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Original Article

Factors Influencing Detection in Occupancy Surveys of a Threatened Lagomorph

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ABSTRACT Successful recovery of populations of rare and cryptic species requires accurate monitoring of changes in their distribution and densities, which in turn necessitates considering detection rates. Development of population monitoring protocols is needed to aid recovery of the New England cottontail (*Sylvilagus transitionalis*; currently the top-priority Species of Greatest Conservation Need in the northeastern United States), which lives in dense shrubby habitat and is difficult to detect. To address this need, we conducted repeated, systematic, presence–absence surveys to determine patch-specific detection probabilities and factors influencing detection of the New England cottontail. We surveyed cottontails during 2–6 visits on 30 sites with known occupancy in the northeastern United States during the winters of 2010 and 2011. For each survey visit, we determined whether cottontails were detected by the presence of fecal pellets on fresh fallen snow and subsequent species identification by genetic analysis. Detection probabilities were modeled in Program PRESENCE to explore the influence of snow condition and depth, temperature, wind, number of pellet deposition days, woody stem density, patch size, and search effort. The overall probability of detecting a New England cottontail during a single survey visit was 0.73. The most influential factor in detection was prior knowledge of site-specific cottontail activity. Snow depth <30.5 cm and the number of days without high winds following a snowfall had a positive influence on detection. Patch size had a negative effect on detection when surveys were restricted to 20 minutes. In the absence of prior knowledge, 2–3 surveys conducted with snowpack <30.5 cm and 2–4 days after a snowfall without high wind should yield reliable occupancy status with 95% confidence in detection. Incorporating our recommendations into monitoring programs will improve the accuracy of patch-specific occupancy data for New England cottontail. Our approach and findings may be applicable to monitoring other rare, cryptic, or threatened species that occupy dense habitats, especially where patch-level occupancy knowledge is required.

KEY WORDS detection, lagomorph, monitoring, New England cottontail, occupancy, patch, *Sylvilagus transitionalis*.

Accurate monitoring of species and populations is requisite for their successful conservation management. One rare and cryptic species for which accurate occupancy monitoring is needed is the New England cottontail (*Sylvilagus transitionalis*). Once widespread throughout the New England states and eastern New York (USA), populations of New England cottontail have declined dramatically in recent decades because of habitat loss and fragmentation; remnant populations occur in 5 geographically and genetically distinct regions within <14% of the species' historical range (Litvaitis et al. 2006, USFWS 2008, Fenderson et al. 2011; Fig. 1). New England cottontails rely on early successional or shrubland habitats with dense understory vegetation (Barbour and Litvaitis 1993, Litvaitis et al. 2003). These habitats are often ephemeral because of their dependence upon disturbance to set back succession. The loss of many historical disturbances (fire, beaver activity, agricultural clearing), combined with land use change, has precipitated a steep decline in these habitats in recent decades (Brooks 2003, Litvaitis 2003, Lorimer and White 2003). Remaining habitats within the species' range have a limited and patchy distribution and <10% are occupied by New England cottontail (Litvaitis et al. 2006). Many potential habitat patches are small, precluding them from sustaining significant cottontail populations; this makes them highly susceptible to local extinction (Litvaitis and Villafuerte 1996). Decreased connectivity of the landscape exacerbates

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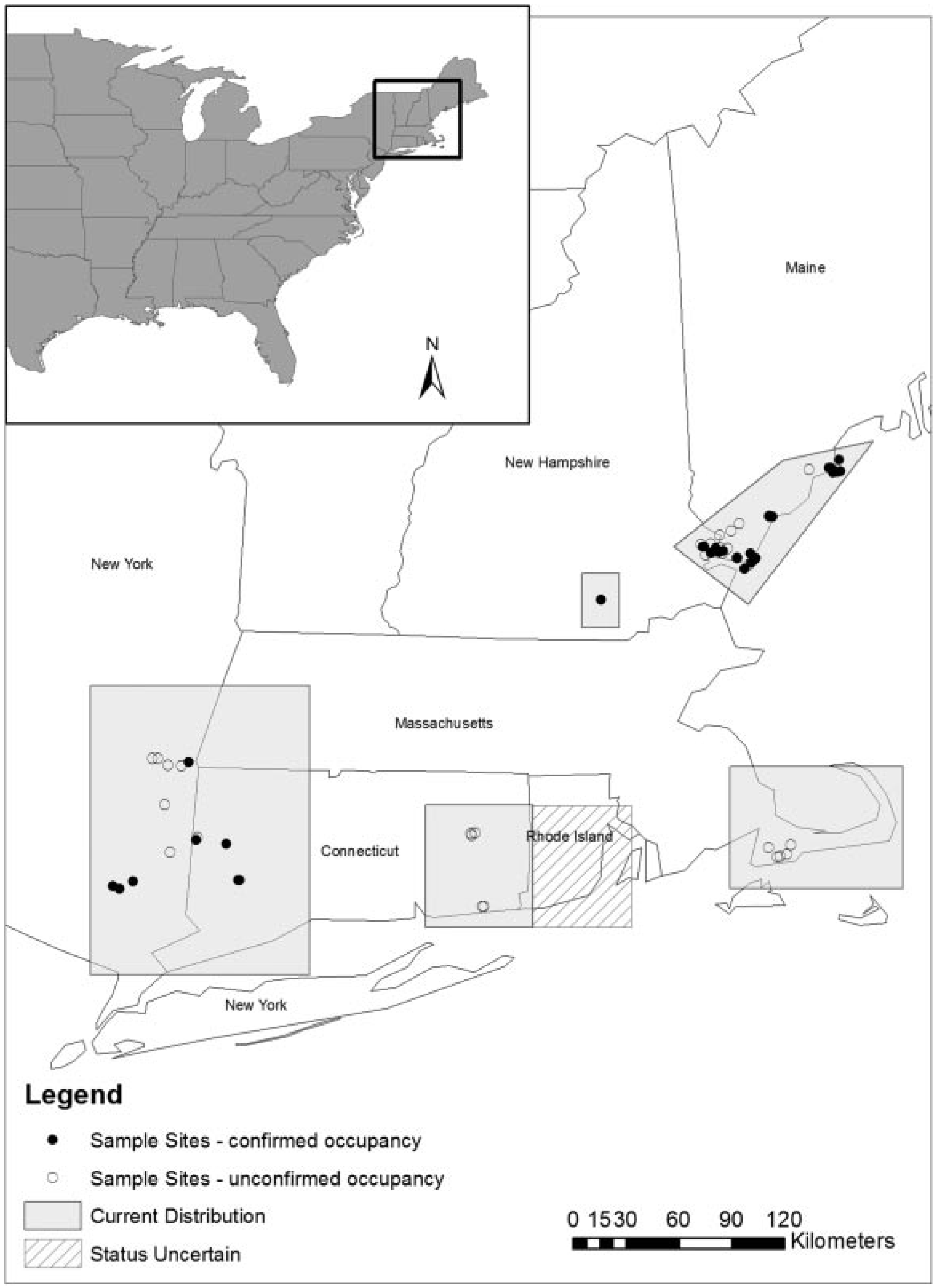

Figure 1. Locations of 60 study sites surveyed for New England cottontail occupancy in the northeastern United States during the winters of 2010 and 2011. Closed circles indicate the 30 sites with confirmed occupancy used in the detection modeling; open circles indicate 30 additional surveyed sites that did not meet our criteria for use in modeling because of unconfirmed occupancy or insufficient survey visits. Gray shaded region indicates the current distribution of New England cottontails based on 2007–2009 surveys in Maine, New Hampshire and Connecticut (Fenderson 2010; H. Kilpatrick, Connecticut Department of Energy and Environmental Protection, personal communication) and the range-wide survey of Litvaitis et al. (2006) for Massachusetts and New York. No study sites were surveyed in Rhode Island because of lack of confirmed occupancy in the past 5 years (A. I. Kovach, unpublished data; Fuller and Tur 2012); cross-hatching indicates the previous distribution in Rhode Island based on Litvaitis et al. (2006).

this problem by impeding re-colonization of increasingly isolated patches (Fenderson 2010). As a result of the extensive decline in habitat, range contraction, and uncertainty for long-term viability of the New England cottontail, the species is a top-priority Species of Conservation Need in the Northeast (Fuller and Tur 2012). The term "Species of Greatest Conservation Need" is a designation given to species with small or declining populations by all states in their federally mandated Wildlife Action Plans (USFWS 2007). In addition, it is also a candidate for federal listing under the Endangered Species Act and is listed as endangered by the states of Maine and New Hampshire (MDIFW 2007, NHFG 2008, USFWS 2008).

To help recover the species, a collaborative network of researchers, managers and state and federal agency biologists from 6 states in the northeastern United States (ME, NH, NY, CT, MA, and RI) have formed the Regional New England Cottontail Conservation Initiative and developed a range-wide conservation strategy (Fuller and Tur 2012). This strategy outlines management actions, including habitat restoration and population recovery goals, to conserve the species. As New England cottontail management activities proceed, accurate monitoring will be necessary to evaluate population status, response to habitat creation and enhancement, response to translocation, and overall progress toward population recovery goals.

Wildlife biologists use winter pellet surveys to track the occupancy status and distribution of New England cottontails (e.g., Litvaitis et al. 2006). Currently, sites are surveyed during single visits after fresh snowfall for the presence of fecal pellets. Diagnostic genetic tests (Litvaitis and Litvaitis 1996, Kovach et al. 2003) are used to distinguish the pellets of New England cottontails from those of the eastern cottontail (*S. floridanus*) or snowshoe hare (*Lepus americanus*), with which it occurs sympatrically throughout portions of its range. Although effective in assessing species' distribution on a broad scale (Litvaitis et al. 2006), single presence–absence surveys may suffer from imperfect detection on the scale of the individual patch, which is the scale at which conservation and management actions take place. The ability to accurately determine patch-specific New England cottontail occupancy is currently hindered by a lack of knowledge of detection rates.

Detectability is a primary source of variation that generates error in presence–absence data (Yoccoz et al. 2001, MacKenzie et al. 2002). Failure to account for detection rates in occupancy surveys can incorrectly identify occupied sites as vacant, and may lead to misinformed management decisions (MacKenzie et al. 2006). Consequently, modified occupancy models have been developed to account for imperfect detection (MacKenzie et al. 2002, 2003; Royle and Nichols 2003). These models are particularly useful for monitoring rare and cryptic species for which detection rates are typically low (Heard et al. 2006, Roughton and Seddon 2006, Durso et al. 2011).

Environmental or survey conditions may be important in influencing detection of rare species that occur in dense vegetative cover, such as New England cottontails and other lagomorphs. Accordingly, identifying the optimal survey conditions for detection should increase the reliability of occupancy monitoring efforts. Accounting for detection rates is of particular importance in the monitoring of threatened species, because knowledge of patch-specific occupancy may be critical when occupied patches occur with low frequency and in a fragmented landscape. High-quality occupancy data are needed to guide conservation and ensure that management actions occur in the areas most likely to result in successful recovery of species of conservation concern. These issues are germane to monitoring New England cottontails, for which detection may be influenced by factors that affect cottontail activity as well as those that affect the efficiency or observational success of the surveyor. Determining detection rates, and uncovering the environmental factors and survey conditions that influence detection of New England cottontails during winter pellet surveys will improve the accuracy of occupancy monitoring efforts, especially at the patch level.

To address these issues, we conducted a systematic study of detection of New England cottontails during presence–absence surveys. Our specific objectives were to 1) estimate the probability of detecting New England cottontails on occupied sites, 2) identify the factors that influence detection, 3) determine optimal survey conditions and survey effort for reliable inference of occupancy, and 4) develop recommendations for accurate patch-level monitoring.

STUDY AREA

The present study was conducted on occupied patches within the New England cottontail's current range, which encompassed an area of about 12,175 km^2 in the northeastern United States (Litvaitis et al. 2006; Fig. 1). These sites were located in York and Cumberland counties in southwestern Maine, Strafford and Rockingham counties of New Hampshire, Windham and New London counties in southeastern Connecticut, Litchfield and New Haven counties in western Connecticut, Barnstable county in eastern Massachusetts, and Putnam, Duchess, and Columbia counties in eastern New York. Occupied sites were found in coastal shrublands, old fields, and shrub swamps and were characterized by a diversity of vegetation cover types, including juniper (*Juniperus* spp.), blackberry (*Rubus occidentalis*), dogwoods (*Cornus* spp.), viburnum (*Viburnum* spp.), high bush blueberry (*Vaccinium corymbosum*), alders (*Alnus* spp.), willows (*Salix* spp.), honeysuckle (*Lonicera* spp.), autumn olive (*Elaeagnus umbellata*), multiflora rose (*Rosa multiflora*), Japanese barberry (*Berberis thunbergii*), and a variety of young deciduous species (*Acer*, *Betula*, and aspen, *Populus tremuloides*).

METHODS

Surveys

In 2010 and 2011, we conducted a series of systematic, repeated presence–absence surveys of 60 selected sites (Fig. 1), ranging in size from 2 ha to 26 ha. Our objective was to determine the factors that influence detection on occupied sites; therefore, we focused only on sites of known or highly probable occupancy, chosen from 2007 to 2009 winter survey efforts in Maine ($n = 26$ sites), New Hampshire ($n = 9$), and Connecticut ($n = 10$; Fenderson 2010; H. Kilpatrick, Connecticut Department of Energy and Environmental Protection, personal communication) and based on the most recent occupancy data (Litvaitis et al. 2006) in New York ($n = 10$) and Massachusetts ($n = 5$). This included a representative sample of recently occupied sites from each of the 5 geographic regions within the species' range. No sites from Rhode Island (continuous with the eastern CT geographic population) were included in this study because of lack of confirmed occupancy in recent surveys (A.I. Kovach, unpublished data; Fuller and Tur 2012).

Sites consisted of patches of continuous habitat, comprised of thick understory habitat with densities of 17,000–62,000 ($\bar{x} = 35{,}000$) woody stems/acre (42,000–153,000; $\bar{x} = 86{,}500$ stems/ha), which cottontails could utilize without venturing into a risky open area (>30 feet wide [9.14 m wide] without suitable winter cover). Patches were delimited by areas of unsuitable vegetation (mature forest, open fields lacking cover), roads, or water bodies. Sites in Maine and New Hampshire were generally more isolated, often surrounded by development, open fields, or, in the case of coastal sites, rocky coastline and open water. Sites in New York and Connecticut were predominantly early successional shrubland or wetlands surrounded by mature forest. Sites in Massachusetts were generally forested wetlands surrounded by forest, uninhabitable wetlands, or development. Maine and New Hampshire sites ($n = 35$) contained only New England cottontail while New York, Connecticut, and Massachusetts sites ($n = 25$) were co-occupied by New England and eastern cottontails.

Surveys occurred in the wintertime, with snow on the ground, and ≥12–24 hours after a snowfall event, following Litvaitis et al. (2006). We surveyed patches systematically for lagomorph fecal pellets, using loose, continuous transects, winding back and forth across the patch with approximately 30-m spacing. For patches >6 acres (2.4 ha), we restricted the search area to 2-acre (0.81-ha) subplots within the patch. To ensure similar search effort, the total area searched for each patch was equivalent to 6 acres (2.4 ha) or 20% of the total patch area, whichever was greater. Searches focused on thicket habitat within the patch and continued until we found a cluster of pellets, or until we had exhaustively searched all potential habitat. For sites with both cottontail species, searches continued until we detected 3–5 distinct pellet clusters separated by ≥100 m. Once detected, pellets were collected for later genetic species identification. To maximize the likelihood that each cluster of pellets originated from a single rabbit, we collected them from an area of ≥1.5 m × 1.5 m.

To assess occupancy status from our pellet surveys, we used diagnostic genetic assays to determine the identity of the species that deposited the pellets. We extracted DNA from pellets using QIAamp® DNA Stool Mini Kits (Qiagen, Valencia, CA) following the methods of Kovach et al. (2003). We amplified an approximately 560 base-pair segment of the mitochondrial control region and used a combination of 2 diagnostic restriction fragment length polymorphism tests, one using the restriction enzyme *Nla III* (Kovach et al. 2003) and one with *Bfa I* (Litvaitis and Litvaitis 1996), to distinguish pellets of New England cottontails from those of the 2 sympatric lagomorph species (eastern cottontails and snowshoe hares). On sympatric sites (sites in CT, MA, and NY), we assayed pellet samples until we identified a New England cottontail or exhausted all collected samples.

Our target was to visit each site 5 times whenever logistically feasible, with a minimum of 3 visits (MacKenzie and Royle 2005). To meet the assumption of population closure with respect to patch occupancy, we attempted to complete the majority of searches within a 6-week window of time, ideally within the first half of the winter (late Dec–mid-Feb). Cottontails in our study area do not breed or disperse during the winter, and mortality may be higher in the late winter when snow cover is persistent (Brown and Litvaitis 1995). Surveys occurred between 23 December and 25 March across all sites. Because of the importance of confirmed occupancy for our study, sites that did not yield detections during the surveys were excluded from modeling, unless occupancy could be verified by other means (e.g., pellets found during other surveys of the site independent from this study). Occupancy could only be verified for 30 of the 60 surveyed sites (17 in ME, 5 in NH, 4 in eastern CT and 4 in NY; none of the sites in MA met our criteria for data analysis because of insufficient survey visits and lack of confirmed occupancy). We visited 29 of the 30 modeled sites ≥3 times: 1 site 3 times, 11 sites 4 times, 15 sites 5 times, and 2 sites 6 times. One site we surveyed twice. The average survey window across all 30 sites was 43 days. All but 2 sites were surveyed during the winter of 2011. Those 2 sites had unconfirmed occupancy in 2011 and we therefore used surveys completed in 2010, when occupancy was detected.

Detection Covariates

During each site visit, surveyors collected data on the following covariates: observer, patch size, search time, search area, snow condition (no snow, powder, wet snow, crusted snow, melted out), snow depth (categorized as <12 inches or >12 inches [30.5 cm]), and days since last snowfall (a measure of the no. of pellet deposition days). We recorded the time spent searching at each patch and calculated the area searched during each survey by buffering a fixed distance, based on average patch woody stem density (a measure of visibility), from the recorded search path. For each visit, we also identified whether the surveyor had prior knowledge of cottontail activity at that site. We considered prior knowledge to be known locations of pellets or rabbit sign from a previous visit that same field season, or from information provided by the landowner concerning specific rabbit locations within the patch. To account for differences in habitat quality, we measured the average stem density at each patch by averaging estimated counts of all woody stems at a height of 0.5 m, obtained for up to 30 evenly spaced 1-m × 2-m plots/patch. Finally, we collected temperature, wind, and precipitation data from Weather Underground (weatherunderground.com) for all potential pellet deposit days, which we identified as any day after the last snowfall but prior to each respective survey. We then used these data to further categorize the number of pellet deposition days as the total number of days since snowfall with winds <40 km/hour and the total number of days since snowfall with temperature $> -10^\circ$ C and also with temperature $> -15^\circ$ C. High winds negatively affect lagomorph activity (Fletcher et al. 1999, Ballinger and Morgan 2002) and this may be true for New England cottontails, particularly in the winter. High winds decrease temperatures through wind chill, and severely cold temperatures may limit cottontail activity. High winds may also cause blowing snow to cover pellets and tracks, thereby reducing visibility of sign.

In total, we collected data on 11 covariates: Observer, Knowledge, SearchTime, SearchArea, PatchSize, StemDensity, SnowPowder, SnowDepth, DaysWind, DaysTemp >-10, DaysTemp >-15. We used preliminary statistical testing to obtain a reduced set of informative factors for detection modeling. We removed Observer from consideration because the logistics of surveying sites across New England produced too many observers to be statistically viable with our sample size. We then used nominal logistic regression to select the most influential factor from correlated sets. These sets included several of the original covariates that were measured as slight variations of the same factor (e.g., multiple measures of pellet deposition days evaluated as iterations of days since snowfall with or without accounting for influence of temp or wind) and covariates that were evaluated as both continuous and nominal variables (e.g., total no. of days since snowfall and >2 days or <2 days since snowfall). From the remaining uncorrelated set of factors, we then used partition modeling, a form of classification and regression tree (CART) modeling, to identify uninformative factors and removed them from further analysis. Partition modeling uses a stepwise regression tree to evaluate the influence of variables, both continuous and categorical, on a target outcome. For categorical responses, such as detection versus non-detection, partitions in the regression tree are made by maximizing the likelihood ratio chi-square statistic. The initial split partitions the data according to the most influential factor and subsequent partitions identify factors with decreasing influence. This analysis resulted in the removal of DaysTemp >-15, SnowPowder, SearchTime, and SearchArea as uninformative factors with respect to detection. We performed a final simple linear regression on the remaining factors and, for subsequent detection modeling, retained those with significant effect likelihood scores: Knowledge ($P < 0.001$), SnowDepth ($P < 0.001$), DaysWind ($P = 0.023$). We also retained PatchSize ($P = 0.099$) and StemDensity ($P = 0.251$) despite non-significant effect likelihood scores because their effects on detection were of particular interest. Despite some multicolinearity with DaysWind, DaysTemp >-10 (hereafter, DaysTemp) was also included in the modeling because we were interested in potential effects of temperature on detection.

Detection Modeling

We modeled New England cottontail detectability in Program PRESENCE 2.0 (Hines 2006) for the 30 known occupied sites as a logit function of the 6 selected covariates: Knowledge, SnowDepth, DaysWind, DaysTemp, PatchSize, StemDensity. We constructed 36 *a priori* models that considered additive combinations of these 6 variables based on our knowledge of cottontail biology and survey logistics. To limit the number of models, we excluded those that contained only the least significant factors from our preliminary covariate analyses and that contained both DaysWind and DaysTemp. Models held occupancy constant at one and allowed detection to be a function of covariates. Given our exclusive use of occupied sites, this approach enabled us to evaluate directly the influence of survey covariates on detection without confounding influence of occupancy status (MacKenzie et al. 2006). To explore the effects of a threshold search time, we also modeled detection probabilities using only detections that occurred within the first 20 minutes of a survey. The 20-minute threshold was chosen because it has been used in past protocols for cottontail occupancy surveys (Litvaitis et al. 2003, 2006) and because we found that 82% of detections in this study occurred within this time period (Fig. 2).

We ranked candidate models according to Akaike's information criteria corrected for small sample size (AIC$_c$). The variance inflation factor, ($\hat{c}$), calculated from a goodness-of-fit test on our global model, was not >1 and did not require a quasi-likelihood modification (Burnham and Anderson 2002). Models with the lowest AIC$_c$ were considered the most parsimonious. Among these models, we did not consider competing models to be informative for drawing inference if they contained the same parameters as the top model plus $\geq$1 additional parameter (Burnham and Anderson 2002, Arnold 2010).

We used Akaike weights to evaluate the probability that a particular model was the best in our candidate set of models. To evaluate the relative influence of each covariate, we summed model weights over all candidate models with that covariate ($w+(i)$; Burnham and Anderson 2002) in the 95% confidence set (all models whose summed weights represented $\geq$95% of the total wt of the candidate set of models). Using PRESENCE, we also calculated untransformed linear logit maximum-likelihood coefficient estimates and standard errors from the best-supported (lowest AIC$_c$) models for surveys conducted with unrestricted search time as well as for detections that occurred within the first 20 minutes of the surveys. Lastly, we used the top model to generate predicted detection rates for different combinations of the influential factors, to represent a variety of survey conditions that a surveyor might encounter, for both unlimited search time

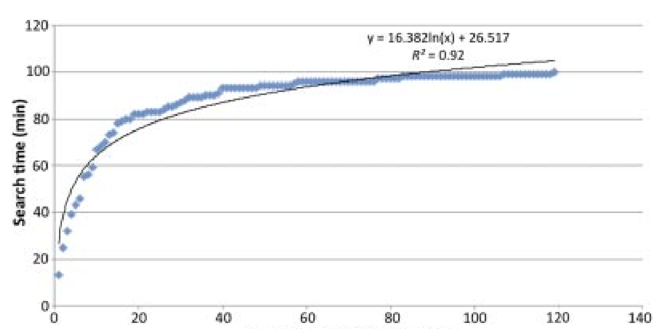

Figure 2. New England cottontail detections as a function of search time during 137 surveys of 30 sites in the northeastern United States during 2007–2009. Diamonds are percentage of observed detections and solid line is the best-fit logarithmic regression line. Positive gains of increased search time begin to diminish at 20 minutes (82%), with only slight gain for increased effort beyond 40 minutes (93%).

surveys and 20-minute search time surveys. From these predicted detection rates, we then estimated the number of surveys needed to obtain 95% confidence in occupancy determination.

RESULTS

We completed 137 surveys over the 30 study sites and detected New England cottontails during 100 of those surveys, resulting in a detection probability of 0.73. Akaike weights, summed across the 95% confidence set of models for the unrestricted search time analysis, indicated that KNOWLEDGE ($w+(i)=1$), SNOWDEPTH ($w+(i)=1$), and DAYSWIND ($w+(i)=0.89$) were the most influential factors influencing cottontail detection probabilities (Tables 1 and 2). All additional models with ΔAIC_c <2 contained these 3 variables, plus 1 or 2 additional variables, indicating little uncertainty in variable importance. The uninformative, nested models (not shown) were not used for drawing inference.

Regression of New England cottontail detections by survey search time showed that there was little benefit of increasing search time beyond 20 minutes. Eighty-two percent of the detections during our study occurred prior to 20 minutes. Additional search time only increased detections slightly, with 87% of total detections occurring within 30 minutes and 93% within 40 minutes. Beyond 40 minutes, the added search time provided very little return in additional detections (Fig. 2). Nonetheless, restricting search time to 20 minutes resulted in a reduction in the overall detection rate from 0.73 to 0.62. In the 20-minute search time model set, KNOWLEDGE ($w+(i)=1$) and DAYSWIND ($w+(i)=0.85$) were again among the most influential factors, and PATCHSIZE ($w+(i)=0.62$) replaced SNOWDEPTH as an influential factor in the 95% confidence set (Tables 1 and 2). These 3 covariates were also the only ones included in the top model. The covariate coefficients for KNOWLEDGE and DAYSWIND were similar for both model sets and showed a positive relationship with detection. SNOWDEPTH also had a positive relationship in the overall model while PATCHSIZE had a slightly negative effect in our 20-minute model; we note also that the effect of PATCHSIZE was poorly constrained, with a large standard error relative to the estimate (Table 3).

Table 2. Summed Akaike Information Criterion weights ($w+(i)$) for all variables in the 95% confidence model sets for detection probability of New England cottontails during surveys with unrestricted search time and surveys with 20-minute search time in the northeastern United States in 2010–2011.

Variable	Unrestricted search model $w+(i)$	20-min search model $w+(i)$
KNOWLEDGE	1	1
SNOWDEPTH	1	0.46
DAYSWIND	0.89	0.85
PATCHSIZE	0.36	0.62
STEMDENSITY	0.32	0.38
DAYSTEMP	0.29	0.33

We used our models to generate predicted detection rates for different combinations of the influential factors (see Table 4 for predicted scenarios). These predictions showed that, for surveys conducted without a time limit, detection rates are high, from 0.85 to 0.99 with prior knowledge, but decrease to a maximum of 0.49 when searches are conducted in the absence of prior knowledge and in deep snow. The detection rate for surveys of a 25-ha patch with 3 wind-free deposit days ranges from 0.68 to 0.33 with and without prior knowledge (Table 4). Detection rates on large patches with limited search times are quite low, and such surveys will require 3–6 visits (depending on deposition days and prior knowledge) for confident occupancy determination.

DISCUSSION

We found that detection of New England cottontails during presence–absence surveys was influenced by the environmental conditions of the survey. When surveys were

Table 1. The 95% confidence sets of candidate models for detection of New England cottontails during winter pellet surveys of 30 sites with confirmed occupancy in the northeastern United States in 2010 and 2011. Model results are shown for surveys with unrestricted search time as well for detections that occurred within 20 minutes of searching. Using additive covariate relationships, we estimated detection probabilities as functions of a surveyor's prior KNOWLEDGE of occupancy, SNOWDEPTH (< or >30.5 cm), number of days since last snowfall with winds <40 km/hour (DAYSWIND), number of days since last snowfall with temperature $>-10^{\circ}$ C (DAYSTEMP), PATCHSIZE, and the number of woody stems (STEMDENSITY—not a factor in our top models). For each model, the Akaike Information Criterion adjusted for sample-size (AIC_c), the difference in AIC_c (ΔAIC_c), AIC_c weight (w_i), the number of parameters (K), and the maximized log likelihood ($-2 \log(\pounds)$) are given. Nested models (those with the same parameters as models with lower AIC_c, plus 1 or 2 additional variables) are not shown.

Model	AIC_c	ΔAIC_c	w_i	K	$-2 \log(\pounds)$
Unrestricted search-time model set					
KNOWLEDGE + SNOWDEPTH + DAYSWIND	111.4	0	0.26	5	100.94
KNOWLEDGE + SNOWDEPTH + DAYSTEMP	115.2	3.79	0.06	5	104.73
KNOWLEDGE + SNOWDEPTH	115.3	3.89	0.05	4	106.98
20-min search-time model set					
KNOWLEDGE + PATCHSIZE + DAYSWIND	170	0	0.16	5	159.54
KNOWLEDGE + DAYSWIND	171.11	1.11	0.09	4	162.8
KNOWLEDGE + PATCHSIZE + SNOWDEPTH	173.03	3.03	0.04	5	162.57
KNOWLEDGE + PATCHSIZE + DAYSTEMP	173.57	3.57	0.03	5	163.11
KNOWLEDGE + SNOWDEPTH	174.03	4.03	0.02	4	165.72
KNOWLEDGE + DAYSTEMP	174.49	4.49	0.02	4	166.18

Table 3. Untransformed linear logit coefficient estimates and standard errors for detection probability of New England cottontails surveyed in northeastern United States in 2010 and 2011. Parameter estimates and standard errors are from the best-supported models for surveys conducted with unrestricted search time as well as for detections that occurred within the first 20 minutes of the surveys. Detection probability was modeled as a function of prior knowledge of cottontail occurrence (knowledge or no knowledge), snow depth (<30.5 cm or >30.5 cm), deposition days (no. of days since last snowfall with winds <40 km/hr; DaysWind), and patch size.

Parameter	Coeff. estimate	SE
Unrestricted search time model set		
Intercept	−1.87	0.58
KNOWLEDGE	3.0	0.57
SNOWDEPTH	2.23	0.63
DAYSWIND	0.61	0.27
20-min search-time model set		
Intercept	−0.70	0.47
KNOWLEDGE	1.45	0.39
DAYSWIND	0.45	0.19
PATCHSIZE	−0.05	0.03

conducted in ideal conditions, New England cottontails could be detected, if present, with high confidence (>95%) in one to three surveys. Surveys conducted during suboptimal conditions, however, were unreliable and required numerous repeat visits for accurate patch-specific occupancy determination. We identified 3 easily measured factors that influence New England cottontail detection. Detection, therefore, must be accounted for to obtain high confidence in occupancy status. This is especially relevant when patch-specific occupancy determination is the goal, as when monitoring for conservation management of this threatened species.

Detection Rates

The overall detection rate in our study was 0.73 across all sites. This is higher than detection rates for other lagomorph species in habitats with similar dense vegetative cover (e.g., eastern cottontail, swamp rabbit [*S. aquaticus*]; Scharine et al. 2011; but see Roy Nielsen et al. 2008) and marsh rabbit (*Sylvilagus palustris;* Eaton et al. 2011), and it is comparable to detection of species in more open habitats with greater visibility (e.g., European rabbit [*Oryctolagus cuniculus*]; van Strien et al. 2011). Our detection rates were also high compared with several other studies of rare or cryptic species (Roughton and Seddon 2006, Durso et al. 2011, Olea and Mateo-Tomas 2011). The higher detection rates in our study, despite the dense vegetative cover, may be due to increased visibility afforded by the winter survey approach. Winter pellet surveys may provide enhanced opportunity for cottontails to be detected by allowing tracks and pellets to accumulate on top of snow for several days. Similarly, Roy Nielsen et al. (2008) found that visibility was high for detecting swamp rabbit pellets on log latrines in the winter time when herbaceous vegetation was lacking, resulting in detection rates (0.7) comparable to that in our study. In comparison, Scharine et al. (2011) performed live capture surveys and detected eastern cottontails at a rate of only 0.44 and swamp rabbits at a rate of 0.12. Although Eaton et al. (2011) used pellet surveys, the environmental conditions did not allow for surveys on snow and their lower detection rates likely reflected the difficulty of detecting pellets in marsh rabbit habitat. The use of sign, in the form of scat and tracks, on top of snow provides a broader detection window per visit compared with surveys where the target species must be actively seen or heard each site visit. This is particularly important for New England cottontails because of the reduced visibility in their preferred thicket habitat. Detection rates of New England cottontail may be much lower if insufficient snow cover is available to aid visibility during surveys. High detection rates in this study may also be a result

Table 4. Predicted single-survey detection probabilities (DetProb) and number of survey visits required to obtain 95% confidence in occupancy determination of New England cottontails during winter pellet surveys with hypothetical survey conditions. Predicted responses are derived for a range of scenarios based on survey covariates in the top models of New England cottontail detection for the unrestricted search-time model set and the 20-minute search-time model set. The unrestricted model set includes Knowledge (1 signifies presence of prior knowledge, 0 signifies absence of knowledge), SnowDepth (1 signifies snow pack <30.5 cm, 0 signifies snowpack >30.5 cm), and DaysWind (modeled as either 1 day or 3 days since snowfall with winds <40 km/hr). All 3 variables have a positive influence on detection. The 20-minute model set includes positive influence of Knowledge and SnowDepth and negative influence of PatchSize (3 ha or 25 ha).

Scenario	Knowledge	SnowDepth	DaysWind	PatchSize (ha)	DetProb	No. visits for 95%
Unrestricted search model						
1	1	1	1		0.98	1
2	1	1	3		0.99	1
3	1	0	1		0.85	2
4	1	0	3		0.95	1
5	0	1	1		0.72	3
6	0	1	3		0.90	2
7	0	0	1		0.22	>6
8	0	0	3		0.49	4
20-min model						
1	1	1		25	0.46	4
2	1	1		3	0.74	3
3	1	3		25	0.68	3
4	1	3		3	0.87	2
5	0	1		25	0.17	>6
6	0	1		3	0.40	6
7	0	3		25	0.33	>6
8	0	3		3	0.62	4

of the positive effect of prior knowledge of occupancy, which we had for most surveys on sites following the first detection.

Detection decreased from 0.73 to 0.62 when the search time was limited to a 20-minute threshold. This reduced detection was negatively associated with increased patch size and suggests that 20 minutes may be inadequate to thoroughly search large patches (e.g., >20 ha). Nonetheless, 82% of all detections occurred within the first 20 minutes of a survey, with minimal additional gains from increasing search effort on most sites. This is consistent with previous findings (Litvaitis et al. 2006). These results suggest a trade-off in balancing survey efficiency with the need for certainty in the occupancy determination. The optimal solution will depend on the survey objective. Efficiency (time-limited search) may be more important for a broad-scale monitoring effort, where regional trends in occupancy are sufficient. On a local scale, where patch-specific knowledge of occupancy is required, the need for a higher degree of certainty will dictate an unlimited search time.

Factors Influencing Detection

Two factors, prior knowledge of cottontail activity and increased pellet deposition days, had a positive influence on detectability for both model sets. Having some knowledge of where cottontails have been active on a site had the strongest effect on each model set. Prior knowledge provides the observer with known areas to focus their search within the patch, sometimes even providing specific locations of cottontail burrows or runs. We also noticed that observers had a tendency to search more intently and more exhaustively on sites where they expected to find rabbits relative to sites where there was no such expectation. Most future monitoring surveys will likely lack prior knowledge, but the strong positive effect it provides suggests that it may be helpful for surveyors to talk with landowners and residents living on or around potential survey sites. This could be particularly true for large sites where anecdotal information could greatly improve search efficiency.

We found that allowing an increased number of days without high winds had a positive effect on detection, because these days reflect the amount of time available for pellets and other sign to accumulate. Deposition days will be most important for small sites (<3 ha) where occupancy determination may rely upon detecting just 1 or 2 individuals on a patch. Measuring deposition time by simply counting the number of days since the last snowfall without consideration of other weather factors may not reflect actual deposition time, because it does not account for the potential reduction in cottontail activity caused by poor weather. We found that the number of days without high winds was more influential than the number of days without extreme cold ($<-10^{\circ}$ C). Cold windy weather may limit cottontails more than cold, calm weather. Even with extremely cold nighttime temperatures, effective daytime temperatures in the sun, particularly on calm days, may be moderate enough not to limit cottontail activity. We also observed that locations with southern exposures had relatively high cottontail activity during cold mornings, suggesting that even on extremely cold days cottontails may be able to utilize microhabitats where temperatures are moderated. Additionally, cottontail activity may be limited in windy weather if noise caused by high winds limits predator detection. Some studies have found decreased lagomorph activity due to high wind (Fletcher et al. 1999, Ballinger and Morgan 2002), while others found no decrease in activity (Wallagedrees 1989, Twigg et al. 1998). It is likely that wind affects lagomorphs differently depending on the climate, season, and species. Our study occurred during the winter when high winds and poor weather likely have a direct impact on movement and survival.

Although detection probability increased with pellet deposition days, there are also negative effects associated with increased deposit days, including DNA degradation (Kovach et al. 2003) and decreased visibility caused by snow melt and accumulation of snow surface debris. These factors could not be modeled in this study because of the limited range of deposition days investigated (1–10 days, with a mean of 2.2 days; and only 3 out of 137 surveys occurred >5 days after snowfall), but they likely negate the benefit of additional deposit days beyond approximately 4 days. This is a particularly important consideration for sympatric sites, where quality DNA is critical for successful genetic species determination.

Snowpack <30.5 cm increased detection rates; this finding fits our expectations. Reduced snowpack provides easier travel for both cottontails and observers. Ease of travel increases cottontail activity, thereby providing additional sign for detection, and allows the observer to cover a greater search area in a given time period, thereby increasing the thoroughness of their search effort. Conversely, deep snow decreases cottontail movement and may promote subnivean travel and foraging, which have both been documented in pygmy rabbits (*Brachylagus idahoensis*; Katzner and Parker 1997). We observed large open-air pockets below the snow on several patches and cottontail runs were seen connecting these areas, so it is likely that a certain amount of subnivean activity occurs on sites where dense vines and vegetation create open space below the snow. Finally, low snowpack is more likely to occur in the early winter and late spring when weather conditions are generally milder, promoting increased cottontail activity.

We expected that patch stem density would affect detectability, but it was not a factor in any of our top models. Stem density may have had multiple confounding effects. Increased stem density is generally associated with increased cottontail density (Barbour and Litvaitis 1993, Litvaitis 2003), which should theoretically improve detection. Dense vegetation, however, reduces visibility of rabbit sign to observers and makes traveling through a patch more difficult. Both of these reduce search efficiency and decrease the likelihood of detection. Although our study was not designed to incorporate cottontail density, we expect that cottontail detection will be reduced on sites with low rabbit densities. The effect of rabbit density on detection is likely also influenced by patch size. Anecdotally, we observed that even large sites had high detection rates as long as they also had relatively large cottontail populations. Conversely, large sites with low rabbit densities had extremely poor detection (density determined from subsequent population surveys; Brubaker 2012). Overall, we found that patch size alone did not influence detection, unless search time was limited.

Other factors that may influence cottontail detectability but were not specifically modeled in this study are search area, geographic location, and sympatry of New England cottontails and eastern cottontails. Our detection results are only applicable to surveys conducted with the intensive protocol we used, in which we searched small to mid-sized patches exhaustively and searched $\geq$20% of the area of patches >6 acres (2.4 ha) in size. A reduction in search effort may decrease detection (Brubaker 2012).

Although we attempted to distribute our survey sites evenly range-wide to account for any potential geographic differences in detection, our final set of modeled sites was biased toward the northern portion of the species' range. This raises the possibility that detection rates may vary by geographic location if relevant environmental conditions, such as habitat or snowfall, vary across the species' range. We did not find stem density to be influential in our detection models, however, suggesting that habitat differences across the range would not affect detection. It is likely that the structural characteristics of the thicket habitats are similar enough across the species' range, despite differences in the specific vegetation assemblages, to have similar impacts on detection. By including both inland and coastal sites with a range of stem densities (our habitat covariate), we likely captured habitat variation. Differences in snowfall amounts between northern and southern portions of the species range also should not affect our conclusions about the influence of snow cover on detection, because we were able to evaluate a range of snow depths across the 30 sites. We note that our survey protocol stipulates that surveys occur after fresh snowfall, and detection is likely much lower without snow cover. Surveying with snow cover is important not only for pellet visibility, but also to preserve DNA quality for species identification (Kovach et al. 2003). The lack of snow cover in some years, particularly in the southern coastal portion of the range could prove challenging.

Another potentially important difference associated with geography is sympatry with eastern cottontails, which was absent from our northern sites. Sympatry may have a negative influence on detection and may require more intensive surveying of a greater proportion of a patch and potentially the collection of larger numbers of samples (Brubaker 2012). To more completely understand the influence of sympatric eastern cottontails on detection of New England cottontails, further investigation on sympatric sites using multi-species occupancy models (Royle and Dorazio 2008) may be warranted.

A final consideration is the extent that over-winter mortality may have influenced our findings. The assumption of closure cannot be met for a survey design that includes multiple visits, because mortality will always be a nontrivial factor in the nonbreeding season. The issue therefore is to what extent mortality might have influenced the outcome of our surveys. Brown and Litvaitis (1995) estimated over-winter survival rates of New England cottontails to be 0.37 on patches $\leq$2.5 ha and 0.7 on patches $\geq$5 ha (for a period of 100 days). Applying these rates, survival rates for the average survey window of 43 days in this study were 0.65 on patches $\leq$2.5 ha and 0.86 on patches $\geq$5 ha. Given that in occupancy determination, only one rabbit need be detected per patch, these survival rates suggest that mortality may only be a factor in detection on very small patches, occupied by only one or a few rabbits. Inspection of our raw data suggested that mortality was not a factor in detection in our surveys, even on small patches, because detection rates did not decrease over the survey window. For the 30 sites, absences were recorded for only 3 of them on the final visit, and all 3 of these also had non-detections in earlier survey visits, whereas non-detections were recorded on 9 sites for the first survey visits. Raw detection rates were higher for the later visits than for the earlier visits: 0.60, 0.67, 0.76, 0.85, and 0.76 for the first 5 visits, sequentially. Therefore, we believe that the effect of closure violations on this study was relatively minor. Moreover, because violations of closure in this study would entail patches that were believed to be occupied becoming vacant through mortality, the overall effect is to make our estimated detection rates slightly conservative. Nonetheless, we recommend that future surveys be conducted in a narrow survey window to minimize potential closure violations on small patches from over-winter mortality.

Recommended Survey Conditions

Environmental and other survey conditions influence detection probabilities of New England cottontails, and detection in turn influences the number of surveys required for accurate patch-specific occupancy knowledge. We found that generally, survey detection rates of 80% or higher occur under optimal survey conditions and will provide 95% confidence in occupancy determination after only 2 site visits. When detection rates range from 65% to 80%, $\geq$3 visits are required to achieve the same accuracy; while detection rates lower than 65%, which occur in suboptimal conditions, may require 4–6 survey visits for accurate occupancy determination.

Prior knowledge of cottontail activity has a very strong positive influence on detection probability and provides the only context in which a single survey visit may be sufficient to yield confident occupancy determination. Prior knowledge will rarely be available in most monitoring situations, so it is important to optimize other survey conditions. Highest detection can be achieved when surveys are conducted with snow depth <30.5 cm and 3–4 days without high winds (>40 km/hr) after a snowfall event. With these conditions, detection rates for a single visit may be as high as 90%, requiring only 2 visits for confident determination of occupancy. Surveying after fewer pellet deposition days decreases the detection rate to 73%, while detection rates for surveys in deep snow are 22% and 49% for 1 and 3 pellet deposition days, respectively, requiring 4–6 survey visits. It is important to keep in mind that the benefit of waiting additional days to allow pellets and sign to accumulate is only realized up to about 4 days, after which negative effects of reduced pellet and track visibility and increased DNA degradation likely outweigh any added benefit of increased deposition time. To optimize detection, we recommend that, to the extent feasible, New England cottontail surveys consist of 3 visits in ideal conditions (low snow depth and with 3–4 pellet deposition days) during as narrow a window as possible, in order to reduce closure violations (e.g., 3 weeks).

If survey effort is limited to 20 minutes, optimal conditions include prior knowledge and 3–4 days for pellet deposition, but detection will be affected by patch size. On small patches (<3 ha), detection rates still approach 90% but are only 70% on patches >25 ha. For time-limited surveys, a lack of prior knowledge reduces detection more significantly, with maximal detection of 62% on small sites and only 33% on large sites. Time-limited surveys on sites without prior knowledge would require 4–6 visits for high-confidence occupancy determination. This suggests that searching large sites with restricted search times may not be an efficient protocol. Further, the negative effect of increased patch size on detection is likely even greater on large sites with low cottontail densities. We therefore do not recommend limiting search time during presence–absence surveys if accurate patch-specific occupancy determination is the objective.

MANAGEMENT IMPLICATIONS

We anticipate that the findings of our study will facilitate more effective and reliable occupancy monitoring of New England cottontails, especially on a patch level. Accurate patch-specific occupancy data will enhance our knowledge of the species distribution, enable tracking changes in population status, assist in the selection of additional management focal areas, and facilitate monitoring responses to habitat management. We recommend therefore that our survey protocol and recommendations be incorporated into an adaptive management program for the species. Our findings also provide insight into the role of detection in monitoring rare and cryptic species that occupy dense habitats. Our approach may be useful in developing monitoring programs for other species of conservation concern, for which accurate patch-level data on occupancy status are necessary for conservation management.

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