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Forest Ecology and Management 325 (2014) 37-48



Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Multiscale habitat selection by a forest-dwelling shorebird, the American woodcock: Implications for forest management in southern New England, USA



Forest Ecology and Management

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ARTICLE INFO

Article history: Received 25 January 2014 Received in revised form 29 March 2014 Accepted 29 March 2014 Available online 23 April 2014

Keywords: Young forest American woodcock Resource selection function Habitat selection New England

ABSTRACT

Declines of young forest and associated populations of wildlife are major conservation concerns in the Northeast, USA. Active forest management is required to conserve declining populations of young forest wildlife and investigating habitat selection by target species can help inform management decision-making. The American woodcock (Scolopax minor) is a key indicator species of young forest whose populations have declined significantly since 1968. We investigated multiscale habitat selection by woodcock in Rhode Island, USA in order to characterize daytime habitat, and to predict state-wide relative probability of use by woodcock of forested land. We used radio-telemetry to monitor the daytime locations of woodcock at three state wildlife management areas from 23 May-25 August 2011 and 2012. Compared to random sites, woodcock selected younger forest where the biomass of preferred food (i.e., earthworms [Haplotaxida]) was 46-67% greater and the density of shrub and sapling stems was about two times greater. Most woodcock home ranges were <50 ha and usually comprised wetland forests and deciduous or mixed upland forests on flatter slopes that were closer to streams, agricultural openings, upland young forests, and moist soils. Using resource selection functions, we found that the majority of forested land in Rhode Island was in the low-moderate classes of relative use, but 92% of older second-growth upland forest in the state is located where woodcock habitat management would be beneficial for increasing relative use. We illustrate how land managers can use resource selection functions to compare expected responses of woodcock to alternative forest management scenarios and so maximize conservation benefits.

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1. Introduction

Reduced extent of early-successional forest and shrubland vegetation types (hereafter young forest) in the Northeast, USA, over the last 60 years has caused declines in populations of wildlife that depend on young forest (Askins, 2001; DeGraaf and Yamasaki, 2003; Dettmers, 2003; Trani et al., 2001). Historically, natural disturbance regimes such as wind, fire, and ice storms, and biological agents including insects, pathogens, beavers (*Castor canadensis*), and Native Americans sustained patchworks of young forest (Askins, 2001; Day, 1953; Foster and Aber, 2004; Lorimer, 2001). Prior to European settlement, young forest may have occupied up to 13% of the land area in some regions of eastern North America (Lorimer, 2001), but following European settlement, intensive log-

http://dx.doi.org/10.1016/j.foreco.2014.03.054 0378-1127/© 2014 Elsevier B.V. All rights reserved. ging and conversion of land from forest to agriculture formed a largely non-forested landscape which eventually produced an influx of young forest across the Northeast. Indeed, in central New England, USA, >75% of remaining forests were <30 years old during the late-1800s (Foster et al., 1998). However, since the 1960s, the amount of young forest in the region declined from about 30– 35% to $\leq 3\%$ (Buffum et al., 2011; Trani et al., 2001). Consequently, active forest management is now required to conserve populations of young forest wildlife (DeGraaf and Yamasaki, 2003; Schlossberg and King, 2007), and habitat selection by target species should be investigated using quantitative methods to promote more informed and efficient forest management decision-making.

Classical approaches to investigating habitat selection involve comparing attributes of habitat or food measured at sites used by target species and sites unused by or available to target species (Johnson, 1980; Manly et al., 2002). For example, studies comparing vegetation structure at nest or roost sites and random sites

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2. Methods

2.1. Study area

tures associated with reproduction or occupancy for forest birds (e.g., McAuley et al., 1996; Miller and Jordan, 2011; Zahner et al., 2012) and mammals (e.g., Hackett and Pagels, 2003; O'Keefe et al., 2009). More recently, studies of habitat selection have transitioned towards using resource selection functions (RSFs) to understand how probability of use by target species is influenced by environmental covariates (Johnson et al., 2006; Manly et al., 2002; McDonald, 2013). Importantly, these analysis methods allow multiple competing hypotheses to be easily tested using an information-theoretic approach (Anderson et al., 2000; Johnson et al., 2006), facilitate studies of habitat selection across multiple spatial scales (e.g., Johnson et al., 2004), and can be used to predict shifts in probability of use by target species in response to environmental change (e.g., Brown et al., 2007). We investigated habitat selection by American woodcock (Scolopax minor) using both traditional and contemporary analysis methods in order to inform young forest management in the Northeast.

using traditional null hypothesis testing help describe habitat fea-

The American woodcock (hereafter woodcock) is a key indicator species of young forest because populations thrive only in landscapes with an appropriate mixture of young forest ranging from forest openings to approximately 30-year-old forest stands (Kelley et al., 2008). Woodcock breed across the eastern USA and adjacent southern and southeastern Canada and winter mainly across the southern half of the eastern USA (Sheldon, 1967), and their populations have declined significantly since 1968 (Cooper and Rau, 2012). Although woodcock are a popular game bird, woodcock survival is similar between hunted and non-hunted sites so recreational hunting is not believed to be contributing to observed population declines (McAuley et al., 2005). Instead, loss and degradation of preferred young forest is the principal factor driving population declines (Dessecker and McAuley, 2001; Kelley et al., 2008; McAuley et al., 2005). High densities of small tree and shrub or sapling stems characteristic of young forests provide protective cover from diurnal predators (Dessecker and McAuley, 2001; Keppie and Whiting, 1994; McAuley et al., 1996; Straw et al., 1986) whereas recent forest clearcuts, maintained or abandoned agricultural fields, tree plantations, and other forest openings provide critical breeding areas during spring crepuscular periods (Sheldon, 1967), safe roosting areas during summer nights (Dunford and Owen, 1973; Masse et al., 2013), and feeding or roosting areas during fall and winter nights (Blackman et al., 2012; Connors and Doerr, 1982; Krohn et al., 1977).

In this study, we investigated habitat selection by woodcock in important state-owned wildlife management areas in Rhode Island, USA, where young forest was limited, but actively being created. Young forest occupies only 3% of the land area in Rhode Island (Buffum et al., 2011) and an estimated 377 km² of new young forest is needed to restore woodcock densities (Kelley et al., 2008). Our objectives were to (1) characterize the daytime habitat selected by woodcock, (2) predict and map the relative probability of use by woodcock of forested land across Rhode Island, and (3) illustrate how land managers can forecast how forest management practices aimed at creating woodcock habitat influence relative use of the surrounding landscape. Addressing these objectives will increase knowledge of woodcock habitat selection in areas where preferred young forest is uncommon and permit more informed forest management decision-making. We predicted that woodcock would select areas of younger forest where preferred food (i.e., earthworms [Haplotaxida]) and shrub or sapling stems were more abundant, and that creating upland young forest and forest openings via forest clearcutting at sites deemed most beneficial for woodcock habitat management would increase relative use of the surrounding landscape.

We investigated woodcock habitat selection in three state wildlife management areas (Arcadia, Big River, and Great Swamp) in Kent and Washington Counties, Rhode Island. Each management area was dominated by forested cover types although the relative proportions of each differed among sites (RIGIS, 2012). Arcadia (41°35′10″N, 71°43′20″W) was 62 km² of which deciduous (33%), mixed (31%), and coniferous upland forest types (24%) predominated, while wetland forest types (7%) were uncommon. Big River (41°37′0″N, 71°36′60″W) was 33 km² and comprised deciduous (8%), mixed (31%), and coniferous upland forest types (45%), while wetland forest types (6%) were scarce. In contrast, Great Swamp $(41^{\circ}27'15''N, 71^{\circ}35'19''W)$ was 15 km² and composed of deciduous (16%), mixed (5%), and coniferous upland forest types (1%), while wetland forest types (55%) were common. Mixed oaks (Quercus spp.), hickories (Carya spp.), and red maple (Acer rubrum) dominated deciduous upland forest types while coniferous and mixed upland forest types were dominated by Eastern white pine (Pinus strobus) and oaks and pines, respectively (Enser and Lundgren, 2006). Red maple swamps were the most widespread wetland forest type and Atlantic white cedar (Chamaecyparis thyoides) swamps occurred locally (Enser and Lundgren, 2006).

During 1995, the Rhode Island Department of Environmental Management initiated a forest cutting program to benefit declining populations of woodcock and other wildlife associated with young forest. A series of 2-5-ha clearcuts in older second-growth forest (e.g., 60-100 years) were initially made at Great Swamp followed by additional forest management at that site during 2007 and 2012. Similar forest management began at Arcadia and Big River during 1996 and 2006, respectively. Future management at each site is expected to involve additional forest cutting at regular (e.g., 10-year) intervals and, where appropriate, the creation of larger (e.g., 10-ha) young forest patches. At the time of this study, Great Swamp contained the highest proportion of combined upland and wetland young forest (15%) whereas young forest was uncommon at Arcadia (2%) and Big River (1%). Forest openings in the form of abandoned meadows and agricultural fields were also maintained to benefit woodcock and other wildlife, but the relative proportions of these at each site were low (i.e., 1-2%).

2.2. Woodcock capture, marking, and tracking

We caught woodcock from 2 April–16 May 2011 and 2012 (IACUC protocol AN10-02-017) by placing mist-nets at known singing grounds where males engaged in crepuscular courtship displays to attract females for breeding (McAuley et al., 1993; Sheldon, 1967). We included only male woodcock in our study because females are difficult to catch with mist-nets during spring (McAuley et al., 1993). We caught 50 males during 2011 and 42 males during 2012, and determined age by examining plumage characteristics of wings (Sheldon, 1967). After capture, we fitted each woodcock with an Advanced Telemetry Systems 2-stage transmitter (Model A5400) using cattle tag cement and a wire belly-band for attachment (package weight \leq 4.0 g; McAuley et al., 1993) and released birds on site.

From 23 May–25 August 2011 and 2012, we monitored the daytime locations of each bird 3–4 times per week. We tracked radiomarked birds on foot using a 3-element antenna and approached each bird until the receiver gave an audible signal without the use of the antenna or headphones. On average, this method allowed us to approach to ≤ 18 m (Masse et al., 2013) and we marked exact locations in the field using a handheld GPS unit. We located each bird once during each monitoring day (0600-1900 EST) and stratified our telemetry schedule by time of day during subsequent weeks to ensure that the majority of the daytime period was represented in the sample of telemetry locations for each bird. Male woodcock generally concentrate daytime activity within small areas (Hudgins et al., 1985), called diurnal coverts, and so we approached marked birds from different directions on subsequent visits in order to circumscribe selected coverts. Since we were interested in summer habitat selection we included in our study only those individuals for which we obtained >25 locations throughout each monitoring period. Consequently, we excluded 40 woodcock because they died (2011: n = 4; 2012: n = 4), slipped their transmitters (2011: n = 3; 2012: n = 4), or moved away from study sites and could not be relocated (2011: n = 16; 2012: n = 9) prior to obtaining sufficient numbers of telemetry locations (Table 1).

2.3. Habitat sampling

We sampled woodcock habitat at two spatial scales in order to investigate third- and second-order selection. Third-order selection pertains to specific sites selected by individuals within their home ranges whereas second-order selection pertains to the positioning of home ranges within a broader landscape or geographical range (Johnson, 1980).

2.3.1. Third-order selection

For analysis of third-order selection, we considered diurnal coverts represented by clusters of telemetry locations for each bird similar to Hudgins et al. (1985). For each woodcock, clusters of \geq 5 locations in which each location was \leq 100 m of another location were defined as a diurnal covert and we delineated the boundaries of diurnal coverts using minimum convex polygons (MCP; Mohr, 1947). We delineated 1-3 diurnal coverts for each woodcock, but each bird generally showed preference for a single diurnal covert and so we designated for each bird a primary diurnal covert that contained the most telemetry locations. If an individual woodcock selected multiple diurnal coverts with equal frequency then we randomly selected one to represent the primary diurnal covert. Primary diurnal coverts for 16 of 52 woodcock overlapped to some degree and so in situations where overlap was >20% we randomly selected one woodcock's primary diurnal covert for inclusion. In addition, one woodcock was tracked during both years so we randomly selected one year to include for this individual. As a result, we promoted independence among the primary diurnal coverts included in this portion of our study and ensured that each woodcock (2011: *n* = 11 at Arcadia, 8 at Big River, and 3 at Great Swamp; 2012: n = 4 at Arcadia, 7 at Big River, and 9 at Great Swamp) was represented equally.

We assessed third-order selection by measuring habitat variables in 5-m radius (0.008-ha) circular plots that were randomly located inside (n = 5) and outside (n = 5) each bird's primary

diurnal covert from 24 August-30 September 2011 and 2012. We used Geospatial Modeling Environment (Beyer, 2013) to randomly select plot locations up to 500 m outside each primary diurnal covert. We enforced a minimum distance of 15 m between plot locations to ensure that plots did not overlap. At the center of each plot, we collected a 10-cm deep soil core and determined soil pH, soil moisture content (% by weight), and soil organic matter content (% by weight) following Masse et al., (2013). We also dug a 900-cm² soil pit to 10-cm deep at the center of each plot and collected all earthworms by hand sorting soil pit contents (Dangerfield, 1997). We estimated earthworm density $(\#/m^2)$ and measured fresh and freeze-dried earthworm weight (g/m^2) to the nearest 0.001 g. We calculated canopy closure (%) at the center of each plot using a spherical densiometer (Lemmon, 1957) and visually estimated overstory height class (i.e., 0-3 m, 3-9 m, or >9 m) for each plot. We measured diameter at breast height (dbh) of all live trees (>10-cm dbh) within each plot to the nearest 0.1 cm and used the program NED-2 (Twery et al., 2011) to determine density (#/ha), basal area (m^2 /ha), and medial dbh (cm) of trees, and overstory size class (i.e., regeneration [<2.5-cm dbh], sapling [2.5-11.4-cm dbh], pole [11.5-26.7-cm dbh], small sawtimber [26.8–41.9-cm dbh], or large sawtimber [\geq 42.0-cm dbh]) for each plot. We also recorded generalized overstory cover type (i.e., deciduous upland forest, coniferous upland forest, mixed upland forest, wetland forest, or herbaceous) for each plot based on dominant vegetation. Lastly, within each plot we counted the number of live shrub and sapling stems (≤10-cm dbh and \geq 1.5-m tall) in four randomly located 1-m² quadrats and calculated mean shrub and sapling density (#/ha) for each plot.

2.3.2. Second-order selection

For analysis of second-order selection, we estimated the diurnal home range and core-use area for each bird during 2011 and 2012 using kernel density methods (Worton, 1989). We used Geospatial Modeling Environment (Beyer, 2013) to generate each home range (95% contour) and core-use area (50% contour) using a Gaussian kernel with likelihood cross-validation bandwidth estimator. The least squares cross-validation bandwidth estimator and ≥30 locations per individual have been recommended for home range studies (Seaman et al., 1999), but the likelihood cross-validation bandwidth estimator produces better fit and less variability with moderate to small sample sizes (i.e., ≤ 50 locations per individual; Horne and Garton, 2006). On average, we obtained 35 and 34 locations per individual during 2011 and 2012, respectively. However, we included four woodcock (2011: *n* = 2; 2012: *n* = 2) with 26–29 locations each because the size of their home ranges and core-use areas were within the range of values for woodcock with \ge 30 locations. Previous research of woodcock movements and habitat selection used MCPs to determine home range size (e.g., Hudgins et al., 1985; Sepik and Derleth, 1993) and so we also calculated these home range estimates to facilitate comparisons with other studies.

Table 1

Initial and remaining number of radio-tagged male woodcock in Kent and Washington Counties, Rhode Island, USA. Woodcock were removed from the initial sample if they died (n = 8), slipped their transmitter (n = 7), or moved away from study sites and could not be relocated (n = 25) prior to obtaining >25 telemetry locations during 23 May–25 August 2011 and 2012. We determined age as either after-second-year (ASY) or second-year (SY) based on plumage characteristics of wings.

Age	2011			2012		
	Arcadia	Big River	Great Swamp	Arcadia	Big River	Great Swamp
ASY						
Initial	11	9	9	7	9	5
Remaining	7	7	3	2	6	3
SY						
Initial	11	5	5	6	5	10
Remaining	6	4	0	4	3	7

We used a design I study with sampling protocol A (Manly et al., 2002) to assess second-order selection. For each site, we delineated a composite area of available woodcock habitat by pooling individual kernel home ranges across years and circumscribing them with a MCP. We delineated available habitat in this way because individuals frequently moved across the landscape during crepuscular periods (Masse et al., 2013) and so encountered, and selected against, areas outside of their diurnal home ranges. We delineated a composite area of used woodcock habitat for each site by pooling individual kernel core-use areas across years. Since woodcock remain in forested coverts during the day (Dessecker and McAuley, 2001; Hudgins et al., 1985) we clipped composite areas of available and used habitat by forest boundaries using ArcGIS 10.1 (Environmental Systems Research Institute, Redlands, CA). We converted composite areas of available and used woodcock habitat into separate raster grids (10-m² pixel resolution) for each management area and generated raster-based habitat data at this standardized cell size. We obtained 1/3 arc-second elevation (Gesch et al., 2002), stream (RIGIS, 2001), soil (RIGIS, 2013), and land cover data (RIGIS, 2012), and generated separate grids for elevation (m), slope (%), forest cover type (i.e., coniferous upland forest, deciduous upland forest, mixed upland forest, upland young forest, coniferous wetland forest, deciduous wetland forest, mixed wetland forest, and wetland young forest), and Euclidean distance (m) to the nearest stream, nearest agricultural opening (i.e., agriculture, pasture, idle agriculture, or tillable crops), nearest upland young forest, and nearest moist soil (i.e., moderately well drained, poorly drained, or very poorly drained). For each site, we randomly selected 10% of available (n = 22,598 at Arcadia, 16,955 at Big River, and 13,431 at Great Swamp) and used (n = 1275 at Arcadia, 537 at Big River, and 1235 at Great Swamp) pixels, and extracted values from the corresponding cells in the elevation, slope, forest cover type, and distance grids.

2.4. Statistical analysis

We treated all variables measured inside and outside primary diurnal coverts quantitatively except for generalized overstory cover type. For each of the interval variables (e.g., overstory size class) we either assigned mid-point values to each interval or, for open-ended intervals (e.g., large sawtimber), assigned a value consistent with the spacing of interval mid-points to permit quantitative analysis. We calculated the mean for each quantitative variable across the five plots inside and outside each primary diurnal covert and log-transformed earthworm density, earthworm fresh weight, and earthworm dry weight to improve normality.

We conducted principle components analysis using the correlation matrix (Johnson and Wichern, 2007) of the 13 quantitative variables to obtain uncorrelated, linear combinations of these variables. We used analysis of variance (Ott and Longnecker, 2010) to test the main effects of plot location (i.e., inside vs. outside), age, site, and year on each retained principle component, and adjusted for multiple comparisons using the Tukey-Kramer method (Kramer, 1956). We also tested for interactions between plot location and other main effects, but dropped interaction terms that were not significant (i.e., P > 0.05). We verified model assumptions of residual normality using the Shapiro-Wilk test (Shapiro and Wilk, 1965) and by inspecting normal probability plots, and homogeneity of variance by inspecting residual plots. We used multinomial logistic regression (Agresti, 2007) to test the main effects of plot location, age, and year on generalized overstory cover type. We set mixed upland forest as the reference category, specified a mixed model by treating bird identity as a random effect, and used the Gauss-Hermite quadrature approximation method to obtain maximum likelihood estimation (SAS, 2011; PROC GLIMMIX). We did not test the main effect of site on generalized overstory cover type because not all cover types were represented at each site and cover type differences were already evident among management areas (see 2.1) so we were not interested in further quantifying these differences.

Kernel home range and core-use area size were strongly correlated (r = 0.99) so we tested for differences in home range size only. Kernel home ranges and core-use areas were often divided into multiple parts as a result of woodcock movement patterns and so we counted the number of home range and core-use area divisions for each bird to help characterize this aspect of second-order selection. The number of home range and core-use area divisions were moderately correlated (r = 0.51) so we retained both variables. We log-transformed kernel home range size in order to improve normality and used analysis of variance to test the main effects of age, site, and year on home range size. We adjusted for multiple comparisons, tested for interactions between main effects, and assessed model assumptions as before. We used loglinear regression assuming a Poisson distribution (Agresti, 2007) to test the main effects of age, site, and year on the number of home range divisions and core-use area divisions. We also tested for interactions between main effects, but dropped interactions that were not significant. We adjusted for slight underdispersion in the number of home range divisions, and slight overdispersion in the number of core-use area divisions, using the deviance scale parameter (SAS, 2011; PROC GENMOD).

We used logistic regression to derive the coefficient values for the exponential form of the RSF $[w(x) = \exp(\beta_1 x_1 + \dots + \beta_p x_p)]$ based on available and used habitat (Manly et al., 2002). Johnson et al. (2006) found this approach to be both theoretically appropriate and quantitatively robust to sample contamination (i.e., available sample containing used and unused resource units) and overlap (i.e., resource units occurring in the available sample and used sample). Contamination of our sample of available habitat was low (6%) and overlap among our samples of available and used habitat was minimal (<1%). Correlations among quantitative variables were weak (|r| < 0.39) and variance inflation factors were low (<1.5) so we retained all variables for model building. We generated 15 a priori logistic regression models relating the probability of use by woodcock of forested land to geographic variables and used the information-theoretic approach based on Akaike's Information Criterion (AIC) and Akaike weights (w_i) to select the best candidate model (Anderson et al., 2000). We used Raster Calculator (ArcGIS 10.1) to map the relative probability of use by woodcock of forested land in Rhode Island based on the best candidate model and reclassified relative use into five ordinal classes using geometrical interval classification. Johnson et al. (2006) noted that typical methods for assessing logistic regression performance and model fit are not appropriate for use-availability designs so we used their validation method to evaluate the best candidate model and to assess proportionality of the RSF to true probability of use. We generated a validation dataset by merging composite areas of used woodcock habitat across sites and randomly selecting 10% of remaining pixels (n = 2494) that were not present in the samples used to build the RSFs. Following Johnson et al. (2006), we determined observed and expected numbers of used pixels in the validation dataset within each ordinal class, converted these into proportions, and used linear regression and chi-square goodnessof-fit to assess the relationship between observed and expected proportions.

Lastly, we illustrated how the RSF can be used to (1) identify areas of older second-growth upland forest in Rhode Island, generally 60–100-years-old (Butler et al., 2012), where management to create woodcock habitat might be most beneficial, and (2) forecast how certain forest management practices influence relative use by woodcock of the surrounding landscape. For the first illustration, we calculated for each quantitative variable retained in the best candidate model, the maximum value within the composite areas of used woodcock habitat. For those variables that reduced the relative probability of use by woodcock, we considered maximum values to represent tolerances beyond which were less suitable for woodcock. For example, if distance to the nearest upland young forest reduced the relative probability of use by woodcock and the maximum distance within composite areas of used woodcock habitat was 1000 m then areas ≤ 1000 m from upland young forest were considered more suitable for woodcock while those >1000 m were considered less suitable. We used the maximum value for each of these variables to select older second-growth upland forest that might be most beneficial for woodcock habitat management. For the second illustration, we considered a 4-km² case study area because management of a woodcock habitat mosaic is recommended at this scale (Williamson, 2010). We chose a site in Arcadia where woodcock were known to occur, forest management practices to improve woodcock habitat have previously been implemented, and the estimated relative use by woodcock varied from low to high. We simulated the creation of about 30 ha of upland young forest patches (n = 7; range = 2–10 ha) and 10 ha of herbaceous forest openings (n = 3; range = 2–6 ha) within areas of deciduous, mixed, or coniferous second-growth forest deemed most beneficial for habitat management, and then re-calculated the RSF to illustrate how relative use changed in response to forest cutting. For simplicity, we placed hypothetical management units adjacent to roads (i.e., access points) and \geq 100 m from the nearest stream. We ignored other criteria which might influence where forest cutting can occur, but vary from region to region (e.g., state or local ordinances).

3. Results

3.1. Third-order selection

We identified 46 diurnal coverts during 2011 and 36 diurnal coverts during 2012. During 2011, 15 of 27 woodcock selected 2–3 diurnal coverts throughout the summer while others selected one diurnal covert. In contrast, during 2012, 14 of 25 woodcock selected one diurnal covert throughout the summer while others selected two diurnal coverts. Diurnal coverts represented small areas of concentrated activity (mean ± SE = 0.64 ± 0.07 ha; median = 0.43 ha; range = 0.02-4.22 ha) and primary diurnal coverts were only marginally larger (mean = 0.86 ± 0.10 ha; median = 0.64 ha; range = 0.12-4.22 ha).

We retained the first three principle components because their eigenvalues were >2.0, whereas all other eigenvalues were <1.0. The first three components accounted for 80% of the total variance. Component 1, forest overstory, was characterized by greater values of canopy closure, overstory height class, tree density, basal area, medial dbh, and overstory size class; component 2, food resource, was characterized by greater values of earthworm density, earthworm fresh weight, and earthworm dry weight; and component 3, forest understory, was characterized by greater values of soil moisture content, soil organic matter content, and shrub and sapling density (Table A.1).

Forest overstory component scores were lower inside primary diurnal coverts (F_1 = 15.18, P < 0.001; Fig. 1a), and we found no evidence for significant effects of age, site, year, or interactions ($P \ge 0.152$). Canopy closure was about 7% lower, and tree density, basal area, and medial dbh were 21–29% lower inside primary diurnal coverts (Table 2). Overstory height class was within the 3–9 m interval inside primary diurnal coverts. Overstory size class was within the 11.5–26.7 cm (i.e., pole) interval inside and outside primary diurnal coverts, but overstory trees outside primary



Fig. 1. Mean scores for the forest overstory (a), food resource (b), and forest understory (c) habitat components sampled inside and outside the primary diurnal coverts of male woodcock in Kent and Washington Counties, Rhode Island, USA, from 24 August–30 September 2011 (n = 22) and 2012 (n = 20). Primary diurnal coverts exhibited lower forest overstory scores (P < 0.001), greater food resource scores (P = 0.009), and greater forest understory scores (P = 0.038). Whiskers represent ± 1 SE.

diurnal coverts tended towards the 26.8–41.9 cm (i.e., small saw-timber) interval (Table 2).

Food resource component scores were similar at Arcadia and Big River, but greater at Great Swamp ($F_2 = 6.87$, P = 0.002), and were greater inside primary diurnal coverts ($F_1 = 5.97$, P = 0.009; Fig. 1b). We found no evidence for significant effects of age, year, or interactions ($P \ge 0.063$). Non-transformed earthworm density (mean ± SE) was 20–24% greater at Great Swamp (18.70 ± 4.56) than Arcadia (14.89 ± 4.68) or Big River (14.14 ± 3.91) while earthworm fresh weight was 48–62% greater at Great Swamp (10.91 ± 4.41) than Arcadia (5.63 ± 1.87) or Big River (4.18 ± 1.21). Earthworm dry weight was 39–51% greater at Great Swamp (2.10 ± 0.80) than Arcadia (1.28 ± 0.41) or Big River (1.02 ± 0.30). Irrespective of site, earthworm density, earthworm fresh weight, and earthworm dry weight were 46–67% greater inside primary diurnal coverts (Table 2).

Forest understory component scores were also similar at Arcadia and Big River, but greater at Great Swamp (F_2 = 14.02,

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Non-transformed range, mean ± SE, and median for the variables associated with the forest overstory, food resource, and forest understory habitat components measured inside and outside the primary diurnal coverts of male woodcock in Kent and Washington Counties, Rhode Island, USA, from 24 August–30 September 2011 (*n* = 22) and 2012 (*n* = 20).

Variable	Inside diurnal coverts			Outside diurnal coverts		
	Range	Mean	Median	Range	Mean	Median
Canopy closure (%)	23.14-98.44	77.79 ± 3.44	87.26	22.83-99.22	83.30 ± 2.23	87.21
Overstory height class (m)	1.50-10.50	7.99 ± 0.42	8.70	5.10-10.50	9.34 ± 0.20	9.60
Tree density (#/ha)	0.00-1196.80	465.63 ± 44.36	382.00	178.30-967.70	591.14 ± 29.23	611.15
Basal area (m ² /ha)	0.00-46.30	22.07 ± 2.30	21.93	5.09-67.84	31.27 ± 2.08	29.98
Medial dbh (cm)	0.00-41.51	20.62 ± 1.75	20.87	12.11-38.77	26.63 ± 0.96	26.98
Overstory size class (cm)	5.80-40.80	22.44 ± 1.45	23.00	11.80-37.80	26.69 ± 0.91	25.60
Earthworm density (#/m ²)	0.00-95.50	23.70 ± 4.30	12.20	0.00-51.10	7.72 ± 2.01	0.00
Earthworm fresh weight (g/m^2)	0.00-41.71	8.29 ± 1.65	3.31	0.00-102.69	4.96 ± 2.51	0.00
Earthworm dry weight (g/m^2)	0.00-8.71	1.84 ± 0.36	0.64	0.00-17.47	1.00 ± 0.45	0.00
Soil moisture content (%)	9.33-86.09	40.04 ± 3.31	35.44	11.12-82.39	41.65 ± 2.86	36.72
Soil organic matter content (%)	1.68-87.64	25.87 ± 3.25	19.46	5.71-63.14	29.86 ± 2.53	29.22
Shrub and sapling density (#/ha)	2500.00-78,500.00	21,452.38 ± 2704.03	15,500.00	0.00-33,000.00	11,488.10 ± 1457.64	7750.00

P < 0.001), and were greater inside primary diurnal coverts ($F_1 = 3.24$, *P* = 0.038; Fig. 1c). We found no evidence for significant effects of age, year, or interactions (*P* ≥ 0.220). Soil moisture content (mean ± SE) was 30–51% greater at Great Swamp (57.56 ± 3.98) than Arcadia (40.35 ± 2.84) or Big River (27.96 ± 2.51) and soil organic matter content was 37–51% greater at Great Swamp (40.57 ± 3.72) than Arcadia (25.76 ± 3.35) or Big River (19.81 ± 2.67). Shrub and sapling density was 44–52% greater at Great Swamp (25,000.00 ± 2821.69) than Arcadia (12,033.33 ± 2419.62) or Big River (14,083.33 ± 2699.20). Regardless of site, soil moisture content and soil organic matter content were similar inside and outside primary diurnal coverts whereas shrub and sapling density was 46% greater inside primary diurnal coverts (Table 2).

Generalized overstory cover type differed by plot location ($F_{4248} = 4.58$, P = 0.001), but we found no evidence for significant effects of age or year ($P \ge 0.124$). Relative to mixed upland forest, the odds of occurring inside primary diurnal coverts were similar for deciduous upland forest (odds ratio = 1.26, 95% CI = 0.68–2.34), wetland forest (odds ratio = 1.61, 95% CI = 0.80–3.21), and herbaceous cover types (odds ratio = 0.52, 95% CI = 0.14–1.90). In contrast, relative to mixed upland forest, coniferous upland forest was less likely to occur inside primary diurnal coverts (odds ratio = 0.16, 95% CI = 0.06–0.44).

3.2. Second-order selection

We found no evidence for significant effects of age, site, year, or interactions on kernel home range size ($P \ge 0.091$). Non-transformed kernel home range size varied from 1.04 to 474.52 ha with a mean ± SE of 51.13 ± 13.81 ha and median of 11.29 ha. Core-use area size varied from 0.19 to 75.49 ha with a mean of 8.45 ± 2.21 ha and median of 2.03 ha. Minimum convex polygon home range size varied from 0.43 to 487.01 ha with a mean of 57.55 ± 12.52 ha and median of 19.24 ha. The number of kernel home range divisions differed by age ($F_{147} = 5.15$, P = 0.023), but we found no evidence for significant effects of site, year, or interactions ($P \ge 0.065$). The home ranges of after-second-year males were divided into 1.59 (95% CI = 1.06–2.41) times more parts than the home ranges of second-year males. We found no evidence for significant effects of age, site, year, or interactions on the number of core-use area divisions ($P \ge 0.246$).

Of the 15 *a priori* logistic regression models that we tested (Table A.2), the top-ranked model produced the lowest AIC and accounted for 94% of the Akaike weight. This model suggested that the relative probability of use by woodcock (1) increased with increasing elevation, (2) decreased with increasing slope, (3) was higher in deciduous upland forest, mixed upland forest, deciduous wetland forest, mixed wetland young forest,

but lower in coniferous upland forest, upland young forest, and coniferous wetland forest, and (4) decreased with increasing distance to the nearest stream, agricultural opening, upland young forest, and moist soil (Table 3). The vast majority of forested land in Rhode Island occurred in the low (445 km²), low-moderate (234 km²), moderate (533 km²), and moderate-high (444 km²) classes of relative use whereas areas of high relative use (46 km²) were widely scattered (Fig. 2a). Our validation of the RSF revealed adequate fit between observed and expected proportions of pixels in each ordinal class ($X_4^2 = 0.083$, P = 0.999). In addition, the linear regression model relating observed and expected proportions of pixels in each ordinal class (y = 0.921x + 0.016) had an intercept similar to 0 (P = 0.718), a slope >0 (P = 0.011), but near 1, and a high R^2 (0.912) indicating that the RSF was proportional to true probability of use.

3.3. Applications of the resource selection function

Older second-growth upland forest (e.g., 60–100 years) in Rhode Island where woodcock habitat management was deemed most beneficial was within the maximum values of used woodcock habitat (i.e., composite core-use areas; see 2.3.2) for each quantitative variable that reduced relative probability of use in the highest

Table 3

Coefficient values (β) for each of the variables included in the three highest-ranked resource selection functions relating the relative probability of use by woodcock of forested land from 23 May–25 August 2011 and 2012 to geographic variables in Rhode Island, USA. Coefficients were derived using logistic regression under a use-availability design. Variables included elevation, slope, forest cover type (ForCov), and Euclidean distance to the nearest stream (D2Strm), agricultural opening (D2Ag), upland young forest (D2UYF), and moist soil (D2MS). Coefficients for forest cover type were estimated using dummy variables with mixed upland forest serving as the reference category.

β	Model 1	Model 2	Model 3
Elevation	0.00210		0.00165
Slope	-0.01870	-0.01760	
ForCov ^a			
CUF	-0.31110	-0.32520	-0.31970
DUF	0.09060	0.08440	0.07260
UYF	-0.22690	-0.26200	-0.19820
CWF	-0.02730	-0.05390	0.03100
DWF	0.68390	0.61330	0.75650
MWF	0.19930	0.15660	0.26160
WYF	0.39340	0.32270	0.47500
D2Strm	-0.00080	-0.00083	-0.00075
D2Ag	-0.00162	-0.00162	-0.00163
D2UYF	-0.00025	-0.00021	-0.00025
D2MS	-0.00117	-0.00106	-0.00135

^a Coniferous upland forest (CUF), deciduous upland forest (DUF), upland young forest (UYF), coniferous wetland forest (CWF), deciduous wetland forest (DWF), mixed wetland forest (MWF), and wetland young forest (WYF).

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Fig. 2. Relative probability of use by woodcock of forested land (a) and areas of older second-growth upland forest, generally 60–100 years, where woodcock habitat management was deemed most beneficial for increasing relative use (b) in Rhode Island, USA. Relative use was derived from the exponential form of a resource selection function based on a use-availability design. Second-growth upland forest was classified as most beneficial for woodcock habitat management if it occurred on slopes \leq 53% and within 1211 m of the nearest stream, 1314 m of the nearest agricultural opening, 1498 m of the nearest upland young forest, and 639 m of the nearest moist soil. Arcadia Wildlife Management Area, the site where an example case study was conducted, is shown for reference.

ranked resource selection function. Generally, management of older second-growth upland forest was deemed most beneficial on slopes $\leq 53\%$ and within 1211 m of the nearest stream, 1314 m of the nearest agricultural opening, 1498 m of the nearest upland young forest, and 639 m of the nearest moist soil. Most (1281 km²) older second-growth upland forest was located in areas where woodcock habitat management was classified as most beneficial while only 109 km² was located in areas where management was classified as least beneficial (Fig. 2b). Across the 4-km² case study area, clearcutting 40 ha (10%) to produce young forest and forest openings reduced the 210 ha of forested land in the low class of relative use to 118 ha, increased the 77 ha in both the low-moderate and moderate classes of relative use to 103 ha and 115 ha, respectively, and increased the 22 ha in the moderate-high class of relative use to 38 ha (Fig. 3).

4. Discussion

4.1. Third-order selection

We found that daytime activity by male woodcock in Rhode Island was highly localized within areas of their home range. In Pennsylvania, USA the diurnal coverts of male woodcock during April–May were about 0.1–1.0 ha (Hudgins et al., 1985). Most (74%) of the diurnal coverts that we identified were within this range, but some were as much as four times larger. Adult females caring for young concentrated daytime activity within areas that were approximately 0.8–2.6 ha in Minnesota, USA (Wenstrom, 1974) and 1.0–2.8 ha in Pennsylvania (Caldwell and Lindzey, 1974) so localized habitat selection is not specific to males. Localized habitat selection has also been found during winter months in Alabama, USA where woodcock activity centers were from 0.4 to 5.7 ha (Horton and Causey, 1979). Historically, young forest likely occurred as relatively small, isolated patches resulting from localized natural disturbances (Askins, 2001) so woodcock and other young forest birds likely adapted to exploit small areas of preferred habitat (Askins et al., 2007).

The structure of preferred young forest provides woodcock protection from predators (Dessecker and McAuley, 2001; Keppie and Whiting, 1994; McAuley et al., 1996; Straw et al., 1986), but older forest might also be selected for nesting, brood-rearing, or feeding if the density of shrub or sapling stems is sufficient to provide similar protective cover (Dessecker and McAuley, 2001; Williamson, 2010). On average, tree density inside the primary diurnal coverts

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Fig. 3. Relative probability of use by woodcock of forested land in a 4-km² case study area in Arcadia Wildlife Management Area in southwestern Rhode Island, USA, that is considered for forest management (a). The hypothetical forest management scenario considered for this site (b) included creating 30 ha of upland young forest and 10 ha of herbaceous forest openings (e.g., wildlife openings or old fields) in areas of older second-growth upland forest (e.g., 60–100 years) deemed most beneficial for woodcock habitat management. Following management (c), the estimated extent of low relative use by woodcock of the managed forest decreased by 92 ha while the estimated extents of low-moderate, moderate, and moderate-high relative use increased by 26 ha, 38 ha, and 16 ha, respectively. White areas represent non-forested cover types in panels (a) and (c), and these cover types along with cover types other than older second-growth upland forest in panel (b).

that we investigated was about 466 stems/ha which was less than the tree density associated with aspen (*Populus* spp.; mean = 760 stems/ha) and mixed deciduous forest types (mean = 890 stems/ ha) selected by woodcock in Michigan, USA (Rabe, 1977), but similar to the tree density associated with nesting and brood-rearing habitat selected by female woodcock (range = 400–783 stems/ha; Dessecker and McAuley, 2001). In Pennsylvania, optimum basal area of trees and sapling density for daytime habitat was estimated to be 14.3 m²/ha and 4900 stems/ha, respectively, and woodcock generally avoided areas where basal area was $\geq 20.0 \text{ m}^2/\text{ha}$ and sapling density was <1500 stems/ha (Straw et al., 1986). We found that mean basal area inside primary diurnal coverts was 22.1 m²/ ha and shrub and sapling density was 21,452 stems/ha. While overstory trees inside primary diurnal coverts tended to be shorter and smaller in diameter (i.e., younger) than those outside (Table 2), woodcock in Rhode Island may currently be selecting the best available forest rather than optimum forest.

The high shrub and sapling density typical of diurnal coverts in Rhode Island may protect woodcock from predators even though the structure of selected coverts differs from young forests that woodcock typically select in other areas of the Northeast. Indeed, in some areas, understory structure rather than species composition may be most useful for identifying sites selected by woodcock (Rabe, 1977). The shrub and sapling density that we observed inside primary diurnal coverts was over four times greater than the sapling density at sites selected by woodcock in Pennsylvania (Straw et al., 1986) and similar to shrub and sapling densities in areas selected by female woodcock in Minnesota (Morgenweck, 1977) and Maine, USA (McAuley et al., 1996). Moreover, shrub and sapling density was nearly two times greater inside than outside primary diurnal coverts. We only documented eight mortalities among the 60 woodcock that we monitored during summers 2011 and 2012 so woodcock survival is relatively high in Rhode Island. Woodcock survival is also relatively high in Maine (Derleth and Sepik, 1990) where optimum habitat is more widespread. Thus, the shrub and sapling density typical of diurnal coverts in Rhode Island apparently provides similar protective cover as forests selected by woodcock in other parts of the Northeast.

Woodcock typically feed in forested coverts during the day (Masse et al., 2013) and so our findings that woodcock consistently selected forest stands where earthworm availability was at least 46% greater than random sites (Table 2) help support this conclusion. On average, earthworm dry weight at heavily-used diurnal coverts in Maine was 18.2 g/m² compared to 15.4 and 7.8 g/m² at commonly- and rarely-used diurnal coverts, respectively (Reynolds et al., 1977). During summer, greater earthworm density or biomass at sites selected by woodcock has also been reported in Pennsylvania (mean = 34.4 earthworms/m²; Hudgins et al., 1985) and Minnesota (range = $4.4-23.0 \text{ g/m}^2$; Morgenweck, 1977). In contrast, Sepik and Derleth (1993) found no relationship between earthworm dry weight and woodcock habitat selection in Maine, but noted that mean earthworm dry weight was 8.9 g/m² at sites selected by woodcock. Mean earthworm density (23.7 earthworms/ m^2) and dry weight (1.8 g/ m^2) inside primary diurnal coverts in Rhode Island were generally lower than those found elsewhere in the Northeast. However, earthworm availability was even more limited outside primary diurnal coverts (Table 2) suggesting that woodcock selected areas that could maximize feeding opportunities.

4.2. Second-order selection

We found that the size of kernel home ranges and core-use areas for male woodcock in Rhode Island were highly variable, but did not differ by age, site, or year. Historically, MCPs have been the standard method used to estimate woodcock home ranges, but the shortcomings of this method have prompted researchers to advocate kernel methods for contemporary studies (Powell, 2000). Yet, MCPs may still be a valid and favored method for delineating areas used by certain taxa (e.g., herpetofauna; Row and Blouin-Demers, 2006) or under certain situations (e.g., our delineation of primary diurnal coverts). During summer, mean diurnal home range size (MCP) for adult (19 ha) and juvenile (13 ha) male woodcock in Maine did not differ (Sepik and Derleth, 1993) which coincides with our conclusion using kernel methods. The mean home range sizes that we observed for woodcock in Rhode Island using either kernel or MCP methods were considerably larger than mean MCP home range estimates for woodcock in Maine (8–19 ha depending on cohort; Sepik and Derleth, 1993) and Alabama (9.2 ha; Horton and Causey, 1979). However, the median home range sizes that we observed were similar to those found in Pennsylvania (median = 3.1–73.6 ha depending on activity level; Hudgins et al., 1985) and more similar to mean home range sizes reported elsewhere. The unusually large home ranges that we observed for some woodcock (e.g., 474.5 ha) inflated our estimates of mean home range size and are clearly not typical of most woodcock in Rhode Island as 73% and 67% of kernel and MCP home ranges, respectively, were <50 ha.

Adult male woodcock have been found to move greater distances between successive daytime locations than juvenile males (Sepik and Derleth, 1993) so this could partially explain why the number of home range divisions was greater for the older cohort in our study. Animal memory is likely an important factor influencing home range use patterns (Van Moorter et al., 2009) and the diurnal home ranges of more experienced (i.e., older) woodcock might be divided into more parts if these birds tend to re-visit familiar sites on the landscape in order to exploit resources which could vary spatially or temporally (e.g., earthworms; Reynolds et al., 1977). For example, the one woodcock that we were able to monitor during subsequent summers was a second-year during 2011 and an after-second-year during 2012. During 2011, his diurnal home range was divided into two parts which were separated by about 146 m whereas his home range during 2012 was divided into four parts which, on average, were separated by about 973 m (range = 137–1628 m). Importantly, this male showed some capacity to re-visit sites used in previous years while also exploiting apparently new areas on the surrounding landscape since one of the four divisions of his 2012 home range overlapped with one of the divisions of his 2011 home range.

All else being equal, relative use by woodcock of forested land tended to be greatest in wetland forest and lowest in coniferous upland forest (Table 3). Wetland forest may be particularly attractive to woodcock as daytime habitat during summer because the moist soils typically associated with this cover type tend to promote higher densities of earthworms and shrub or sapling stems (Williamson, 2010). The fact that relative use was most negatively influenced by coniferous upland forest coincides with our finding that this cover type was less likely to occur inside primary diurnal coverts. Consequently, relative use by woodcock can effectively be increased if older, second-growth, coniferous upland forests are harvested and replaced with upland young forest, or deciduous or mixed upland forest. However, coniferous upland forest may be selected by woodcock during periods of summer drought (Sepik et al., 1983) so some of this forest type should be maintained on landscapes within or around woodcock habitat mosaics.

We also found that relative use by woodcock of forested land decreased at higher slopes and farther distances from the nearest stream, moist soil, upland young forest, and agricultural opening. Woodcock habitat suitability also declined on steeper slopes in West Virginia, USA (Steketee, 2000). In general, woodcock habitat management is considered most beneficial on flatter slopes (Dessecker and McAuley, 2001) perhaps because these areas can better support earthworm populations (Steketee, 2000). Our findings that proximity to streams and moist soils influences relative use supports the views that creating woodcock habitat closer to streams (Williamson, 2010) or across moisture gradients (Dessecker and McAuley, 2001) is most beneficial. The affinity of woodcock to young forest has been well-documented across the Northeast (Hudgins et al., 1985; McAuley et al., 1996; Sheldon, 1967) so we expected relative use to decrease as distance to the nearest upland young forest increased. However, we were somewhat surprised to find that relative use also decreased as distance to the nearest agricultural opening increased because greater proportions of agriculture on the surrounding landscape reduced woodcock habitat suitability in West Virginia (Steketee, 2000) and were not associated with areas used by woodcock during spring in Pennsylvania (Klute et al., 2000). Variation in the response of woodcock populations to agricultural openings likely relates to the predominant type of agriculture in a region or considered in a given study, but this subject has yet to be investigated. Some agricultural openings provide critical breeding sites for woodcock during spring (Sheldon, 1967) and roosting sites during summer (Dunford and Owen, 1973; Masse et al., 2013) so the proximity of these landscape features to forests used by woodcock has some ecological relevance. Declines of woodcock populations in Pennsylvania from the 1960s–1970s mirrored declines in the extent of pastureland and other cover types used by woodcock (Gutzwiller et al., 1980) so it seems reasonable that forests further from certain agricultural openings are generally less ideal than those closer to these forest openings.

4.3. Applications of the resource selection function

Given the link between declines of woodcock populations and young forest, the American Woodcock Conservation Plan (AWCP) established habitat goals for restoring woodcock densities to those of the 1970s (Kelley et al., 2008). Across the Northeast, >22,000 km² of young forest is needed to restore woodcock densities (Kelley et al., 2008) so widespread, active forest management will be required if the goals of the AWCP are to be met. Forest clearcutting is generally regarded as the most efficient method for creating quality woodcock habitat (Dessecker and McAuley, 2001; McAuley et al., 1996; Williamson, 2010). On the one hand, non-game birds which require similar young forest would likely benefit from woodcock habitat management. On the other hand, removing all trees from select areas may be aesthetically displeasing (Gobster, 2001) or viewed as harmful to populations of wildlife that require more mature forest (Wallendorf et al., 2007). Consequently, forest management efforts to create quality woodcock habitat should be strategically-coordinated and scientificallyinformed so that conservation benefits are maximized while negative impacts are minimized.

Managing young forest to increase relative probability of use by woodcock of surrounding landscapes can help improve connectivity between habitat patches thereby reducing the negative impacts of habitat patch isolation. Moderate-high and high classes of relative use were widely scattered across Rhode Island (Fig. 2a) and metapopulation theory dictates that immigration to habitat patches decreases as isolation of habitat patches increases (Hanski, 1998). We used our RSF to identify 1281 km² of older second-growth upland forest where habitat management might be most beneficial for increasing relative use by woodcock (Fig. 2b). About 377 km² of young forest must be managed in Rhode Island to restore woodcock population densities (Kelley et al., 2008), but this represents roughly 14% of the total land area and is about four times larger than the current extent of young forest in the state (Buffum et al., 2011). A more feasible goal might be to first stabilize the extent of non-coastal upland young forest by clearcutting about 136 ha of older second-growth forest per year over the next 20 years (Buffum et al., 2011). We recommend that forest clearcutting to create habitat for woodcock and other young forest wildlife (e.g., New England cottontail [Sylvilagus transitionalis]) should take place in areas identified as most beneficial for management in order to help meet the goals of the AWCP. In addition, other land management practices such as allowing \ge 30 m buffers around agricultural openings to regenerate into young forest benefit woodcock (Williamson, 2010) and increase the extent of young forest without requiring older forest to be cut down.

In the Northeast, woodcock best management practices focus on creating habitat mosaics that provide all necessary components of quality habitat within a 4-km² landscape (Williamson, 2010). About 25% of each habitat mosaic should be maintained as young forest by clearcutting blocks >2 ha on a 40-year rotation (McAuley et al., 1996), and occasional herbaceous forest openings (e.g., wildlife openings or old fields) should be maintained to provide breeding sites (e.g., >0.2 ha each; about eight per 40 ha) and roosting sites (e.g., >2 ha each; about one per 40 ha; Williamson, 2010). Clearcutting forest blocks >1 ha has also been recommended to conserve other species of young forest birds (Schlossberg and King, 2007). Moreover, wildlife openings such as old fields provide adequate habitat for some of these species (King et al., 2009). We used our RSF to show that creating 30 ha of upland young forest and 10 ha of herbaceous forest openings at key sites in a 4-km² case study area increased relative use by woodcock of surrounding forested land (Fig. 3).

Clearcutting older second-growth upland forest to enhance woodcock habitat is not suitable in all areas so tools that can distinguish where management efforts are likely to be most effective will be useful in forest management decision-making. The RSF that we developed represents such a tool for biologists managing woodcock habitat across Rhode Island or similar landscapes in the Northeast. Geographic data sets can be easily manipulated allowing biologists to simulate competing forest management plans, forecast the response of target woodcock populations using our RSF, and then select the management plan that produces the greatest increase in relative probability of use. Resource selection functions can accommodate various study designs and data collection methods (Manly et al., 2002) so biologists in other regions can develop their own RSFs provided they have basic data on used and available or unused sites. Employing quantitative tools such as RSFs during the decision-making process will help to maximize conservation benefits and facilitate more efficient and effective forest management planning.

Acknowledgments

Funding for this project was provided by the following sources: Rhode Island Agricultural Experiment Station, the US Department of Agriculture McIntyre-Stennis (MS-975) and Hatch (H-333) grants, the Rhode Island Department of Environmental Management via USFWS Federal Aid to Wildlife Investigations Project W-23R, and the Department of Natural Resources Science at University of Rhode Island. Many volunteers assisted with woodcock captures and we thank them for their help. We also thank T. Heywood, S. Camillieri, J. Veale, J. Travers, A. Hunt, A. Padula, W. Shean, L. Barnard, D. Duffin, and D. McAuley for their help in the field. Finally, we thank A. Smith and L. Gonzalez for statistical advice, and the two anonymous reviewers that provided helpful comments on an earlier version of this paper. This is contribution number 5397 of the Rhode Island Agricultural Experiment Station.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014. 03.054.

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