

## RESEARCH ARTICLE



# Sex-specific differences and long-term trends in habitat selection of American woodcock

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## Abstract

Effective wildlife management requires an understanding of how individuals select environmental factors, although few studies assess how habitat selection may differ over time or between sexes. During the post-breeding period (15 May to 1 Sep), we tracked 146 male American woodcock (*Scolopax minor*) in Rhode Island, USA, from 2010–2021 to assess how habitat selection varied over time, and 17 females and 51 males during the final 2 years of the study to document sex-specific differences in habitat selection. Males generally had smaller home ranges ( $35.0 \pm 10.7$  [margin of error] ha) and preferred habitat mosaics that consisted of forested wetlands, young forest patches, areas of deciduous forest, moist soils with gentle slopes, and riparian corridors. We detected subtle differences between sexes in selection for wetland young forest, upland young forest, percent slope, distance to upland young forest, distance to streams, and distance to moist soils. During 2020–2021, females tended to have larger home ranges ( $78.7 \pm 46.4$  ha) than males ( $35.0 \pm 10.7$  ha) and more strongly selected sites closer to riparian corridors, while males selected areas that were closer to upland young forest with flatter slopes than the available surrounding landscape. Such sex-specific differences in habitat selection may be related to males and females prospecting for potential breeding sites during this post-breeding period for the following spring. We used the top-ranked habitat selection models for males and females to produce a spatially explicit state-wide map that identifies low-to-high likelihood of use areas that can be used to guide

forest management decisions in southern New England to maximize benefits for American woodcock.

#### KEYWORDS

probability of use maps, radio telemetry, Rhode Island, *Scolopax minor*, shorebirds, young forest

Understanding the resources individuals select is an important component of effective habitat management, especially for declining species (Johnson 1980, Johnson et al. 2006, Northrup et al. 2022). Often, habitat selection is investigated at multiple spatial scales to understand the hierarchical selection process that occurs as an individual, or group of individuals, interacts with and assesses their environment (Rettie and Messier 2000, Manly et al. 2002, Masse et al. 2014, Fattbert et al. 2018). For migratory birds, habitat selection is often assessed during periods that biologists perceive as more important portions of the annual cycle (e.g., breeding, nesting), even though each period is inextricably linked (Bowlin et al. 2010). As a result, one of the more understudied periods of the annual cycle is the post-breeding period directly after young have fledged when adults become more quiescent (e.g., reduced mating displays and vocalizations) and disperse from breeding sites. In well-studied groups like waterfowl, post-breeding habitat selection is markedly different from other portions of their annual cycle, and the availability and quality of these sites plays an important role in their readiness for fall migration (Batt et al. 1992, Savard and Petersen 2015, Lamb et al. 2019). Furthermore, sex-specific spatial segregation during the non-breeding season has been observed in diverse species including marine fish, reptiles, birds, and mammals (Wearmouth and Sims 2008). The importance of such intraspecific differences in habitat selection for land management and conservation is rarely examined. Therefore, it is especially important to investigate habitat use of both males and females during the post-breeding season when negative effects of poor habitat quality (i.e., the suitability of resources to support populations) may affect survival or preparation for fall migration (Batt et al. 1992, Savard and Petersen 2015, Lamb et al. 2019, Graham et al. 2022).

Sex-specific spatial segregation (i.e., sex segregation) has been studied in plants, birds, fishes, and mammals, with most studies focused on ungulates (Bowyer et al. 2001, Long et al. 2009, Dutt et al. 2020). Pronounced sexual dimorphism in ungulates promotes spatial segregation that allows each sex to procure resources necessary for survival and to meet their varied energetic demands while limiting intraspecific competition (Bowyer 2004). Like ungulates, most shorebird species are sexually dimorphic, although they more often exhibit reverse sexual size dimorphism such that females are larger than males (Jehl and Murray 1986). Aside from distinctions in overall body size, female shorebirds are often disproportionately longer billed than their male counterparts, which may facilitate partitioning of resources (Jehl and Murray 1986, Nebel 2005, Stein et al. 2008). Sex segregation in shorebirds may occur at both geographic and local scales (Cristol et al. 1999). At geographic scales, females of some shorebird species travel farther south than males during winter migration (Gill et al. 1995, Cristol et al. 1999, Nebel 2005, Catry et al. 2006), whereas at local scales, males and females may forage at different water depths allowing them to simultaneously procure resources at shared feeding sites (Both et al. 2003, Nebel 2005, Alves et al. 2013). As a result, understanding sex segregation in relation to habitat use is necessary for effective population management, especially at local scales.

American woodcock (*Scolopax minor*) exhibit a strong degree of sexual dimorphism that is much greater than most other shorebird species, yet the selective pressures that have led to this male-female size disparity remain unclear (Keppie and Redmond 1988). Woodcock inhabit forested landscapes (Sheldon 1961) and are considered a species of conservation concern in the northeastern United States because of population declines related to loss and degradation of young forests (Dessecker and McAuley 2001, McAuley et al. 2005, Masse et al. 2014, Seamans and Rau 2022). In southern New England, male woodcock prefer areas with higher elevation, flatter slopes, and closer to upland forest openings, streams, and moist soils (Masse et al. 2014). Most male woodcock translocated

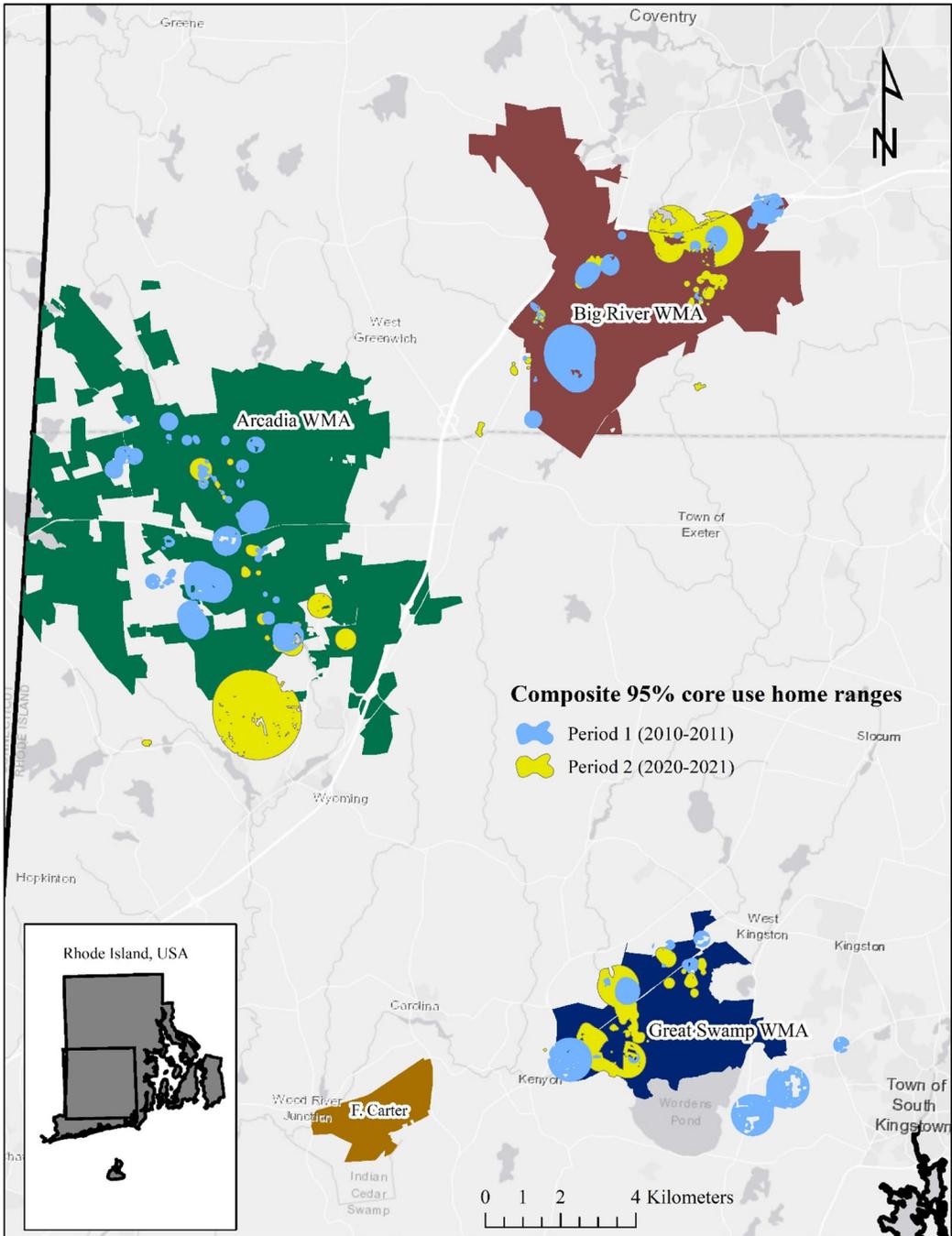
from high- to low-quality sites (i.e., areas distinctly different in relative probability of use scores) quickly moved back to high-quality sites and most birds translocated to high-quality sites remained at the release site, suggesting that males rapidly assessed the quality of forest types and landscape composition in ways consistent with that predicted from habitat selection models (Brenner et al. 2019). Studies of woodcock habitat use have primarily focused on males (Horton and Causey 1979, Hudgins et al. 1985, Masse et al. 2014, Seamans and Rau 2018, Brenner et al. 2019) in part because of the difficulty associated with capturing females during the spring breeding season (McAuley et al. 1993a, Masse et al. 2014). Aside from a lack of female data, many studies of male habitat selection span only 2–3 years (Horton and Causey 1979, Hudgins et al. 1985, Sepik et al. 1993, Masse et al. 2014, Brenner et al. 2019). Qualitative assessments of forests used by woodcock are common (Horton and Causey 1979, Sepik and Dwyer 1982, Hudgins et al. 1985, Dwyer et al. 1988, Sepik et al. 1993), but few researchers have quantitatively assessed which environmental factors are most important (Masse et al. 2014, Allen 2017), especially simultaneously for both male and female woodcock.

In this study, we used our long-term (9 years over an 11-year period) radio-telemetry tracking data to assess how male woodcock habitat selection during the post-breeding season may change over a decade. For the last 2 of these 9 years, we also quantified male and female habitat selection during the post-breeding season when the resource needs of males and females may differ. Based on body size and associated daily energy expenditure differences between the sexes (Keppie and Redmond 1988), we predicted that females would more strongly select food-rich, wet areas compared to males. Our specific objectives were to determine changes in male habitat selection between 2010–2011 and 2020–2021 in relation to changes in availability of young forest, determine whether male and female habitat selection differed for individuals tracked at the same spatiotemporal scale, and assess long-term male habitat selection and produce habitat selection models for males and females to guide forest management practices and enhance post-breeding habitat quality for woodcock in southern New England.

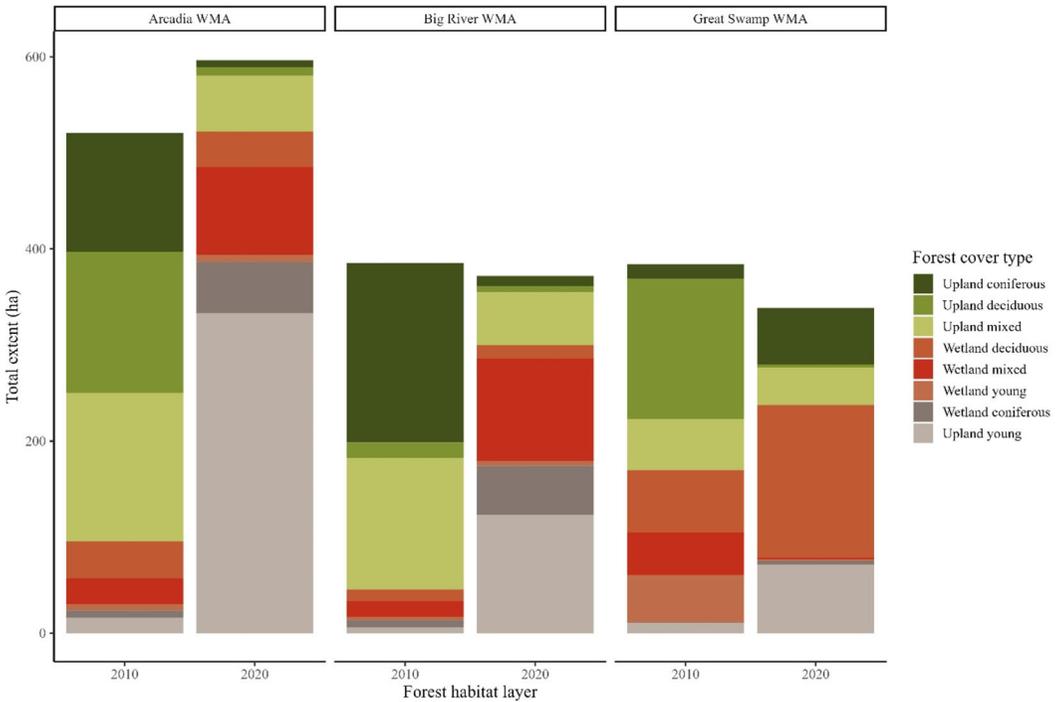
## STUDY AREA

We assessed male woodcock habitat selection during the post-breeding period (15 May–1 Sep) from 2010–2021 in 3 state-owned Wildlife Management Areas (WMAs) and 1 Preserve in Kent and Washington counties, Rhode Island, USA (Figure 1). Specifically, we studied male habitat selection at Big River and Great Swamp during 9 years (2010–2012, 2015–2016, 2018–2021), at Arcadia for 7 years (all years except 2018–2019), and Francis Carter Preserve for 6 years (all years except 2010–2012). For 2 years (2020–2021), we focused on documenting sex-specific habitat selection of males and females at these same 4 study areas.

In this region of southern New England, mixed oaks (*Quercus* spp.), hickories (*Carya* spp.), and red maple (*Acer rubrum*) typically dominate in deciduous upland forests, whereas eastern white pine (*Pinus strobus*) was common in coniferous forests, and mixed forests typically contained combinations of oaks and white pine; red maple and Atlantic white cedar (*Chamaecyparis thuyoides*) swamps were common in forested wetlands (Enser and Lundgren 2006). Common fauna in southern New England forested areas include white-tailed deer (*Odocoileus virginianus*), eastern cottontail (*Sylvilagus floridanus*), eastern gray squirrel (*Sciurus carolinensis*), and gray catbird (*Dumetella carolinensis*; <https://www.inaturalist.org>, accessed 4 Jul 2023) in young forests, and veery (*Catharus fuscescens*; Masse et al. 2015) in mature forests. Common understory flora in these mixed-age forests include rugosa rose (*Rosa rugosa*), oriental bittersweet (*Celastrus orbiculatus*), multiflora rose (*Rosa multiflora*), and common milkweed (*Asclepias syriaca*; <https://www.inaturalist.org>, accessed 4 Jul 2023). Elevation in Rhode Island ranges from 0–247 m ( $\bar{x}$  = 61 m) and consists of 3 topographical divisions: narrow coastal plain, gentle rolling uplands, and hilly uplands (<https://dem.ri.gov/climate/climate-overview-ri.php>, accessed 4 Jul 2023). During the summer season in Rhode Island, mean monthly temperatures range from 13–23°C and mean monthly rainfall ranges from 7.1–8.1 cm from May to August annually (30-year normal; <https://prism.oregonstate.edu/normals/>, accessed 4 Jul 2023). All study areas were forest-dominated and were actively managed to create and maintain stands of young forest for woodcock and



**FIGURE 1** The 3 Wildlife Management Areas (WMAs) and 1 preserve used in our 3 analyses of woodcock habitat selection in Rhode Island, USA, 2010–2021, with composite male home ranges from the first (2010–2011) and second (2020–2021) periods.



**FIGURE 2** Total extent (ha) of each forest cover type within the pooled 95% home ranges of woodcock at Arcadia, Big River, and Great Swamp Wildlife Management Areas (WMAs) in Rhode Island, USA, during the 2 time periods (2010–2012 and 2016–2021).

other associated species of conservation concern (Buffum et al. 2019). Each of these study areas varied in the extent of different forest cover types and especially young forest (Figure 2). To assess spatial coverage of the various forest cover types from 2010–2021, we used the 2010 forested cover layer for the period of 2010–2012 and an updated 2020 layer for the period of 2016–2021 (Rhode Island Geographic Information System [RIGIS] 2023).

## METHODS

### Woodcock capture, marking, and tracking

During the entire study, we operated mist-nets daily during evening crepuscular periods from 5 April–1 June to capture male woodcock while they performed their aerial courtship displays (Sheldon 1961, McAuley et al. 1993a, Masse et al. 2014, Brenner et al. 2019, Graham et al. 2022). In our area, woodcock typically returned as early as late-February or early-March although many males caught and marked before 5 April do not remain in the area and presumably continue migrating north (Masse et al. 2014, Brenner et al. 2019). We received historical reports of nesting females as early as 15 March from hunters who ran practice trials with pointing dogs on WMAs, so we chose an earlier start date for capturing females (15 Mar) compared to that for males (5 Apr). From 15 March–1 June 2020 and 2021, we used 3 techniques to capture woodcock females because female woodcock are occasionally captured with mist-nets operated during evening periods (McAuley et al. 1993a). In both years, we placed mist-nets at male singing grounds to catch the occasional females at night, and we used pointing dogs to locate brooding females

during the day (Ammann 1974, 1977; McAuley et al. 1993a; Daly et al. 2015; Huinker 2020). During 2021, we also used thermal cameras (FLIR Scout III 320 or FLIR Scion OTM230, Teledyne FLIR, Wilsonville, OR, USA) after sunset to locate additional brooding females (Keller et al. 2019). Whenever we located a brooding female, we would return later that same day to attempt a capture with a long-handled net (Ammann 1974, 1977; McAuley et al. 1993a, b; Daly et al. 2015; Huinker 2020). This allowed us to gather the capture equipment and to use the newly tagged chicks as a way to cautiously approach and net the females before she flew. If we found a nesting female, we waited until the nest hatched before attempting a capture to avoid nest abandonment (Horton and Causey 1984). We captured 35 females ( $n_{2020} = 18$ ;  $n_{2021} = 17$ ) using these various capture methods (44% in mist-nets, 41% with pointing dogs, and 5% with thermal camera). We captured and marked an additional 4 females ( $n_{2020} = 3$ ;  $n_{2021} = 1$ ) because other wildlife researchers incidentally flushed brooding females while working in the field. We determined age and sex of woodcock in the field using the methods described in Martin (1964). For each captured bird, we measured mass, wing chord, width of outer 3 primaries, and culmen length (Greeley 1953, Martin 1964, Masse et al. 2014). We then attached an A5400 ATS (Advanced Telemetry Systems, Isanti, MN, USA) very high frequency (VHF) transmitter using a crimped wire belly band and cattle tag cement (McAuley et al. 1993a). Mass of the transmitter and attachment materials was  $\leq 4.0$  g, which was approximately 2.4–3.3% of the body mass of males in our study and 1.7–2.6% of the body mass of females in our study.

We tracked males ( $\bar{x} = 33.66 \pm 1.98$  locations) and females ( $40.94 \pm 2.12$  locations)  $\geq 3$  times/week from 15 May–1 September so that we could construct home ranges and assess post-breeding habitat selection (McAuley et al. 1993a, Masse et al. 2014, Brenner et al. 2019, Graham et al. 2022). We chose 15 May as the start of the post-breeding period because we observed declines in male breeding activity (e.g., singing; Brenner et al. 2019) and female breeding activity (e.g., brooding young; C. R. Slezak, University of Rhode Island, personal observation) after this date, and we ensured that all females included in this analysis had completed nesting. The weekly locations for each individual were stratified across the day so that approximately equal numbers of diurnal locations were recorded in the morning (before noon) and afternoon. We assessed the location of each bird by walking in on individuals until we could hear the telemetry signal without the Yagi antenna attached (mean distance to bird was  $\leq 18$  m; Masse et al. 2014); often this technique got us within view of marked birds without causing birds to flush. If a bird was flushed, we took a global positioning system point from the location the bird flushed from, and we exercised greater caution when approaching the bird during subsequent checks to ensure that we did not cause undue disturbance. For some birds ( $n_{\text{males}} = 16$ ;  $n_{\text{females}} = 7$ ) during 2020–2021, when access was limited or we could not get landowner permission, we recorded bearings from 3 separate locations ( $>30$  degrees apart) using Avenza maps and then triangulated the bird's location using the package sigloc (version 0.0.4; Berg 2015) in Program R (R Core Team 2022). For many of these birds ( $n_{\text{males}} = 8$ ;  $n_{\text{females}} = 7$ ), we gained property access or found an alternative entry point during the same tracking bout, allowing us to walk-in and confirm the accuracy of our triangulations. We located all males and females included in the analyses ( $n_{\text{males}} = 146$ ;  $n_{\text{females}} = 17$ )  $\geq 25$  times between 15 May–1 September, when woodcock begin to undergo physiological changes in preparation for fall migration (Owen and Krohn 1973, Graham and McWilliams 2021). Of the 210 radio-tagged males and 22 females still present at the beginning of the study period (15 May), we excluded 64 males and 5 females across all years that provided  $\leq 25$  locations for the following reasons: 33 males and 3 females died, 9 males slipped transmitters, and 22 males and 2 females were absent from the study area for an extended period (Table S1, available in Supporting Information). The final dataset included only 1 male and 1 female that were tracked for more than a single summer.

## Habitat selection over time and between sexes

We compared third-order habitat selection (usage made of various habitat components within the home range; Johnson 1980) for males between 2 time periods (2010–2011, 2020–2021; objective 1). We generated kernel

density home ranges (KDEs; 95% contours) for individuals with  $\geq 25$  telemetry locations using the Geospatial Modelling Environment (Geospatial Modelling Environment version 0.7.4, <http://www.spatialecology.com/gme>, accessed 1 Nov 2022) and the least-squares cross-validation bandwidth method suggested by Horne and Garton (2006), which is applicable for animal relocation data with  $\leq 50$  telemetry points. After filtering our telemetry dataset to include only individuals that had  $\geq 25$  locations, we had 41 males ( $n_{2010} = 15$ ;  $n_{2011} = 26$ ) in the first period and 42 males ( $n_{2020} = 22$ ;  $n_{2021} = 20$ ) in the second period across 3 study areas (i.e., Arcadia, Big River, and Great Swamp WMAs). Because woodcock are typically found in forested areas during the day, we clipped our home ranges to forested boundaries (Hudgins et al. 1985, Dessecker and McAuley 2001, Masse et al. 2014) using ArcMap (version 10.3.1; Esri, Redlands, CA, USA). Prior to clipping home ranges to these forested boundaries, we buffered the forest cover layer by 20 m to account for our intentional  $\leq 18$ -m approach distance. This buffer allowed us to assign a forest cover type to telemetry locations (used points) that fell just outside of all forested cover types that we deemed available to woodcock. We then randomly generated 5,000 available points within the estimated 95% KDEs for each bird. From all our used and available points, we extracted values for each of our environmental factors. We later weighted this availability sample by 2 within our generalized linear mixed models to ensure that our availability sample had correctly characterized all available habitats within each bird's home range, and that our coefficient estimates had converged (Northrup et al. 2013). We used the original environmental layers from Masse et al. (2014) and newer 2020 versions of these layers when available for the study herein (2020–2021) as outlined below. To determine the change in forest cover type area within our availability sample (Figure 2), we calculated the area of each forest cover type within the composite 95% home range (Figure 1; pooled 95% KDEs) for the 3 main study areas separately in each period. Then for each study site, we calculated the change in area for each of the forest cover types between periods 1 (2010–2011) and 2 (2020–2021) within the pooled home ranges (Figure 1).

We repeated the above analysis of third-order selection to compare male and female habitat selection from tracking data collected during the final 2 years (2020–2021) of the study (objective 2). After filtering our telemetry dataset to include only individuals that had  $\geq 25$  locations, we had 51 ( $n_{2020} = 26$ ;  $n_{2021} = 25$ ) males and 17 ( $n_{2020} = 8$ ;  $n_{2021} = 9$ ) females. For the male-female comparison, we included all 4 study areas because we tracked both males and females there during these years. We used the same methods as described above for males to estimate KDEs, clip and assign used points to a forested cover type, and estimate forest cover types available within the 95% KDEs. We also created minimum convex polygon home ranges (MCPs) in Geospatial Modelling Environment for males and females during 2020–2021 so that we could compare our home range sizes to other studies of woodcock habitat use (Hudgins et al. 1985, Sepik and Derleth 1993, Masse et al. 2014).

We repeated the above analyses on our long-term (2010–2021) male-only dataset ( $n = 146$  males; objective 3). We compiled tracking data from 4 separate studies of woodcock in Rhode Island. Like our male-female comparison, we included all 4 study areas in this analysis, although birds from Francis Carter Preserve were tracked only since 2016. From 2010–2012, Masse et al. (2014) tracked 66 males ( $n_{2010} = 15$ ;  $n_{2011} = 26$ ;  $n_{2012} = 25$ ) 3 times/week from 15 May–1 September to assess male habitat selection. From 2016–2017, Brenner et al. (2019) tracked 10 males ( $n_{2016} = 6$ ;  $n_{2017} = 4$ ) 3 times/week from 15 May–15 August as part of a reciprocal transplant study. From 2018–2019, Graham et al. (2022) tracked 22 males ( $n_{2018} = 9$ ;  $n_{2019} = 13$ ) 3 times/week from 15 May–31 August to assess the influence of pre-migratory habitat use on fall migration strategies. During 2020–2021, we tracked 48 males ( $n_{2020} = 25$ ;  $n_{2021} = 23$ ) 3 times/week from 15 May–1 September to assess changes in habitat use over the last decade of woodcock research.

## Resource layers used for the analysis of third-order selection

We used the most current available land cover layers to address each of the 3 objectives. These layers included 1/3 arc elevation (Gesch et al. 2002, U.S. Geological Survey 2020) and RIGIS layers for 1:5000 streams, soils, and

forested cover data (RIGIS 2023). The 1:5000 stream layer was the only dataset that had not been updated during the time our data were collected (2010–2021); thus, we used the same layer in our more contemporary and vintage raster datasets. For each of the 2 periods (2010–2011 and 2021–2021), we created separate rasters (10-m scale) for elevation, percent slope, forest cover type, and Euclidian distance (m) to 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).

To investigate shifts in habitat selection for males over time (2010–2012 vs. 2020–2021), we used older layers for woodcock tracked during 2010–2012: elevation (2002), streams (2001), soils (2013), and forested cover (2010). We used newer versions of these layers when available for data collected 2016–2021: elevation (2020), streams (2001), soils (2020), and forested cover (2020). We assume that the pairing of the male telemetry data for a given year with the resource layers that most closely corresponded in time adequately corrected for any changes in forested cover from 2010–2021 (no changes were evident in other resource layers). For our study of sex-specific differences in habitat selection (2020–2021), we used the most current available resource layers: elevation (2011), streams (2001), soils (2020), and forested cover (2020). Finally, for our long-term study of male habitat selection, we used older layers coinciding with Masse et al. (2014): elevation (2002), streams (2001), soils (2013), and forested cover (2010). We used newer versions of these layers (when available) coinciding with Brenner et al. (2019), Graham et al. (2022), and the study herein: elevation (2020), streams (2001), soils (2020), and forested cover (2020).

## Statistical analysis

For our 2 comparison studies (objectives 1, 2), we wanted to determine if KDE home range size estimates differed between the 2 periods or sexes, respectively. We first log-transformed KDE home range size to improve normality. To compare home range sizes between the 2 periods, we ran a multiple linear regression using the function `lm()` in the stats package in R (R Core Team 2022). We considered period, study area, and the interaction of these 2 terms as predictors of home range size using all males tracked with  $\geq 25$  locations from 2010–2011 and 2020–2021. To compare home range sizes between males and females, we ran a multiple linear regression with sex, study area, age (second year, after second year), and the interactions of these terms as predictors of home range size for our dataset of males ( $n = 51$ ) and females ( $n = 17$ ) tracked with  $\geq 25$  locations from 2020–2021. We limited the male-female home range comparison to 2 study areas (Great Swamp and Arcadia WMAs) because these were the only study areas that had enough males and females to facilitate comparison.

To determine the best explanatory habitat selection model, we generated 5 sets of the same 15 *a priori* generalized linear mixed-effects logistic regression models (Table S2, available in Supporting Information) and conducted model comparison for each of the 3 analyses separately in Program R (R Core Team 2022). For the 2 comparison studies (objectives 1, 2), we modeled habitat selection models separately for males and females and during periods 1 and 2. We first calculated Spearman rank correlation for all of our continuous variables using the function `rcorr()` in the package Hmisc (version 5.1-1; Harrell and Dupont 2023) to check for highly correlated covariates ( $r_s \geq 0.7$ ). None of our continuous variables in either the male or female tracking datasets were highly correlated (all  $r_s \leq 0.2$ ), so we retained all variables for model creation. We scaled and centered ( $\bar{x} = 0$  and  $SD = 1$ ) our continuous variables using the `scale()` function in Program R (R Core Team 2022). Our model sets had the same combinations of variables as Masse et al. (2014) for direct comparison to this earlier study of post-breeding male habitat selection and because, after a careful review of the literature, there were no other habitat layers available that were relevant to woodcock third-order selection. Woodcock require moist soils within forest mosaics consisting of both young and mature forest (Sepik et al. 1981, Dessecker and McAuley 2001, Williamson 2010, Masse et al. 2014), interspersed with clearings that are used by woodcock for both male courtship activities and female nest sites (Sepik et al. 1981, 1993; Sepik and Dwyer 1982; Dessecker and McAuley 2001; Keller et al. 2019).

Like Masse et al. (2014), we used mixed upland forest as the reference category in all our generalized linear mixed-effects logistic regression models. We fitted each of our logistic regression models with a binomial error distribution (used: 1; available: 0) and logit link using the function `glmer()` in the package `lme4` (version 1.1-34; Bates et al. 2015). Each model included a random intercept for both bird ID and the study area where the bird was tracked (i.e., 3 WMAs and 1 preserve) to account for unequal sample sizes and correlations from within hierarchical groupings (Gillies et al. 2006, Hebblewhite and Merrill 2008).

We performed model selection using Akaike's Information Criterion adjusted for small sample sizes ( $AIC_c$ ; Burnham and Anderson 2002) using the function `aictab()` in the `AICcmodavg` package (version 2.3-2; Mazerolle 2020). We selected models with  $\Delta AIC_c$  values  $\leq 2$  (Burnham and Anderson 2002) and for these selected models computed model-averaged estimates with shrinkage using the `modavgShrink` function (`modavgShrink`) in the `AICcmodavg` package when there was  $>1$  competing top model (Burnham and Anderson 2002, 2004; Lukacs et al. 2010; Mazerolle 2020). Because we wanted to make probability of use predictions for 2 of our analyses (objectives 2, 3) and check that our models were not overfit, we ensured that each of the top models ( $\Delta AIC_c \leq 2$ ) from the 3 analyses had high predictive power and performed well on both training and test datasets before model averaging as indicated by a moderately high Spearman rank correlation coefficient ( $r_s \geq 0.6$ ; Boyce et al. 2002). We performed a 5-fold cross validation where we withheld 20% of the data in each fold using the function `kfoldRSF()` in the package `IndRSA` (Boyce et al. 2002, Bastille-Rousseau and Wittemyer 2019, Bastille-Rousseau et al. 2020, Nagl et al. 2022). Each of the 4 female top models from objective 2 and the 2 male top models from objective 3 performed well at predicting woodcock habitat selection so we continued with model averaging of coefficient estimates. Finally, we calculated 95% confidence intervals for each of our coefficient estimates. We multiplied the model-averaged coefficient estimates for each environmental factor (selection strength) by all 10-m cells within the raster datasets for the different environmental factors that we assessed. We added each raster together using the raster calculator in ArcMap to produce relative probability of use maps for females and our long-term tracking study of males. For our 2 comparison studies (objectives 1, 2), we plotted our coefficient estimates with confidence intervals for each group to illustrate the differences between periods and sexes, respectively (Ellington et al. 2020, Clontz et al. 2021, Yang et al. 2021). To test for statistical differences between coefficient estimates, we calculated the proportion of overlap of the confidence intervals between groups. We considered overlap of  $\leq 0.5$  to signify a statistically significant difference ( $P < 0.05$ ) between groups (Cumming and Finch 2005, Gerber et al. 2012, Frantz et al. 2018, White et al. 2021).

## RESULTS

### Home range size and forest cover types over time

We found no statistical differences in average KDE male home range size by either period or study area (all  $P > 0.05$ ). The average KDE home range size for males in period 1 ( $39.8 \pm 9.0$  [margin of error] ha) was similar to the average KDE home range size for males tracked during period 2 ( $41.5 \pm 13.3$  ha). Similarly, we found no statistical difference ( $P > 0.05$ ) in average home range size for males and females tracked at all sites during 2020–2021. During 2020–2021, the KDE home range estimate for males was on average  $35.0 \pm 10.7$  ha with a median of 12.1 ha (range = 1.0–473.0 ha), whereas for females the mean was  $78.7 \pm 46.4$  ha with a median of 20.0 ha (range = 2.2–773.1 ha). During 2010–2011, MCP size for males averaged  $48.1 \pm 6.0$  ha with a median of 18.0 ha (range = 0.7–295.3). During 2020–2021, MCP size for males averaged  $38.8 \pm 6.0$  ha with a median of 26.7 ha (range = 0.7–153.1) and for females MCP size averaged  $61.5 \pm 21.2$  ha with a median of 20.1 ha (range = 1.2–263.7 ha).

Forest cover types within the composite 95% home ranges of males tracked within all study areas changed between the first (2010–2011) and second period (2020–2021) of the study (Figure 2). Within the composite 95% home range area for birds tracked at Arcadia WMA, the extent of upland coniferous forest, upland

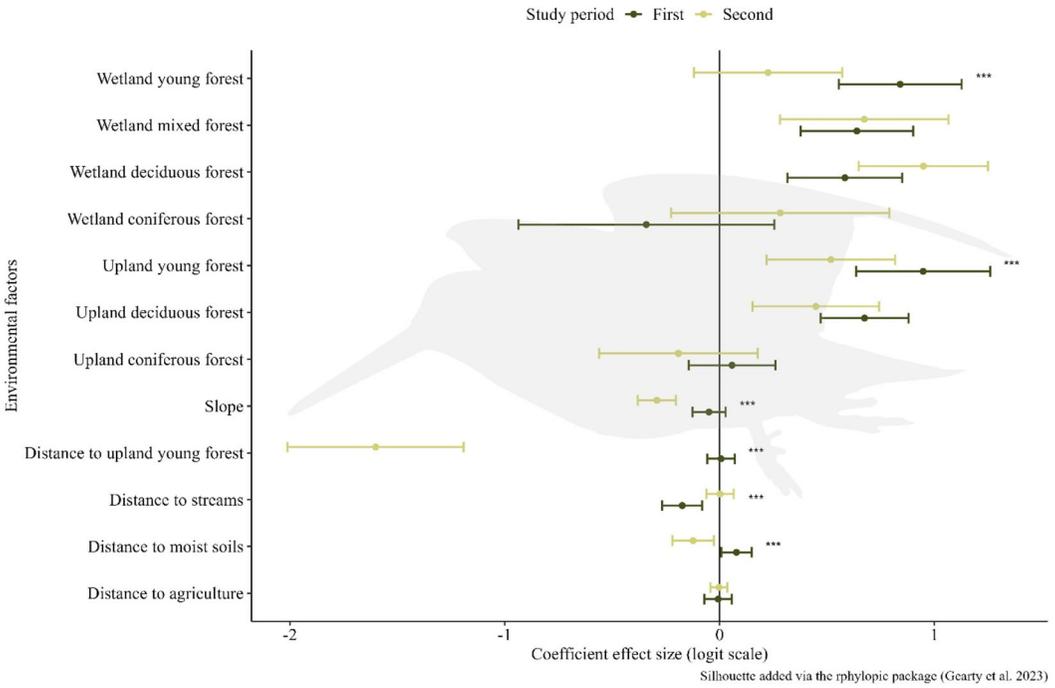
deciduous forest, upland mixed forest, and wetland deciduous forest decreased, while upland young forest, wetland coniferous forest, wetland mixed forest, and wetland young forest increased in extent (Figure 2). At Big River WMA, upland coniferous forest, upland deciduous forest, and upland mixed forest decreased in area, while upland young forest, wetland coniferous forest, wetland deciduous forest, wetland mixed forest, and wetland young forest increased in total area (Figure 2). At Great Swamp WMA, the amounts of upland coniferous forest, wetland mixed forest, and wetland young forest decreased, while upland coniferous forest, upland mixed forest, upland young forest, wetland coniferous forest, and wetland deciduous forest increased (Figure 2). At all 3 of the management areas, there were very large changes within upland young ( $\geq 573\%$ ) and wetland coniferous ( $\geq 451\%$ ) forest types (Figure 2).

## Male habitat selection between periods (objective 1)

Of the 15 *a priori* generalized linear mixed-effects logistic regression models that we tested for period 1 (2010–2011) and period 2 (2020–2021; Table S2), there were 3 competing top-ranked models in the first period and 2 competing top-ranked models in the second period (Table 1). The model-averaged results for these top-ranked models for each of the 2 periods suggested significant differences in selection between periods for

**TABLE 1** Top 5 models compared using the change in Akaike's Information Criterion corrected for small sample sizes ( $\Delta AIC_c$ ), number of parameters ( $K$ ), and model weight ( $\omega_i$ ) for radio-tracked woodcock in Arcadia, Big River, and Great Swamp Wildlife Management Areas, Rhode Island, USA, in the first (2010–2011;  $n = 41$ ) and second periods (2020–2021;  $n = 42$ ). We conducted 5-fold cross validation on each model used for model averaging ( $\Delta AIC_c \leq 2$ ) to ensure models were not overfit and that our model predictions were highly predictive and present Spearman rank correlation coefficients ( $r_s$ ). Factors included elevation slope, forest cover type, and distance (dist.) to several features.

Environmental factors	$K$	$\Delta AIC_c$	$\omega_i$	$r_s$
First period				
Slope, forest cover type, dist. to stream, dist. to upland young forest, dist. to moist soils	14	0.00	0.37	0.84
Slope, forest cover type, dist. to stream, dist. to agriculture, dist. to upland young forest, dist. to moist soils	15	1.77	0.15	0.82
Forest cover type, dist. to stream, dist. to upland young forest, dist. to moist soils	13	1.88	0.14	0.82
Slope, forest cover type, dist. to streams, dist. to upland young forest	13	2.64	0.10	
Elevation, slope, forest cover type, dist. to stream, dist. to agriculture, dist. to upland young forest, dist. to moist soils	16	3.33	0.07	
Second period				
Slope, forest cover type, dist. to stream, dist. to upland young forest, dist. to moist soils	14	0.00	0.58	0.90
Slope, forest cover type, dist. to stream, dist. to agriculture, dist. to upland young forest, dist. to moist soils	15	1.92	0.22	0.88
Elevation, slope, forest cover type, dist. to stream, dist. to agriculture, dist. to upland young forest, dist. to moist soils	16	2.85	0.14	
Slope, forest cover type, dist. to streams, dist. to upland young forest	13	4.67	0.06	
Forest cover type, dist. to stream, dist. to upland young forest, dist. to moist soils	13	49.71	0.00	



**FIGURE 3** Habitat selection coefficient estimates and 95% confidence intervals for radio-tagged male woodcock in Arcadia, Big River, and Great Swamp Wildlife Management Areas in Rhode Island, USA, for the first (2010–2011) and second (2020–2021) study periods. Environmental factors with confidence intervals encompassing 0 are not significant. Positive coefficients indicate selection for an environmental factor, whereas a negative coefficient indicates selection against an environmental factor. Significant differences between groups are indicated (\*\*\*).

wetland young forest, upland young forest, percent slope, distance to upland young forest, distance to streams, and distance to moist soils (Figure 3). In contrast, we detected no differences in selection for wetland mixed forest, wetland deciduous forest, wetland coniferous forest, upland deciduous forest, upland coniferous forest, and distance to agriculture (Figure 3).

In the first period, woodcock selected for wetland young forest, wetland mixed forest, wetland deciduous forest, upland young forest, and upland deciduous forest and increased distance to moist soils and decreased distance to streams (Figure 3). In the second period, woodcock selected for wetland mixed forest, wetland deciduous forest, upland young forest, and upland deciduous forest along with areas with lower percent slope, that were closer to upland young forest and moist soils (Figure 3).

### Male and female habitat selection (objective 2)

Of the 15 *a priori* generalized linear mixed-effects logistic regression models that we tested for males and females (Table S2), there were 3 competing top models for males and 4 competing top models for females (Table 2). The model-averaged results for these top-ranked models for males and females suggested significant differences in selection for slope, distance to upland young forest, and distance to streams (Figure 4). Males and females showed no differences in their selection of wetland young forest, wetland mixed forest, wetland coniferous forest, upland young forest, upland deciduous forest, upland coniferous forest, elevation, distance to moist soils, and distance to agriculture (Figure 4).

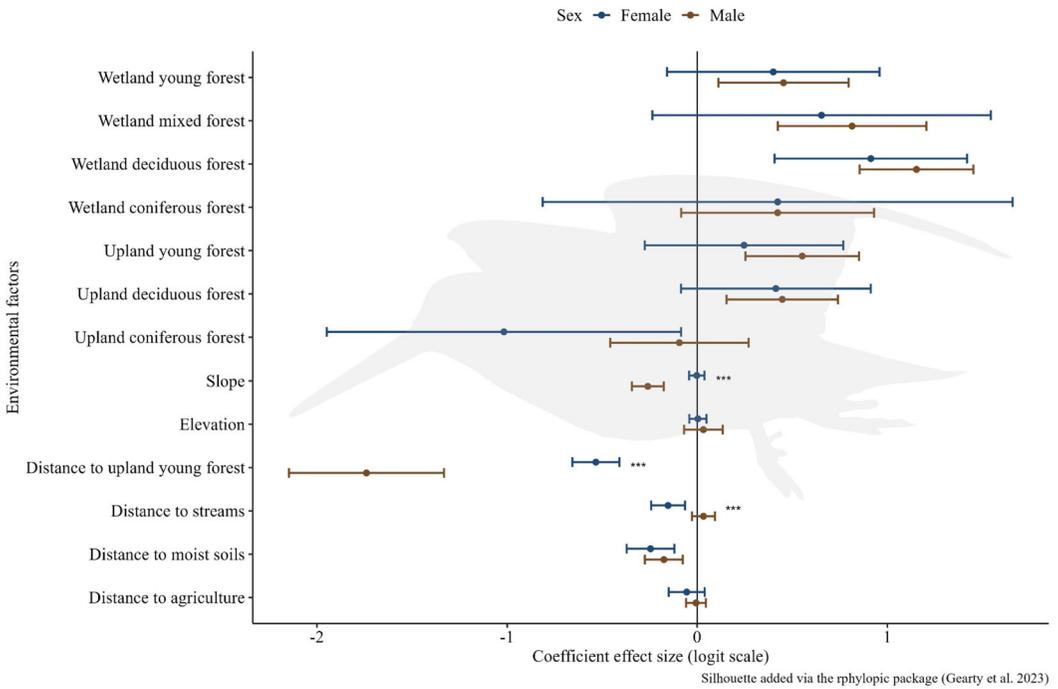
**TABLE 2** Top 5 models compared using the change in Akaike's Information Criterion corrected for small sample sizes ( $\Delta AIC_c$ ), number of parameters ( $K$ ), and model weight ( $\omega_i$ ) for male ( $n = 51$ ) and female ( $n = 17$ ) woodcock tracked in Arcadia, Big River, and Great Swamp Wildlife Management Areas, and Francis Carter Preserve Rhode Island, USA (2020–2021). We conducted 5-fold cross validation on each model used for model averaging ( $\Delta AIC_c \leq 2$ ) to ensure models were not overfit and that our model predictions were highly predictive and present Spearman rank correlation coefficients ( $r_s$ ). Factors included elevation slope, forest cover type, and distance (dist.) to several features.

Environmental factors	$K$	$\Delta AIC_c$	$\omega_i$	$r_s$
Females				
Forest cover type, dist. to stream, dist. to agriculture, dist. to upland young forest, dist. to moist soils	14	0.00	0.36	0.75
Forest cover type, dist. to stream, dist. to upland young forest, dist. to moist soils	13	1.07	0.21	0.61
Elevation, forest cover type, dist. to stream, dist. to agriculture, dist. to upland young forest, dist. to moist soils	15	1.81	0.15	0.75
Slope, forest cover type, dist. to stream, dist. to agriculture, dist. to upland young forest, dist. to moist soils	15	1.94	0.14	0.65
Slope, forest cover type, dist. to stream, dist. to upland young forest, dist. to moist soils	14	2.97	0.08	
Males				
Slope, forest cover type, dist. to stream, dist. to upland young forest, dist. to moist soils	14	0.00	0.44	0.86
Elevation, slope, forest cover type, dist. to stream, dist. to agriculture, dist. to upland young forest, dist. to moist soils	16	0.69	0.31	0.95
Slope, forest cover type, dist. to stream, dist. to agriculture, dist. to upland young forest, dist. to moist soils	15	1.21	0.24	0.93
Slope, forest cover type, dist. to streams, dist. to upland young forest	13	12.28	0.00	
Forest cover type, dist. to stream, dist. to upland young forest, dist. to moist soils	13	42.39	0.00	

Males and females selected for wetland deciduous forest, areas closer to upland young forest, and areas closer to moist soils, whereas on average females selected areas closer to streams and avoided upland coniferous forest (Figure 4). In addition, males selected for wetland young forest, wetland mixed forest, upland young forest, and upland deciduous forest, and areas with lower percent slope.

### Long-term male habitat selection (objective 3)

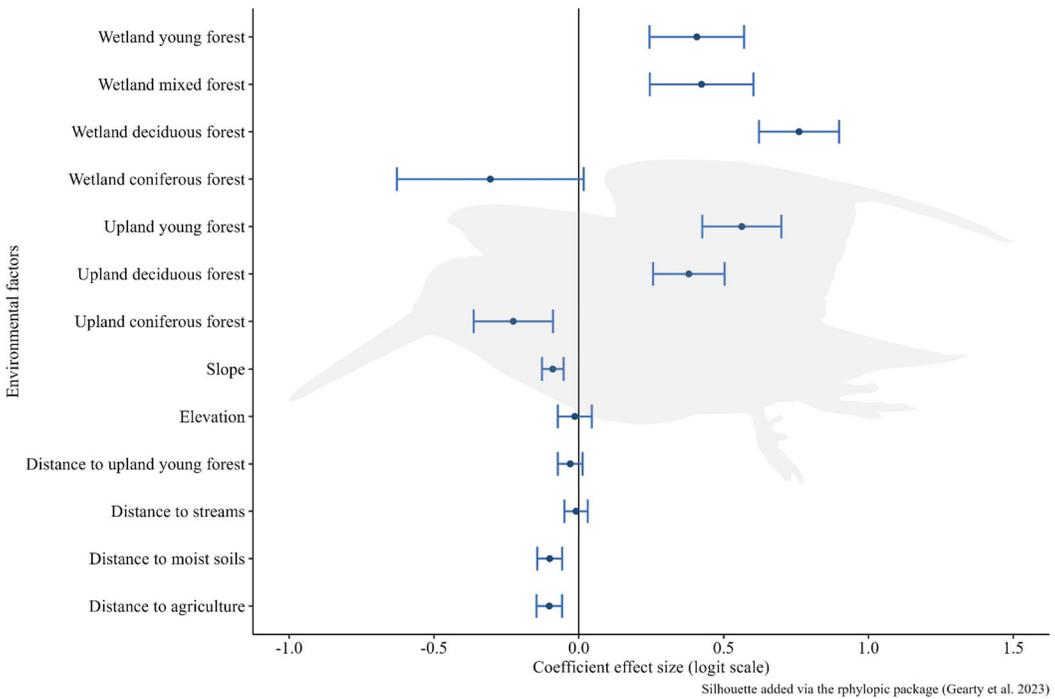
Although we detected some differences between time periods in male habitat selection (see above), we wanted to additionally create a more robust model that best estimated selection variation across males using the complete tracking dataset that was collected during a period of active forest management. Of the 15 *a priori* generalized linear mixed-effects logistic regression models that we tested (Table S2), there were 2 competing top-ranked models (Table 3). Over the entire period, males selected for wetland young forest, wetland mixed forest, wetland deciduous forest, upland young forest, and upland deciduous forest, and areas with flatter slopes, closer to moist soils, and closer to agriculture (Figure 5). The only forest cover type that male woodcock avoided was upland coniferous forest (Figure 5). Male woodcock showed no selection for elevation, distance to upland young forest, or



**FIGURE 4** Habitat selection coefficient estimates and 95% confidence intervals for radio-tagged male and female woodcock in Arcadia, Big River, and Great Swamp Wildlife Management Areas, and Francis Carter Preserve in Rhode Island, USA, 2020–2021. Environmental factors with confidence intervals encompassing 0 are not significant. Positive coefficients indicate selection for an environmental factor, whereas a negative coefficient indicates selection against an environmental factor. Significant differences between groups are indicated (\*\*\*).

**TABLE 3** Top 5 models compared using the change in Akaike's Information Criterion corrected for small sample sizes ( $\Delta AIC_c$ ), number of parameters ( $K$ ), and model weight ( $\omega_i$ ) for male woodcock tracked in Arcadia, Big River, and Great Swamp Wildlife Management Areas, and Francis Carter Preserve Rhode Island, USA (2010–2021). We conducted 5-fold cross validation on each model used for model averaging ( $\Delta AIC_c \leq 2$ ) to ensure models were not overfit and that our model predictions were highly predictive and present Spearman rank correlation coefficients ( $r_s$ ). Factors included elevation slope, forest cover type, and distance (dist.) to several features.

Environmental factors	$K$	$\Delta AIC_c$	$\omega_i$	$r_s$
Slope, forest cover type, dist. to stream, dist. to agriculture, dist. to upland young forest, dist. to moist soils	15	0.00	0.63	0.80
Elevation, slope, forest cover type, dist. to stream, dist. to agriculture, dist. to upland young forest, dist. to moist soils	16	1.10	0.37	0.76
Forest cover type, dist. to agriculture, dist. to upland young forest, dist. to moist soils	13	19.52	0.00	
Slope, forest cover type, dist. to stream, dist. to upland young forest, dist. to moist soils	14	19.69	0.00	
Elevation, forest cover type, dist. to agriculture, dist. to moist soils	13	20.20	0.00	



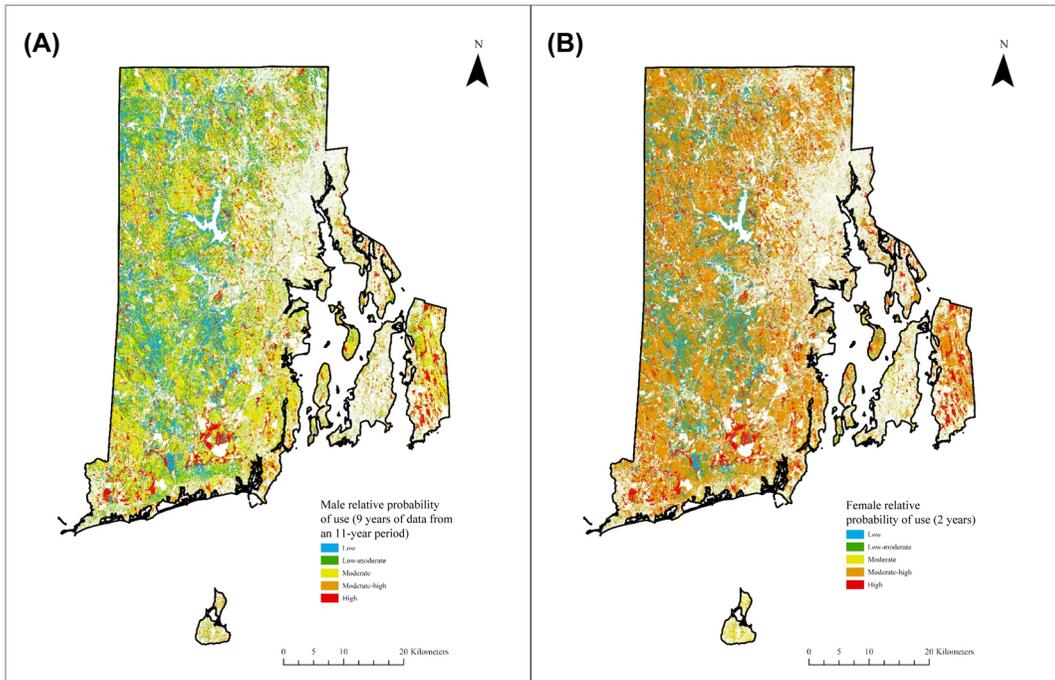
**FIGURE 5** Habitat selection coefficient estimates and 95% confidence intervals for radio-tagged male woodcock tracked at Arcadia, Big River, and Great Swamp Wildlife Management Areas, and Francis Carter Preserve in Rhode Island, USA, 2010–2021. Data were collected for 9 years over an 11-year period. Environmental factors with confidence intervals encompassing 0 are not significant. Positive coefficients indicate selection for an environmental factor, whereas a negative coefficient indicates selection against an environmental factor.

distance to streams (Figure 5). We used the model-averaged coefficient estimates from the 2 top competing models from all males in the study (Table S3, available in Supporting Information) to produce an updated relative probability of use map with 5 natural breaks (Figure 6) in ArcMap that can help guide forest management decisions for males during the non-breeding period in southern New England. For comparison, we used the model-averaged coefficient estimates (Table S4, available in Supporting Information) from the 4 top competing models for females tracked during the same time period to produce a relative probability of use map with 5 natural breaks for females only (Figure 6).

## DISCUSSION

### Home range size and forest cover types over time

The KDE and MCP home range sizes of male woodcock that we estimated (~40 ha and 38–48 ha, respectively) were similar over space and time (2010–2011 and 2020–2021). Mean MCP home range estimates for males in Rhode Island were much larger than those reported in Maine, USA (13–19 ha; Sepik and Derleth 1993). Median MCP estimates for males (26.7 ha) during 2020–2021 were consistent with those from males tracked during 2010–2011 (18.0 ha) in Rhode Island and males in Pennsylvania, USA, which varied from 3.1–73.6 ha (Hudgins et al. 1985, Masse et al. 2014). We think the greater range of KDE home range sizes and the larger median MCP home range estimates that we observed in the second period (2020–2021) of the study could be a result of the marked changes



**FIGURE 6** Male (A) and female (B) relative probability of use maps for woodcock in in Arcadia, Big River, and Great Swamp Wildlife Management Areas and Francis Carter Preserve in Rhode Island, USA. Relative use maps were derived from the exponential form of coefficient estimates from the habitat selection functions developed for radio-tracked males (2010–2021) and radio-tracked females (2020–2021). Radio-tracking data for the male relative probability of use map was collected for 9 years over an 11-year period. White areas are developed areas deemed unavailable to woodcock (non-forested).

in habitat availability between periods 1 and 2 (Figure 2). The unusually large KDE home range estimates for some of the males tracked by Masse et al. (2014; e.g., 474.5 ha) and for some of the males (e.g., 473.0 ha) in this study are reflective of Rhode Island's highly developed landscape where present-day woodcock habitat is highly fragmented and dispersed across the landscape. This may also explain why our home range estimates are larger than those found elsewhere in the woodcock's range.

Average home range size estimates (KDEs) for females tended to be larger and much more variable than the male average home range size during this same time and study area. Age and year were not good predictors of home range size for either sex. Mean MCP home range estimates for males ( $38.8 \pm 6.1$  ha) and females ( $61.5 \pm 21.2$  ha) during 2020–2021 were much larger than those reported in Maine (8–13 ha; Sepik and Derleth 1993). We think the larger and highly variable female home range sizes compared to males may be a result of the female woodcock's pronounced sexual size dimorphism (Keppie and Redmond 1988), and that larger home ranges may allow females to satisfy their daily energy requirements.

### Male habitat selection between periods (objective 1)

The models that best explained male woodcock habitat selection for each period contained the same set of environmental factors (Table 1) that together indicated 5 habitat components were important for male woodcock during the post-breeding period. Similar to other woodcock studies, we found that habitat mosaics with the

following habitat components were important: forested wetlands (Sheldon 1967, Straw et al. 1986, McAuley et al. 1996, Dessecker and McAuley 2001, Masse et al. 2014), young forest patches (Sheldon 1967, Hudgins et al. 1985, Dessecker and McAuley 2001, Kelley et al. 2008, Masse et al. 2014), areas of deciduous forest (Reynolds et al. 1977, Horton and Causey 1979, Sepik et al. 1981, Straw et al. 1986, Masse et al. 2014), moist soils with gentle slopes (Reynolds et al. 1977, Straw et al. 1986, Owen and Galbraith 1989, Steketee 2000, Masse et al. 2014), and riparian corridors (Sepik et al. 1981, Williamson 2010, Masse et al. 2014). Woodcock likely select young forest, upland deciduous forest, and forested wetlands because these areas have greater earthworm densities (Reynolds et al. 1977) and denser vegetation that offers additional protection from predators than drier and more sparsely vegetated sites (Williamson 2010, Masse et al. 2014). Like other studies in the northern portion of the breeding range, tagged males in our study did not select for coniferous forests (Figure 3; Williamson 2010, Masse et al. 2014). Soil conditions in coniferous forests are not as conducive to earthworm abundance and may explain their lack of selection (Reynolds et al. 1977, Owen and Galbraith 1989); however, coniferous forest soils dry out more slowly than those in other forest types so woodcock may use these forests during drought (Sepik and Owen 1983). We also found no selection for distance to agriculture in either period (Figure 3). On the northern breeding grounds, woodcock are rarely observed within agricultural areas except during aerial courtship flights (Sheldon 1961, Dwyer et al. 1988, Sepik et al. 1993) or when roosting at night (Dunford and Owen 1973, George and Causey 1987, Sepik et al. 1993, Masse et al. 2013). Steketee et al. (2000) similarly found that woodcock in West Virginia, USA, were not associated with agricultural land during the summer months (May–Sep). Contrary to our findings, Masse et al. (2014) found that woodcock select areas closer to agriculture; however, Masse et al. (2014) assessed habitat selection at the landscape scale, whereas we investigated habitat selection at the home range scale. We suggest future research investigates how woodcock respond to agricultural practices at multiple spatial scales for given regions because this has received little attention (Masse et al. 2014).

Although the environmental factors important to woodcock were consistent in both periods (Table 1), the effect size for several of the selection coefficients were significantly different between the 2 periods (Figure 3). Given that the random study area effect in our top models explained 5% or less of the variation in period 1 and period 2, many of these differences in selection strengths between periods are best explained by the change in habitat availability between 2010–2011 and 2020–2021 (Figure 2). For example, upland young forest increased dramatically between the 2 study periods (Figure 2). The significantly weaker selection for upland young forest during period 2 is consistent with the expectation of decreased selection with increased availability (Beyer et al. 2010). Woodcock in period 2 may have been significantly closer to upland young forest because it was more common on the landscape, and the distance to it would likely decrease. The amount of wetland young forest was consistently rare in both periods (Figure 2). Thus, even low levels of use during period 1 could have caused the stronger selection coefficient we observed during this time (Beyer et al. 2010). Displaying male woodcock can rapidly occupy new forest clearings in Maine and Rhode Island (Sepik and Dwyer 1982, Dwyer et al. 1988, Masse et al. 2014). Furthermore, translocated woodcock quickly assessed habitat quality and remained at, or returned to, better quality study areas depending on the quality of the area in which they were placed (Brenner et al. 2019).

Several other differences in selection strengths between periods (Figure 3) seem related to factors other than changes in habitat availability over time. For example, during period 2, male woodcock selected flatter sites that were closer to moist soils, but during period 1, woodcock were found farther from moist soils and in areas closer to streams (Figure 3). Although we found no significant difference in temperature or precipitation between time periods, riparian areas provide woodcock with consistent supplies of earthworms (Kelley et al. 2008). Prior studies have observed woodcock moving into areas with slow soil desiccation (i.e., coniferous forests) in response to localized drought (Sepik and Owen 1983), and our findings suggest that woodcock may have similar relationships with riparian corridors. Although the effect sizes for the selection coefficients associated with riparian areas (i.e., slope, distance to streams and moist soils) were relatively modest (Figure 3), the significant changes over time in the magnitude of selection suggests that male woodcock subtly and sensitively respond to habitat attributes related to soil water content as suggested by Sepik and Owen (1983).

## Male and female habitat selection (objective 2)

The majority of studies that document woodcock habitat selection are related to areas used during the breeding season (Sepik and Dwyer 1982, Gutzwiller et al. 1983, Straw et al. 1986, Sepik et al. 1993, McAuley et al. 1996). To our knowledge, our study is the first to characterize the post-breeding habitat selection of female woodcock and to directly compare the habitat requirements of males and females at the same temporal and spatial scale. Although Sepik et al. (1993) concurrently tracked males and females during the post-breeding period, they only discussed differences related to home range size and nocturnal roosting activity and did not assess habitat selection for males or females. Only 2 previous studies of woodcock have directly assessed habitat selection (sensu Manly et al. 2002) during the post-breeding period, although neither study was able to identify which environmental factors females selected for or how this may differ from males (Steketee 2000, Masse et al. 2014). Masse et al. (2014) focused on male woodcock habitat selection because of the difficulties associated with catching females. Steketee et al. (2000) assessed habitat selection of woodcock by comparing areas where woodcock (sex unknown) were flushed by pointing dogs, to randomly selected points that were searched, but no woodcock were found.

In general, male, and female woodcock during the post-breeding period in 2020–2021 selected habitat mosaics consisting of similar components, although we detected subtle sex-specific differences in selection for slope and distance to streams, and more marked differences in selection for distance to upland young forest (Figure 4). Post-breeding resource partitioning has been observed in several other shorebird species and appears to be caused by sex-specific differences in prey preferences (Both et al. 2003, Nebel 2005, Catry et al. 2012, Alves et al. 2013). No similar studies of sex-specific resource partitioning have been conducted for woodcock. The stronger selection for riparian corridors by females could be related to the more consistent supply of earthworms found in these areas (Sheldon 1967, Kelley et al. 2008) and coincides with our prediction that females would select areas with increased food availability. Female woodcock in Maine lost approximately 75% of their body mass and were in negative energy balance during the incubation period (Vander Haegen 1992). Post-breeding females may require consistently abundant food resources provided by riparian areas to replenish fat stores used during nesting and needed for fall migration. Furthermore, female post-breeding habitat selection may be related to nest prospecting behavior as documented for spotted sandpiper (*Actitis macularius*; Reed and Oring 1992) and Eurasian oystercatcher (*Haematopus ostralegus*; Cramp and Simmons 1983). In Rhode Island, female woodcock typically select nest sites along streams and these areas are closer to upland young forest than the surrounding available habitat (C. R. Slezak, unpublished data). Similarly, male woodcock, especially juveniles, may use the post-breeding period as a time to select singing grounds for the following spring (Dunford and Owen 1973), which in our area are on average closer to upland young forest and have flatter slopes compared to the surrounding available habitat. These post-breeding habitat selection strategies during previous years may allow courting males and nesting females to commence their breeding activities rapidly and efficiently upon arrival to their northerly breeding areas (Reed and Oring 1992).

## Long-term male habitat selection (objective 3)

To date, our long-term study is the most robust assessment of male woodcock habitat selection (i.e., 146 males). The same set of variables that together were important for male woodcock habitat selection in the 2-period comparison study were also important during this long-term study, albeit elevation was only included after the addition of a new study area (Francis Carter Preserve; Figure 1) and the addition of 57 males that were tracked during 2012 and from 2016–2019. During this period, male woodcock selected for mosaics consisting of forested wetlands, young forest patches, areas of deciduous forest, moist soils with gentle slopes, and areas that were closer to agriculture compared to the available surrounding habitat (Figure 5). Elevation in Rhode Island is relatively low

(range = 0–247 m;  $\bar{x}$  = 61 m), which we think drove the shift in relative importance for this environmental factor (although non-significant; Figure 5). The addition of Francis Carter Preserve along Rhode Island's coastal plain, and the addition of 57 males, likely allowed us to better characterize subtle elevation gradients given the increase in spatial and temporal coverage and better capture the nuanced aberrations found within the state. The male woodcock's association with agricultural areas that we found when analyzing the entire dataset was different than what we found when separately analyzing fewer years (i.e., the 2-period comparison study), and more similar to the findings of Masse et al. (2014) who assessed woodcock habitat selection at the landscape scale. We believe that the addition of an agriculturally dominated study area (Francis Carter Preserve; Figure 1) led to this selection for areas closer to agriculture because woodcock were inherently closer to agriculture at any given time and these areas serve additional roles as singing grounds (Sheldon 1967) and nocturnal roost sites (Sheldon 1967, Dunford and Owen 1973, Masse et al. 2013). Thus, these findings suggest that in addition to use as nocturnal roost sites, male woodcock may prospect agricultural areas when young forest is rare (i.e., Francis Carter Preserve) to assess a site's suitability for aerial courtship displays during the subsequent spring.

## MANAGEMENT IMPLICATIONS

Forest management planning to benefit woodcock populations during the post-breeding period (May–Sep) should account for sex-specific differences in habitat use. In particular, management that results in young forest or shrubland vegetation types adjacent to streams will likely provide females with necessary cover in areas conducive for feeding. Forest management that is primarily focused on drier upland sites may provide too little benefit to females during this post-breeding portion of their annual cycle. Forest management that benefits both male and female woodcock likely also benefits other wildlife that depend on young forest and should be both time and cost-effective. For this reason, we applied habitat selection coefficient estimates derived from our 2 most robust male and female tracking datasets to produce probability of use maps that predict areas most likely to be selected by woodcock relative to habitat availability in Rhode Island. By focusing management efforts on areas that are currently low or only moderately suitable for both male and female woodcock, management goals focused on increasing woodcock abundance, and the abundance of associated young forest wildlife, can be attained more effectively and efficiently. Although these probability of use maps were produced for woodcock in Rhode Island, our methodologies could be used elsewhere to help predict where habitat management could be most beneficial for this declining species.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## ETHICS STATEMENT

All woodcock trapping, handling, and tagging activities were conducted in accordance with the University of Rhode Island Animal Care and Use Guidelines under Animal Care and Use Protocol AN#10-02-017.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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