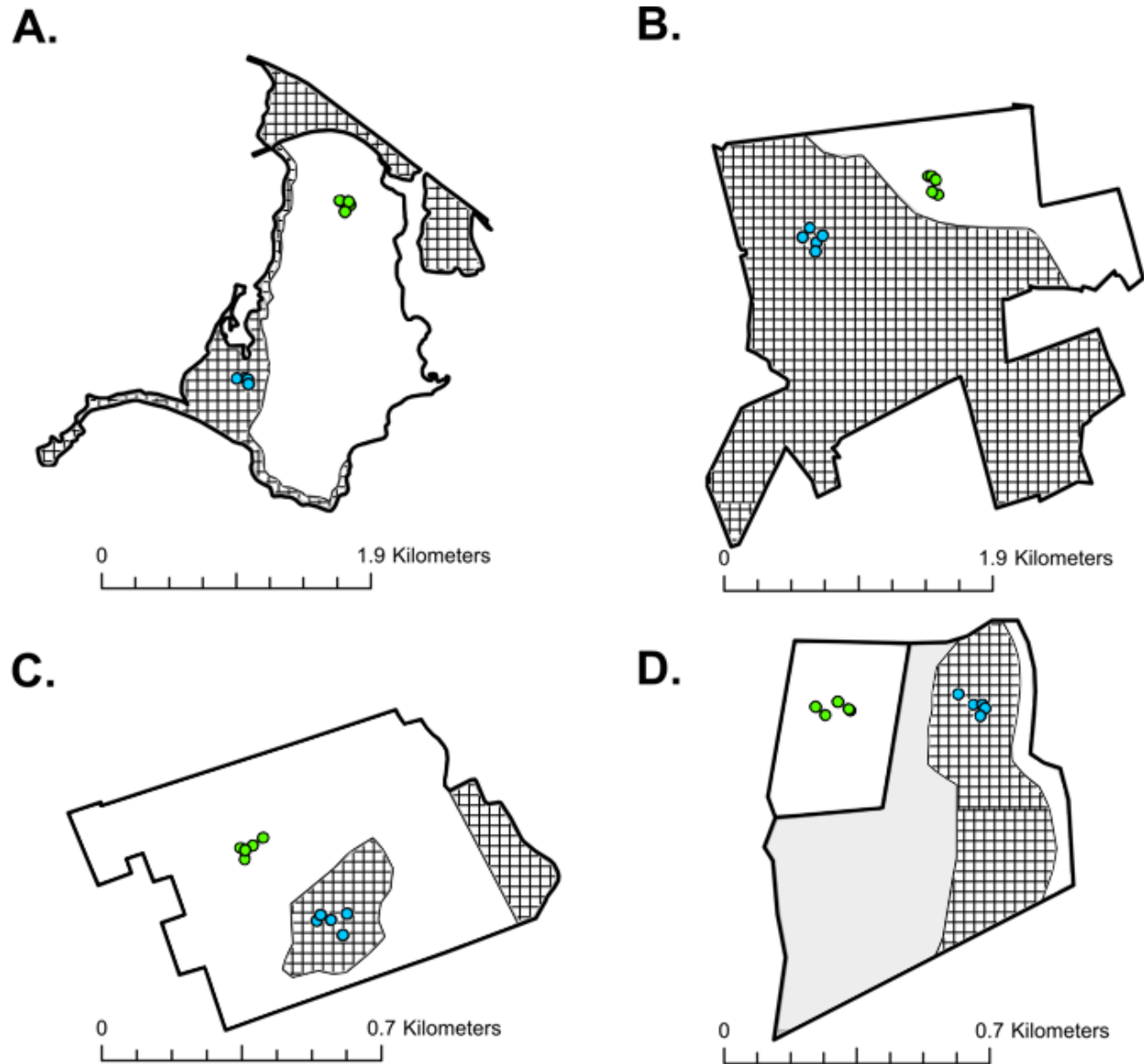


Figure 1. Placement of camera arrays at: A. Bluff Point State Park, B. Pachaug State Forest, C. Spignesi Wildlife Management Area, and D. Nichols. Arrays placed in early successional habitat are displayed in blue, and arrays placed in mature forest habitat are displayed in green. Early successional habitat is indicated in cross-hatching, mature hardwood forest in white. The shaded area at site D is agricultural pasture.

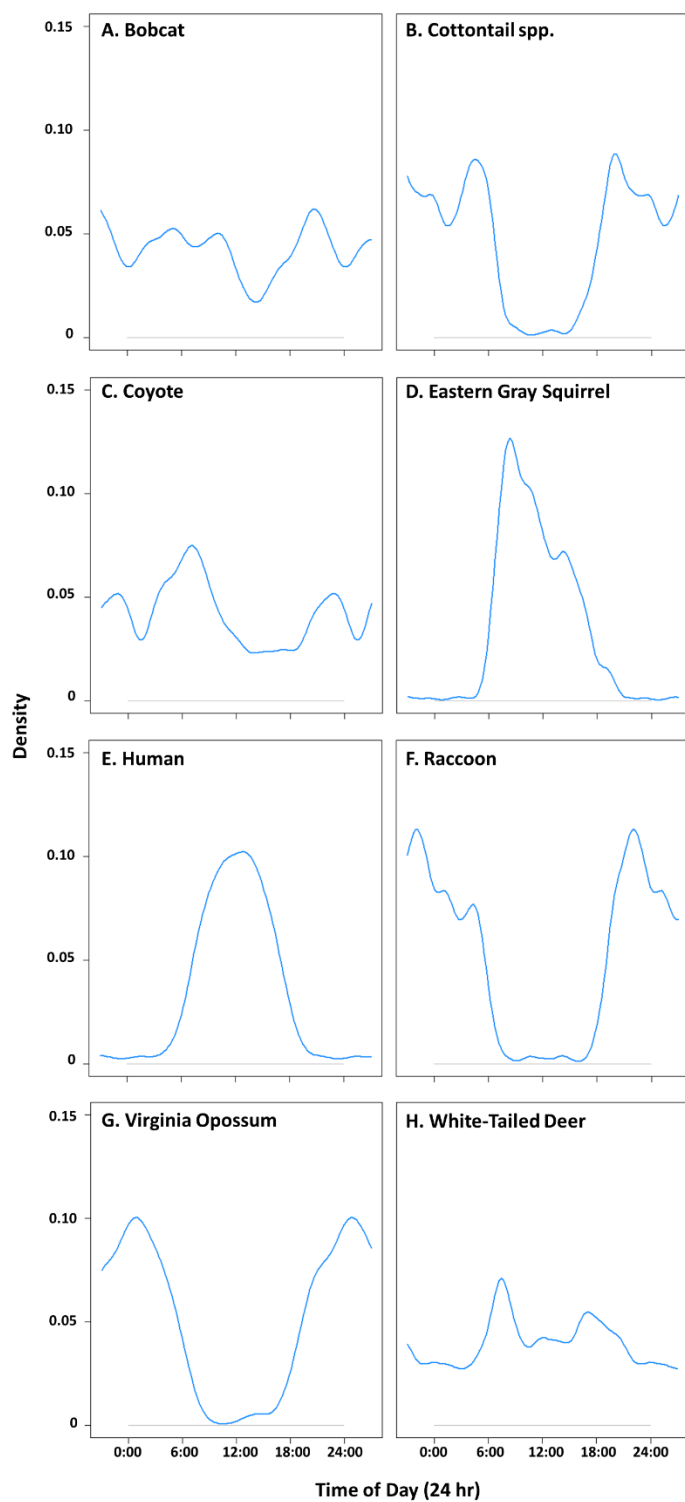


Figure 2. Daily activity distributions for eight mammal species, including detected humans.

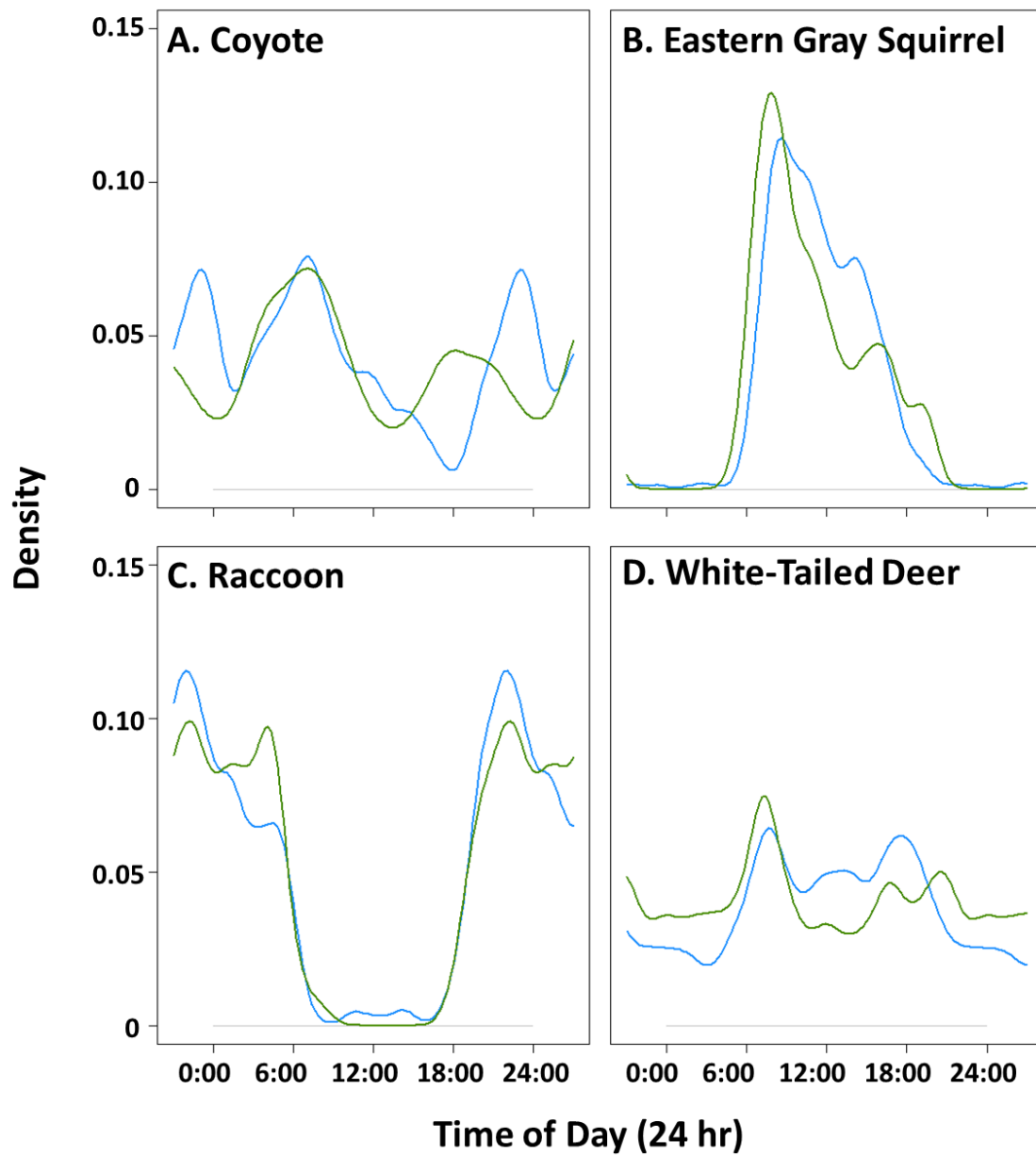


Figure 3. Comparison of activity distributions in early successional (blue) and mature upland hardwood (green) habitats for four mammal species.

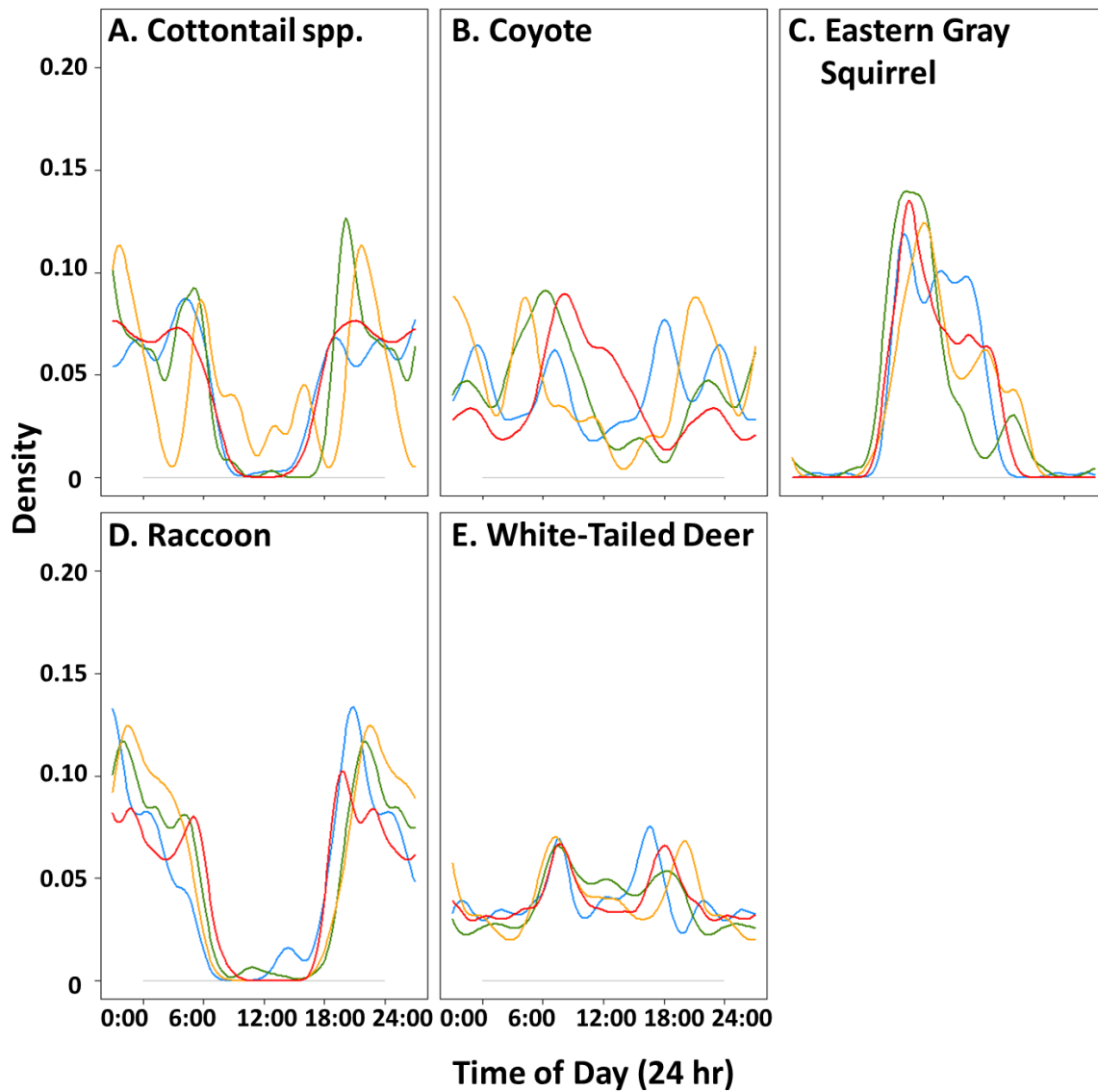


Figure 4. Activity distributions fit for five mammalian species across three-month seasons: Spring (March-May, green), summer (June-August, orange), fall (September-November, red), and winter (December-February, blue).

