

Mismatch between strong nest-site selection and low survival of nests and broods for *Scolopax minor* (American Woodcock) and its implications for conservation

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ABSTRACT

Nest-site selection may reduce predation and enhance recruitment, especially in ground-nesting birds. Few studies have examined both nest-site selection and its potential effects on nesting success, even though predation risk and exposure to inclement weather may limit the effectiveness of nest-site selection. We assessed home-range and local-scale nest-site selection of *Scolopax minor* (American Woodcock) as well as nest and brood survival in Rhode Island, USA during the breeding seasons (March 15 to June 15) of 2020–2022. Specifically, we employed a use/available design and conditional logistic regression models to evaluate nest-site selection and used the Program MARK to estimate nest and brood survival. At the home-range scale, we found that nesting woodcock selected for early successional cover types (i.e., pastures, grasslands, or regenerating clearcuts) and areas closer to upland young forest and reverting agricultural openings. They also occupied forests and wetlands of varied species composition and age (i.e., upland young forests as well as upland and wetland deciduous forests, and emergent wetlands). At the local scale, females selected nest sites that provided visual concealment of the nest. Despite nest-site selection at 2 spatial scales, nest and brood survival were low (10% and 16%, respectively) and were not influenced by vegetation, landscape configuration, and weather. Given that woodcock nest-site selection is driven by vegetative structure and concealment, yet reproductive success was low, future management should experimentally alter forests to identify forest configurations that help mitigate predation and increase cover in fragmented landscapes, such as Rhode Island.

Keywords: American Woodcock, brood survival, concealment, nest survival, nest-site selection, predation, *Scolopax minor*, shorebirds

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LAY SUMMARY

- Nest-site selection can reduce predation rates and improve recruitment in ground-nesting birds, but few studies have examined its impact on nesting and brood success.
- We tracked female *Scolopax minor* (American Woodcock) and their young using very high-frequency radiotelemetry in southern New England throughout the spring to assess 3 key aspects of breeding ecology: nest-site selection, nest survival, and brood survival.
- At the home-range scale, females selected nest sites near upland young forests and at the local scale they selected nest sites where the nest could be hidden.
- Nest and brood survival were extremely low, and neither were predicted well by habitat or weather variables.
- To enhance breeding success, managers should create and maintain diverse habitats that include early successional areas, mature forests, and wetlands and promote dense vegetation transition between habitat patches for better connectivity.

Desajuste entre una fuerte selección de sitios de anidación y una baja supervivencia de nidos y crías en *Scolopax minor* y sus implicaciones para la conservación

RESUMEN

La selección de sitios de anidación puede reducir la depredación y mejorar el reclutamiento, especialmente en aves que anidan en el suelo. Pocos estudios han examinado tanto la selección de sitios de anidación como sus posibles efectos en el éxito reproductivo, aunque el riesgo de depredación y la exposición a condiciones climáticas adversas pueden limitar la eficacia de esta selección. Evaluamos la selección de sitios de anidación de *Scolopax minor* a escala de rango de hogar y local, así como la supervivencia de nidos y crías en Rhode Island, EUA, durante

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las temporadas de cría (15 de marzo al 15 de junio) de 2020 a 2022. Específicamente, utilizamos un diseño de uso/disponibilidad y modelos de regresión logística condicional para evaluar la selección de sitios de anidación y usamos el programa MARK para estimar la supervivencia de nidos y crías. A escala de rango de hogar, encontramos que los individuos que anidan de *S. minor* seleccionaron coberturas en etapas sucesionales tempranas (i.e., pastizales, praderas o claros en regeneración) y áreas cercanas a bosques jóvenes de tierras altas y a aperturas agrícolas en recuperación. También ocuparon bosques y humedales con composición de especies y edades variadas (i.e., bosques jóvenes de tierras altas, así como bosques deciduos de tierras altas y de humedales, y humedales emergentes). A escala local, las hembras seleccionaron sitios de anidación que ofrecían camuflaje visual para el nido. A pesar de la selección de sitios de anidación a dos escalas espaciales, la supervivencia de nidos y crías fue baja (10% y 16%, respectivamente) y no estuvo influida por la vegetación, la configuración del paisaje y el clima. Dado que la selección de sitios de anidación de *S. minor* está impulsada por la estructura de la vegetación y el camuflaje, a pesar de que el éxito reproductivo fue bajo, la gestión futura debería alterar experimentalmente los bosques para identificar configuraciones que ayuden a mitigar la depredación y aumentar la cobertura en paisajes fragmentados, como Rhode Island.

Palabras clave: aves playeras, camuflaje, depredación, *Scolopax minor*, selección de sitios de anidación, supervivencia de crías, supervivencia de nidos

INTRODUCTION

Breeding ecology of birds is influenced by multiple factors, including predation rate, habitat selection, and abiotic conditions. These limitations have shaped nest-site selection (Martin 1993), optimal clutch size (Cody 1966, Martin 1995), and a diversity of breeding behaviors (e.g., injury feigning) that combined maximize reproductive output (Martin et al. 2000, Ghalambor and Martin 2002). Ground-nesters are particularly susceptible to nest depredation because they are vulnerable to a broad suite of predators, and often construct simple nests that provide little protection from predators and the elements (Smith and Edwards 2018). The high nest failure rates of ground-nesting birds have been selected for traits that increase crypsis. These traits include egg coloration (Kilner 2006) that camouflages the eggs against their background (Stevens et al. 2017), selection of nest sites that provide vegetative concealment (Schieck and Hannon 1993, Dion et al. 2000, Albrecht and Klvaňa 2004, Westmoreland and Kiltie 2007) which limit predator detection and access to nest sites (Martin 1995), high rates of incubation constancy (Ghalambor and Martin 2002), and aggressive or deceptive behaviors that help drive or mislead predators away from the nest and chicks (Smith and Edwards 2018). However, studies have shown that wildlife cannot always discern quality and thus may choose suboptimal habitats (Battin 2004). Also known as an ecological trap, breeding in these suboptimal habitats leads to low recruitment of young and/or survival of adults (Battin 2004, Robertson and Hutto 2006). The disconnect between perceived and actual habitat quality demonstrates the complexity of habitat selection in fragmented landscapes, where habitat may appear suitable but has unperceived/undetected deficiencies or risks (Rocha et al. 2021).

Spatial variability in predator activity and abundance and thus predation risk influences nest-site selection by ground-nesting birds (Kurki et al. 1997, Wilson and Arcese 2006, Schmidt et al. 2006, Mönkkönen et al. 2009) and the likelihood of losing a nest or brood to predators. High predator abundance often leads to low breeding success (Kurki et al. 1997, Wilson and Arcese 2006). Spatial variability in predator abundance and predation rates can arise from both landscape and local-scale features, such as forest patch size or amount of edge (Robinson et al. 1995, Chalfoun et al. 2002, Thompson et al. 2002). For example, predation rates are higher along edges when the surrounding forested landscape is highly fragmented but not when the surrounding landscape is contiguous (Donovan et al. 1997, Lloyd et al. 2005). The effects of edge on nest predation appear to be particularly strong for ground-nesting species (Chalfoun et al. 2002, Lloyd et al. 2005). This edge effect is broadly problematic given that most remaining forests globally are composed of fragments and

edges (Luskin et al. 2023) and such areas have typically lost apex predators causing mesopredator release and population declines of prey species (Crooks and Soule 1999). Given that bird populations are often limited by recruitment (Desante 1990), an understanding of the underlying mechanisms that affect rates of nest success and brood survival are particularly important to achieve effective species-specific management strategies (Chalfoun et al. 2002).

Abiotic factors as well as biotic factors other than predators, such as parasites, can also play a crucial role in influencing reproductive success. Weather conditions, such as temperature and precipitation, can impact nest and brood survival separately from predation risk (Dinsmore et al. 2002). For example, harsh weather can cause nests to fail or chicks to die independent of the extent of predation (Dinsmore et al. 2002, Andreasson et al. 2020). Additionally, vegetative structure can influence microclimate around nests (Martin 1998), and the availability of resources can influence breeding success (Holmes and Robinson 1988). Abiotic factors, such as temperature and precipitation, and biotic factors, such as predation risk, food availability, and habitat structure, collectively influence nest-site selection in ground-nesting birds across multiple scales (Martin 1995).

Charadriiformes is a large, diverse group of ground-nesting shorebird species (Thomas et al. 2006) that experience high yet variable rates of clutch failure (Evans and Pienkowski 1984, Colwell 2006) and use a diversity of cover types for nesting (Colwell and Oring 1988). Shorebird nests are cryptic and typically include 4 dull-colored, spotted eggs (Maclean 1972), suggesting an anti-predatory evolutionary response to high nest failure rates (Lack 1968, Lee et al. 2010). Increases in nest predation rates during the last 70 years have been implicated as the likely cause for the precipitous population declines in shorebirds worldwide (Kubelka et al. 2018). However, migratory shorebirds also face other significant threats, such as habitat loss (Wang et al. 2022) and trophic mismatches during crucial periods of the annual cycle, including the breeding season, caused by a warming climate (Kwon et al. 2019, Lameris et al. 2022). Shorebirds may select their nest sites to reduce the likelihood of nest loss during incubation and in response to perceived suitability of the area for rearing their precocial chicks (Blomqvist and Johansson 1995, Anteau et al. 2012, Wiltermuth et al. 2015). Therefore, adequately assessing reproductive success requires understanding how nest-site selection influences predation rates during both the nesting and brood-rearing stages.

Scolopax minor (American Woodcock) is an upland shorebird that primarily feeds on earthworms and resides in deciduous forests and wetlands throughout eastern and central North America. Since monitoring began in the 1960s, their

populations have declined (Seamans and Rau 2023). Although initiatives focused on increasing forest management activities (e.g., timber harvests and prescribed burns as part of the young forest initiative) for woodcock have increased during recent decades, populations have not stabilized or increased, leading researchers to believe that factors related to breeding season survival and productivity may be limiting (Whiting *et al.* 2005, Kelley *et al.* 2008, Case and Sanders 2010, Huinker 2020, Seamans and Rau 2023). This realization has motivated researchers to prioritize investigations of breeding habits and habitats (Case and Sanders 2010). Because woodcock have such a broad breeding distribution (McAuley *et al.* 2020, Slezak *et al.* 2024a), the level of concealment of nests by vegetation varies across their range (Sepik *et al.* 1993, McAuley *et al.* 2020), but nests are typically in or near young forests that provide females with the visual concealment required for nesting and brood rearing (Sepik *et al.* 1993, Dessecker and McAuley 2001). Nest sites are also often near male singing grounds (i.e., forest openings or abandoned agricultural land) that are selected in part by males for their proximity to nesting cover (Dwyer *et al.* 1988, Williamson 2010). Past studies of woodcock nesting habitat were largely qualitative, and there have been few studies of woodcock nest-site selection (McAuley *et al.* 1996, Miller and Jordan 2011, Huinker 2020). Our study is distinct in that it directly relates nest-site selection to nest and brood survival.

We studied the breeding ecology of woodcock in Rhode Island, USA, at sites typically considered to be the southern edge of the primary breeding range (Sheldon 1967). Our goals were to quantify the habitat selection of nesting female woodcock at 2 spatial scales (local and home-range scale) and to determine how environmental factors related to landscape configuration, vegetation, and weather, specifically temperature and precipitation, influenced nest and brood survival rates. We tested the hypothesis that woodcock considers both landscape-level and local characteristics when selecting nest sites. We predicted that females would select for home ranges comprising early successional cover types close to wetland forests that support their preferred food source (Dessecker and McAuley 2001), and at the local scale for sites with more visual concealment near the nest compared to the surrounding available habitat. We also tested the hypothesis that nest and brood survival for this ground-nesting bird may be determined by mostly unpredictable abiotic events. We predicted that nest and brood survival would be strongly related to weather, such as temperature and precipitation, due to their direct impact on the viability of nests and the overall environment for the young chicks and less to vegetation and landscape configuration. Documenting these aspects of the breeding ecology of woodcock establishes the foundation for developing effective management prescriptions and conservation goals.

METHODS

Marking and Tracking Female Woodcock, Nest Searches, and Brood Tag Attachment

Locating nests and broods

Over a 3-year period (2020–2022), we assessed female woodcock nest-site selection and nest and brood survival during the core of the female woodcock breeding period (March 15 to

June 15; McAuley *et al.* 2020, Slezak *et al.* 2024b, a) in 4 state-owned Wildlife Management Areas (WMAs) and 3 Preserves in Kent and Washington Counties, Rhode Island, USA (Figure 1). In this region of southern New England, *Quercus* spp. (mixed oaks), *Carya* spp. (hickories), and *Acer rubrum* (red maple) typically dominated in deciduous upland forests, whereas *Pinus strobus* (eastern white pine) was common in coniferous forests, and mixed forests typically contained combinations of oaks and white pine; red maple and *Chamaecyparis thyoides* (Atlantic white cedar) swamps were common in forested wetlands (Enser and Lundgren 2006). Nests and brood sites found within management areas were forest-dominated and were actively managed to create and maintain stands of young forest for woodcock and other associated species of conservation concern (Buffum *et al.* 2019).

We used mist nets to capture females visiting male singing grounds (2020–2021) and used pointing dogs (2020–2022) and thermal cameras (2021–2022) to locate brooding females incubating eggs or with chicks. We placed mist nets at male singing grounds to capture and tag females ($n = 20$), although only a few ($n = 5$) were later found nesting. We used pointing dogs 5 or more days per week in areas that were managed as young forests to locate and tag brooding females ($n = 25$) during the day (Ammann 1974, 1977; McAuley *et al.* 1993, Daly *et al.* 2015, Huinker 2020). We also used thermal cameras (FLIR Scout III 320, Teledyne FLIR, Wilsonville, OR, USA; FLIR Scion OTM230, Teledyne FLIR, Wilsonville, OR, USA) after sunset to locate additional brooding females ($n = 8$) (Keller *et al.* 2019). We incidentally located 5 additional brooding females when observers flushed them from the nest during fieldwork. If a nesting female was found, we collected information about the nest site and waited until the eggs hatched before attempting to capture the female with a long-handled net to avoid nest abandonment (Horton and Causey 1984). We 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 to all females (McAuley *et al.* 1993). The mass of the transmitter and attachment materials was 1.7–2.6% of the body mass of females in our study.

When nests were located, we took a global positioning system (GPS) coordinate, placed a flag in the area, and floated 2 eggs from each clutch to estimate the percentage of incubation completed (Liebezeit *et al.* 2007) and thereby nest initiation dates assuming a 25-day nesting period including 4 days of egg laying and ~21 days of incubation (McAuley *et al.* 2020). To estimate nest initiation dates, we used the egg floatation methodology outlined in Liebezeit *et al.* (2007), which seemed to approximate the hatch date within a few days. However, when we floated eggs in 2 nests that hatched the next day, the eggs floated 6 mm higher above the water surface than estimated by Liebezeit *et al.* (2007) for other shorebird eggs on the final day of incubation (C.R. Slezak, personal observation). This relatively higher floatation height of eggs just before hatch was within the range reported by other studies of nesting woodcock (Ammann 1974). We monitored nests attended by incubating females every 2–3 days to determine nest fate. Woodcocks are unique in that their eggs hatch longitudinally, allowing us to identify depredation events by the absence of eggs or the presence of shells cracked in non-characteristic configurations (Wetherbee and Bartlett 1962). If a nesting female was inadvertently flushed during

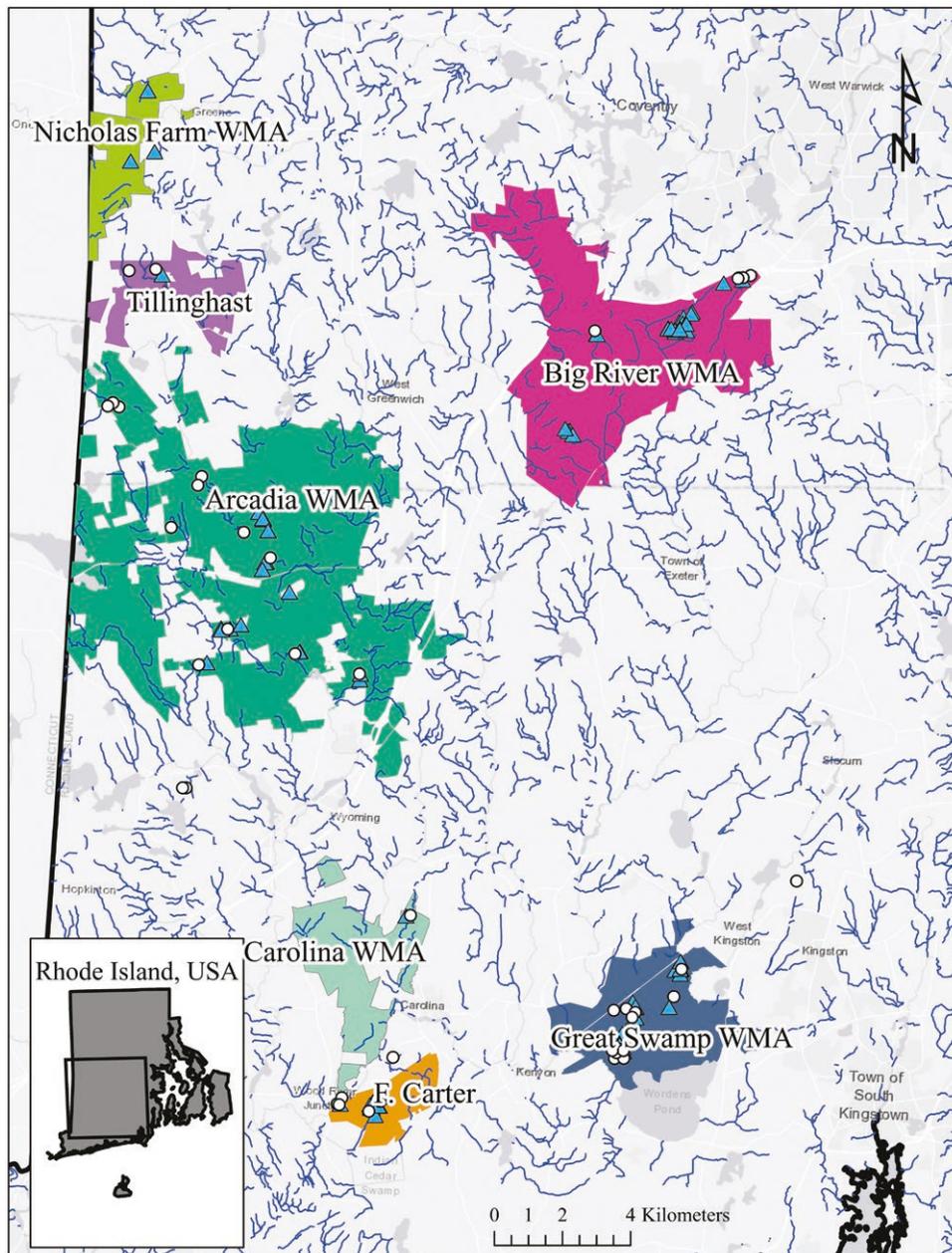


FIGURE 1. The 4 WMAs and 3 preserves used in our 2 analyses of female *Scolopax minor* (American Woodcock) nest-site selection and analysis of nest and brood survival in Rhode Island, USA from 2020 to 2022. Nest site locations are overlaid as dots on the map and streams are represented as lines. Males were captured at their singing grounds (triangles) in 2020–2021 as part of a companion study and female nest sites were usually near one or more documented singing ground(s). No nests were found at Nicholas Farm preserve, although there were several male singing grounds. Four nests were located incidentally by dog handlers and other observers outside our study areas.

a nest check, then at subsequent visits we would observe the site from a more discrete location and exercised greater caution. In total 50 nests ($n_{2020} = 16$, $n_{2021} = 18$, $n_{2022} = 16$) were found using a combination of capture techniques including trained pointing dogs, thermal cameras, tracking of tagged females, as well as incidental finds from other observers. All failed woodcock nests showed indication of depredation (i.e., non-latitude-cracked eggshells, missing eggs, or missing eggshells).

Aging chicks and estimating hatch dates and survival rates

When chicks were located with dogs or thermal cameras, we measured culmen length, recorded body mass, and banded

each chick with a butt-end size 3 USFWS leg-band. Woodcock chicks can be reliably aged because they hatch with a culmen length of 14 mm that grows at a rate of 2 mm per day until ~2 weeks of life (Ammann 1982). This documented growth rate of culmen allowed us to estimate the date of hatching, as well as nest initiation (i.e., hatch date minus 25 days) for each brood. In addition, 1–2 chicks per brood were tagged with a VHF transmitter so we could track their subsequent movements and survival. For chicks with a mass ≥ 16 g, we attached a VHF transmitter (0.5 g, <3% body mass; Holohill Systems BD-2XC VHF, Carp, Ontario, Canada). During 2020, we also attached some larger VHF transmitters (1.1 g, <3% body mass; Holohill Systems BD-2XC VHF, Carp, Ontario,

Canada) on chicks weighing ≥ 27 g, but we discontinued the use of these heavier tags after 2020, given the small difference in transmitter lifespan between the 2 tag types. In total, 62 broods ($n_{2020} = 16$; $n_{2021} = 21$; $n_{2022} = 25$) were found through trained pointing dogs, thermal cameras, tracking of tagged females, and incidental finds.

We tracked females without broods to locate their nests, tagged females with broods, and tagged chicks ~ 3 times weekly from the first time of capture until tag failure, bird mortality, or until chicks fledged at ~ 21 days old. We used chick-fledging data to assess the pre-fledge survival of broods. The 3 weekly locations for each individual were stratified across the day so that approximately equal numbers of diurnal locations were recorded before and after 1200 Eastern Standard Time (EST). The location of each female and chick was assessed by walking in on individuals until the telemetry signal could be heard without the Yagi antenna attached (\bar{x} distance to a bird was ≤ 18 m; Masse *et al.* 2014). Subsequently, we cautiously approached until the tagged individual was seen or we could determine that the female and chicks were still together because their VHF signals were originating from the same general location. When females were no longer seen with chicks, we flushed the female to observe whether her flight behavior (i.e., drooping legs and/or decoy display) indicated she still had a brood. When we were unable to locate VHF signals from tagged chicks that were with an untagged adult female, we drove on paved and unpaved roads nearby to scan for VHF radio signals in an area much larger than the detection distance of the tag. When these searches failed to identify an audible VHF signal, we assumed that the brood had died. We were confident that these broods had died because chicks under the age of 21 days cannot fly and will remain in the vicinity of the nest. In the case of suspected mortality of tagged females or chicks, we attempted to locate the VHF tag and/or carcass to identify a potential cause of death. All recovered chicks showed evidence of depredation (e.g., bite marks on the neck or missing body parts) or their VHF tags had visible signs of predator damage (i.e., damaged harness or teeth marks; Derleth and Sepik 1990). However, some chicks might have died due to exposure to adverse climatic conditions and could have been subsequently scavenged by predators.

Nest-Site Selection at the Scale of the Home Range

We assessed home-range-scale nest-site selection from 2020 to 2022 by comparing environmental factors at each nest site to 5,000 paired available sites within a 1,001-m diameter circle centered around each nest (Supplementary Material Table S1). Our dataset included 50 nests (used points; $n_{2020} = 16$; $n_{2021} = 18$, $n_{2022} = 16$) across 6 of the study sites (Figure 1; Arcadia, Big River, Carolina, and Great Swamp WMAs and Tillinghast and Francis Carter Preserves). We chose a 1,001-m diameter circle because this produced an area that was equivalent to the average 95% kernel area used by females during the summer (May to September) in Rhode Island (78.7 ± 46.4 ha), as there are no home-range size estimates available for female woodcock during the nesting period (Slezak *et al.* 2024b). To assess the spatial extent of the various forest cover types surrounding the nest, we created a 10-m raster grid in ArcMap (version 10.3.1; Esri, Redlands, CA, USA) using the 2020 forest habitat layer for Rhode Island (RIGIS 2020). We used the clipping tool in ArcMap 10.3.1

to clip our 1,001 m diameter circles (available area) to the 3 cover types with nests: agricultural (pasture/hay and idle agriculture), emergent wetlands, and forested areas excluding wetland coniferous forest. We created a separate raster for each forest cover type, emergent wetlands, distance to agriculture, distance to stream, distance to upland young forest, elevation, and distance to moist soils, as these environmental factors are suspected to play a role in nest-site selection, food availability, and subsequent space use by females during brood rearing (Sheldon 1967, Gregg and Hale 1977, Kinsley and Storm 1989, McAuley *et al.* 1996, Kelley *et al.* 2008, Keller *et al.* 2019). We then randomly generated (paired by nest) 5,000 available points for each nest site and extracted values for each of our environmental factors from both the used and available points.

Local-Scale Nest-Site Selection

For 31 (used points; $n_{2021} = 17$; $n_{2022} = 14$) of 34 nests found during 2021–2022, we collected local-scale vegetation data 46 (± 2) days after the estimated nest initiation date within a 15-m radius circular plot centered on each nest site following the methods in Yeldell *et al.* (2017). Three nests were excluded because time constraints limited our ability to collect vegetation data. Within each of the circular plots, we measured percent canopy cover, percent ground cover, stem density (number m^{-2}), visual obstruction height (m), and maximum height of vegetation (m). We used a convex spherical densiometer (Lemmon 1956) held at ground level to measure the percent canopy cover at 15 cm from the ground, the approximate height of a woodcock. We measured canopy cover at both the nest bowl and 15-m away in each cardinal direction to characterize vegetation at and near the nest site. We also placed a 1- m^2 quadrat frame on the ground centered on the nest bowl, as well as 15 m away in each cardinal direction. We viewed each quadrat directly overhead and estimated the percent ground cover (in categories of 5%) that was composed of bare ground, grasses, herbaceous plants, and woody stems (taller than 0.5 m and shorter than 0.5 m). We also counted the number of woody stems in both categories within each quadrat as a measure of stem density. For all these measures conducted at both the nest bowl and 15 m away in each cardinal direction, we calculated the mean of the 5 readings to estimate vegetation characteristics at and near the nest site. In addition, we used a 2-m Robel pole (Robel *et al.* 1970) to quantify visual obstruction and the maximum height of vegetation. For both measures, we placed the Robel pole in the nest bowl and took readings through a 1-m tall seeing eye pole standing 4 m away in each cardinal direction. For each reading, we estimated the height to the nearest 10 cm, at which the pole was fully obstructed by vegetation, as well as the maximum height to the nearest 10 cm, at which any vegetation covered some part of the pole. We averaged the 4 Robel pole readings for each nest to estimate the mean maximum vegetation height and visual obstruction height at and near the nest site. For each nest site, we then randomly chose a paired location within 50–100 m of the actual nest site and conducted the same set of vegetation surveys as described above for nest sites (Supplementary Material Table S1). This available location was presumably a site that a female could have selected as an alternative nest site. Paired comparisons of vegetation characteristics at and near nest sites vs. available locations are commonly used to estimate nest-site selection

TABLE 1. The 5 models from the home-range scale *Scolopax minor* (American Woodcock) nest-site selection analysis and the 4 models from the local-scale nest-site selection analysis. Models were compared using the change in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c), number of parameters (k), model weight (w_i), and Deviance. All nests were located in Rhode Island, USA (see Figure 1) in 2020–2022. Forest cover type is a categorical variable with 7 levels: upland coniferous forest, grassland/herbaceous, wetland deciduous forest, palustrine wetland, pasture/hay, and upland young forest.

| Model | Structure | k | ΔAIC_c | w_i | Deviance ($-2\log l$) |
|---------------------------------------|--|-----|----------------|-------|----------------------------|
| Home range nest-site selection models | ~cover (forest cover type + distance to upland young forest + distance to agriculture) | 9 | 0.00 | 0.92 | 811.01 |
| | ~global (forest cover type + dist. to ag + dist. up young forest + dist. to stream + elevation + slope + dist. to moist soil) | 13 | 4.84 | 0.08 | 807.85 |
| | ~1 | 0 | 22.72 | 0.00 | 851.74 |
| | ~distance to stream | 1 | 24.72 | 0.00 | 851.73 |
| | ~food (distance to stream + elevation + slope + distance to moist soil) | 4 | 27.91 | 0.00 | 848.92 |
| Local nest-site selection models | ~nest concealment (visual obstruction height + max vegetation height + % herbaceous plants + % canopy cover) | 4 | 0.00 | 0.95 | 53.42 |
| | ~global (% herb. plants + % grass + % open + no. woody stems < 0.5 m + no. woody stems > 0.5 m + % canopy cover + max vegetation height + visual obstruction height) | 8 | 6.04 | 0.05 | 50.54 |
| | ~1 | 0 | 24.20 | 0.00 | 85.95 |
| | ~stem density (number of woody stems < 0.5 m + number of woody stems > 0.5 m) | 2 | 26.72 | 0.00 | 84.37 |

or nest-site characteristics at the local scale (McAuley et al. 1996, Harris et al. 2009, Yeldell et al. 2017, Huinker 2020).

Statistical Analysis

Nest-site selection at the scale of the home range

To determine the best explanatory model for nest-site selection at the home-range scale, we generated 5 a priori conditional logistic regression models (strata: nest ID) using the *survival* package (version 3.5-7; Therneau and Lumley 2024) in Program R (version 4.2.2; R Core Team 2022). These models compared the actual nest sites to the available sites to identify the factors influencing selection. The environmental variables chosen for model development had been previously shown as important for females during the breeding and/or post-breeding period, when females may be prospecting for future nest sites (Slezak et al. 2024b). We first calculated Pearson correlations for all continuous variables using the *rcorr* function in the *Hmisc* package (version 5.1-1; Harrell and Dupont 2023). None of our continuous variables were highly correlated (all with $r \leq 0.7$; Dormann et al. 2013) so we retained all variables for the model creation. We scaled and centered ($\bar{x} = 0$ and $SD = 1$) our continuous variables. The 5 a priori models included a null model, a global model, and 3 models with combinations of environmental variables related to food availability (i.e., proxies for earthworm abundance), forest cover type (reference category: upland coniferous forest), and proximity to rivers and streams (Table 1). The cover model included cover types in which woodcock nests were located, as well as variables related to landscape configuration (distance to nearest upland young forest and to nearest agriculture) that may relate to the amount of vegetative cover. We performed model selection using Akaike Information Criterion adjusted for small sample sizes (AIC_c ; Burnham and Anderson 2002) using the *aictab* function in the *AICcmodavg* package (version 2.3-2; Mazerolle 2020). We selected models with ΔAIC_c values ≤ 2 (Burnham and Anderson 2002) and plotted the coefficient estimates with 85% confidence intervals (85% CIs). Unlike 95% confidence intervals (95% CIs), 85% CIs

are compatible with a ΔAIC_c cutoff of 2 and are particularly useful for determining whether a variable is informative (Arnold 2010). Furthermore, forest management for woodcock leads to the creation of young forest openings that may be beneficial to many other species that rely on early successional cover types (Masse et al. 2015). This supported our decision to use 85% CIs given the relatively non-controversial nature of such management.

Local-scale nest-site selection

To determine the best explanatory model for nest-site selection at the local scale, we generated 4 a priori conditional logistic regression models (strata: nest ID) using the *survival* package (version 3.5-7) in Program R (version 4.2.2; R Core Team 2022). These models compared the actual nest sites to available sites to identify the factors influencing selection. Similar to the home-range-scale analysis, we initially calculated Pearson correlations for all continuous variables using the *rcorr* function in the *Hmisc* package (version 5.1-1; Harrell and Dupont 2023) to check for highly correlated covariates ($r \geq 0.7$). We found that the % woody stems > 0.5 m was highly correlated with both the number of woody stems > 0.5 m and the number of woody stems < 0.5 m, so we retained only the number of woody stems > 0.5 m and the number of woody stems < 0.5 m for model development. We scaled and centered ($\bar{x} = 0$ and $SD = 1$) our continuous variables using the scale function in Program (version 4.2.2; R Core Team 2022). The 4 a priori models included a null model, a global model, and 2 models with combinations of environmental variables related to concealment at the nest site and stem density (Table 1). The nest concealment model assessed the effect of variables related to vegetative cover and concealment at the nest site (i.e., fine-scale vegetation data), while the stem density model assessed the extent, to which stem abundance influenced nest-site selection at the local scale (Table 1). Our cover and stem candidate models were compared against a global model containing each of the variables contained in these 2-candidate model sets along with a

TABLE 2. Mean values and 95% CIs for each of the local-scale vegetation measures collected at a subset of *Scolopax minor* (American Woodcock) nest sites ($n = 31$) from 2021 to 2022. Mean values and CIs were calculated using the measurements that we collected at the nest site as well as in the 4 cardinal directions surrounding the nest. For each measure, we averaged the 5 values (4 values for maximum vegetation height and visual obstruction) across all 31 sites for nests in Rhode Island, USA, 2021–2022.

| Vegetation measures in 1-m ² plot | Mean (95% CIs) |
|--|---------------------|
| % Woody stems > 5 (m) | 11.10 (7.72–14.47) |
| % Woody stems < 5 (m) | 5.74 (4.24–7.24) |
| % Herbaceous plants | 23.90 (20.12–27.69) |
| % Grass | 21.39 (16.96–25.81) |
| % Open | 37.87 (32.95–25.81) |
| % Canopy cover | 34.95 (29.94–39.96) |
| Max vegetation height (m) | 1.35 (1.19–1.50) |
| Visual obstruction height (m) | 0.24 (0.15–0.33) |

null model (Table 1). Similar to the home-range-scale selection analysis, we selected top models with ΔAIC_c values ≤ 2 (Burnham and Anderson 2002) and plotted the coefficient estimates with 85% CIs to ensure they were informative and did not contain 0 (Arnold 2010, Scraftford *et al.* 2018). For each used nest site, we calculated the mean value with 95% CIs for each of the vegetative measures we collected to demonstrate typical nest-site characteristics for female woodcock in Rhode Island (Table 2). We chose 95% CIs for descriptive statistics in the manuscript, which were not model predictions to provide a more conservative estimate of the uncertainty around the population parameters.

Nest survival

We estimated nest daily survival rates (DSR) for 39 of the 50 nests with encounter histories from 2020–2022 using nest-survival models in the *RMark* package (version 3.0.0, Laake 2022) in Program R (version 4.2.2; R Core Team 2022). *RMark* is an R program interface for Program MARK (White and Burnham 1999, Laake 2022). Eleven nests were excluded because they were found after hatch or depredation ($n = 5$) or were abandoned by the female possibly as a result of human interference ($n = 6$). Similar to other studies of nesting woodcock, we found that females caught on the nest were very likely to abandon the nest even during the final days of incubation (McAuley *et al.* 1993). For each field season (2020–2022), we formatted the number of occasions so that the first day a nest was found was labeled as “day 1” and sequentially numbered through to the last day a nest was checked during that nesting season. We generated 9 candidate models for nest survival (grouped by year) for the full dataset ($n = 39$ nests) to assess the effect of precipitation and temperature, landscape configuration, and time (daily intervals) of the nesting season (T) on woodcock nest survival (Table 3). We retrieved minimum and maximum temperature, as well as rainfall and snowfall data from the Kingston, RI coop station using past weather archived on the National Oceanic and Atmospheric Administration website (<https://www.weather.gov/wrh/Climate?wfo=box>). We chose this weather station given its central location considering the 7 study sites (Figure 1) and because it is more representative of the weather conditions in southern Rhode Island (≤ 30 km from all study sites) than the

more urban Providence Airport weather station farther north. We also assessed how proximity to forest clearings created for agricultural fields or for timber harvest (proxies for distance to nearest male singing ground) may influence woodcock nest survival. We compared our set of candidate models against a null model (Table 3). During 2021 and 2022, we used the local-scale vegetation data we collected at the 25 nests with encounter histories to assess the potential effect of each fine-scale vegetative measure on nest survival (Table 3). The 4 nests potentially abandoned because of human disturbance were excluded, as well as 2 nests for lack of vegetation data. After calculating Pearson correlations for all continuous variables using the *rcorr* function in the *Hmisc* package (version 5.1-1; Harrell and Dupont 2023), we retained all variables in our models. We scaled and centered ($\bar{x} = 0$ and $SD = 1$) our continuous variables. We compared the set of candidate models to a null model, as well as a global nest concealment model that combined each of the 4 vegetative measures using AIC_c (Table 3). We selected models with ΔAIC_c values ≤ 2 (Burnham and Anderson 2002) and evaluated whether the 85% CIs on the beta coefficients were significant and did not contain 0 (Arnold 2010, Scraftford *et al.* 2018). For our nest-survival analysis, we estimated the probability that a nest survived the entire incubation period (25 days) by raising the DSR estimate from our null model of constant daily survival to the 25th power (Freeman *et al.* 2023).

Brood survival

We estimated brood DSR (≥ 1 chick surviving to fledge) using nest-survival models in the *RMark* package (version 3.0.0, Laake 2022) for 56 of the 62 broods with encounter histories from 2020 to 2022. Six broods were excluded from the analysis because the brood was caught after fledging (i.e., 21 days old) and capable of sustained flight ($n = 1$), the transmitters were faulty at deployment ($n = 2$), or the hen was injured during the capture and banding process ($n = 2$). We used nest-survival models in *RMark* to assess brood survival, as we did not track broods at regular time intervals and instead monitored them ~ 3 times weekly. Thus, nest-survival models worked well because we did not know the exact date of death in cases where the brood was not successful (White and Burnham 1999). For our brood survival models, we applied the same formatting for the number of occasions as used in our nest-survival models. We used the same set of 9 survival models from the full nest-survival dataset (Table 3), in part because female woodcock, similar to other ground-nesting species, select a nest site based on its perceived suitability for raising a brood. We used the same environmental variables as in the nest-survival analyses. In addition to the 9 survival models used in the nest-survival analysis, we included a cover model (Table 3; % young forest in the localized use area for each brood) because brooding woodcock may prefer young forest sites based on the vegetative structure and concealment they provide. We assigned a % young forest value to each brood by averaging the longitude and latitude values (WGS 84) for each individual brood in Program R (version 4.2.2; R Core Team 2022). Using ArcMap (version 10.3.1; Esri, Redlands, CA, USA), we added a circular buffer to each averaged longitude and latitude location of radius equivalent to the average step length between subsequent GPS locations for our entire dataset of tracked broods. We then clipped these individual buffers to the forest habitat 2022 layer and

TABLE 3. The 9 models compared for *Scolopax minor* (American Woodcock) nest survival full dataset ($n = 39$; 2020–2022) analysis, the 6 models compared for the nest survival subset analysis with local-scale vegetation measures ($n = 25$; 2021–2022), and the 10 models compared for the brood survival analysis ($n = 56$) for nests and broods in Rhode Island, USA in 2020–2022. Model comparisons were based on the change in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c), number of parameters (k), and model weight (w_i).

| Model | Structure | k | ΔAIC_c | w_i |
|---------------------------------------|--|-----|----------------|-------|
| Nest survival (full dataset) models | ~1 | 1 | 0.00 | 0.22 |
| | ~distance to agriculture | 2 | 0.76 | 0.15 |
| | ~time (T) | 2 | 1.15 | 0.12 |
| | ~minimum temperature | 2 | 1.28 | 0.12 |
| | ~snowfall | 2 | 1.45 | 0.11 |
| | ~rainfall | 2 | 1.48 | 0.11 |
| | ~distance to young forest | 2 | 2.01 | 0.08 |
| | ~maximum temperature | 2 | 2.03 | 0.08 |
| Nest survival (subset dataset) models | ~1 | 1 | 0.00 | 0.34 |
| | ~% herbaceous plants | 2 | 0.65 | 0.25 |
| | ~maximum vegetation height | 2 | 1.82 | 0.14 |
| | ~visual obstruction height | 2 | 1.97 | 0.13 |
| | ~% canopy cover | 2 | 1.97 | 0.13 |
| | ~nest concealment (visual obstruction height + maximum vegetation height + % herbaceous plants + % canopy cover) | 5 | 5.38 | 0.02 |
| Brood survival models | ~1 | 1 | 0.00 | 0.17 |
| | ~maximum temperature | 2 | 0.15 | 0.15 |
| | ~minimum temperature | 2 | 0.28 | 0.15 |
| | ~distance to young forest | 2 | 0.74 | 0.12 |
| | ~cover (% young forest) | 2 | 1.31 | 0.09 |
| | ~rainfall | 2 | 1.36 | 0.08 |
| | ~time (T) | 2 | 1.51 | 0.08 |
| | ~distance to agriculture | 2 | 1.56 | 0.08 |
| | ~snowfall | 2 | 1.97 | 0.06 |
| | ~weather (snowfall + rainfall + maximum temperature + minimum temperature) | 5 | 3.55 | 0.03 |

summarized the percentage of young forest in the activity center of each brood. We compared our set of candidate models to a null model using AIC_c (Table 3), selected models with ΔAIC_c values ≤ 2 (Burnham and Anderson 2002), and evaluated whether the 85% CIs on the beta coefficients were significant and did not contain 0 (Arnold 2010, Scraftford et al. 2018). We estimated the probability that a brood survived either the entire brood-rearing period (21 days) by raising the DSR estimate from our null model of constant daily survival to the 21st power (Freeman et al. 2023).

RESULTS

Home-range Scale Nest-site selection

Of the 5 a priori conditional logistic regression models for nest-site selection at the home-range scale (Table 1), the model containing variables related to forest cover type and landscape configuration predicted nest-site selection best with 95% AIC_c model weight (Table 1). This model suggests that at the home-range scale, females were selected for wetland deciduous forest, upland deciduous forest, upland young forest, pasture/hay, grassland/herbaceous, and emergent wet-

land cover types (Figure 2). The second-ranked model had a $\Delta AIC_c > 4$. Females were also selected for areas closer to upland young forest and agriculture. The only variable that was weakly related to nest-site selection was upland mixed forest (Figure 2).

Local-Scale Nest-Site Selection

Of the 4 a priori conditional logistic regression models for nest-site selection at the local scale (Table 1), the model containing variables related to nest-site concealment predicted woodcock nest-site selection best with 92% AIC_c model weight (Table 1). This model suggests that at the local scale, females were selected for nest sites with higher percentages of herbaceous cover, canopy cover, and surrounding vegetation that was taller (Figure 3). The only variable that was weakly related to nest-site selection was percent visual obstruction (Figure 3). The second-ranked model had a $\Delta AIC_c > 6$.

Nest Survival

The average nest initiation date for woodcock in Rhode Island derived from 41 nests and 45 broods was April 1, although nest initiation was estimated to be as early as March 7 and

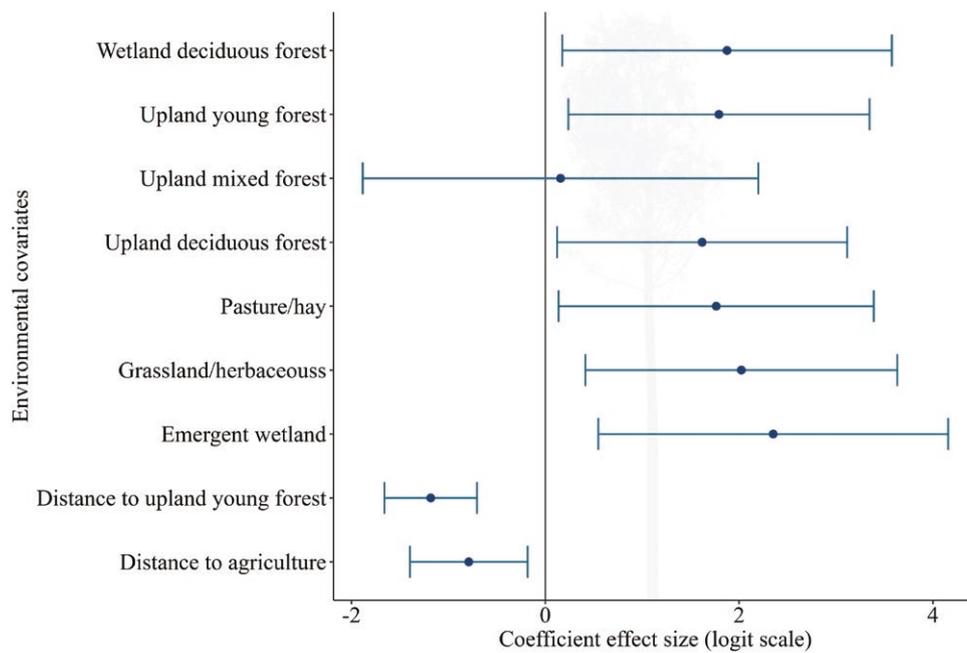


FIGURE 2. Home-range scale nest-site selection coefficient estimates on the logit scale and 85% CIs from our cover model for 50 *S. minor* nest sites in Rhode Island, USA in 2020–2022. Nest sites were located in wetland deciduous forest, upland young forest, upland deciduous forest, pasture/hay, grassland/herbaceous, emergent wetlands, and were close to upland young forest and agriculture. Upland mixed forest was considered weakly related to home-range scale nest-site selection because the CIs encompassed 0.

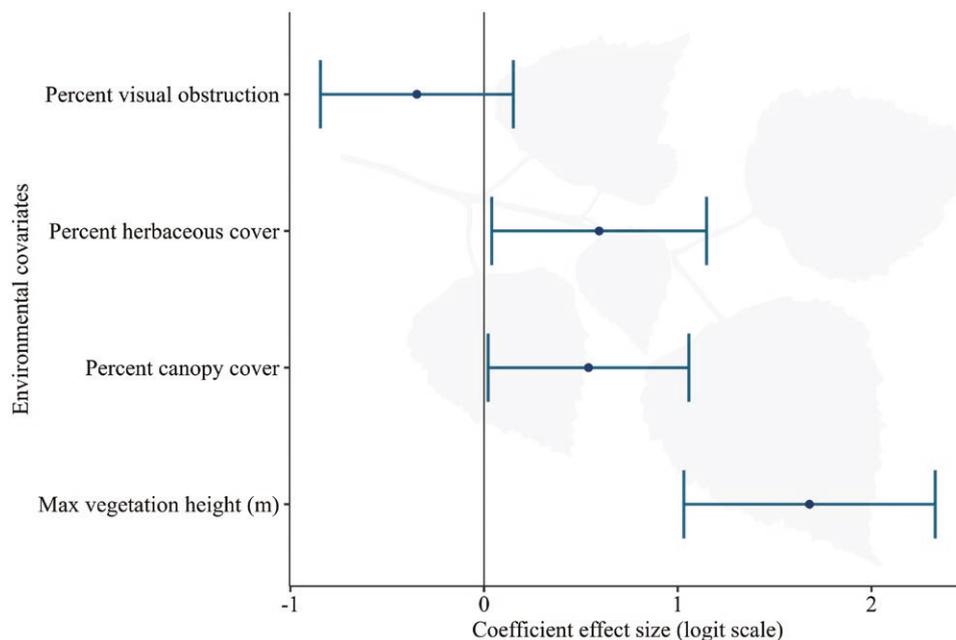


FIGURE 3. Local-scale nest-site selection coefficient estimates on the logit scale and 85% CIs from our nest concealment model for 31 *S. minor* nest sites in Rhode Island, USA in 2021–2022. Nest sites had a higher percentage of herbaceous cover, canopy cover, and surrounding taller vegetation. Percent visual obstruction was considered weakly related to local-scale nest-site selection because the CI encompassed 0.

as late as May 15 during the 3 years of the study (Figure 4). The null model was the top-ranked model for both the full nest-survival dataset and the subset of nests with local-scale vegetation measures, suggesting that none of the assessed factors affected nest survival (Table 3). Each of the competing models ($\Delta AIC_c \leq 2$) ranked lower than the null model, so none of these variables were considered important for nest survival. The probability of a nest surviving the entire nesting

period was low, with only 10% making it to hatch (95% CI: 2–21%).

Brood Survival

The average hatch date for broods in Rhode Island ($n = 62$) was April 25 although hatching began as early as April 1 and as late as June 9 during the 3 years of the study (Figure 4). Similar to the 2 nest-survival analyses, the null model was the

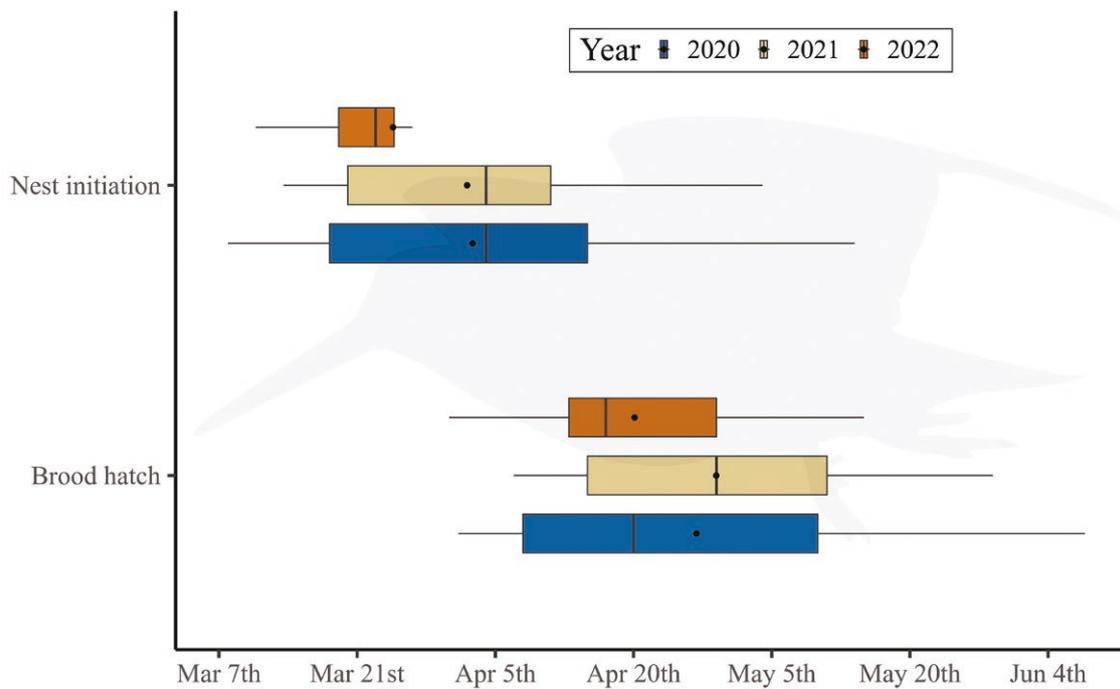


FIGURE 4. Nest initiation ($n_{\text{ nests }} = 41$; $n_{\text{ broods }} = 45$) and brood ($n = 62$) hatch date phenology by year for *S. minor* nests and broods located in Rhode Island, USA from 2020 to 2022. Boxes indicate median, mean (black point within box plot), 25%, and 75% quartiles. Whiskers represent the highest and lowest values within 1.5 times the interquartile range over the 75th percentile. In Rhode Island, nests are initiated in mid-March and continue through late-April, whereas broods typically begin hatching in mid-April and continue through mid-May.

top-ranked model, suggesting that the assessed factors did not affect brood survival (Table 3). Each of the competing models ($\Delta\text{AIC}_c \leq 2$) ranked lower than the null model, so none of these variables were considered important for brood survival. The probability of a brood surviving to fledge was low with only ~16% (95% CI: 8–27%) of broods surviving the entire 21-day period.

DISCUSSION

Our study is one of the first to document woodcock nest-site selection at 2 spatial scales and to the best of our knowledge, the first to explicitly test the hypothesis that female nest-site selection relies on home-range characteristics, as well as visual concealment of the nest at the local scale. As predicted, females were strongly selected for landscape characteristics related to forest cover and landscape configuration, and nest sites that provided high percentages of herbaceous and canopy cover, and tall surrounding vegetation. Despite this strong nest-site selection at 2 spatial scales, nest and brood survival were extremely low, and contrary to our predictions, neither were adequately explained by weather or habitat variables. These low survival rates may indicate a need for softer edges (i.e., undulating boundaries or removal of mature trees where 2 boundaries meet) in areas where woodcock and other ground-nesting birds reside.

Home-Range Scale Nest-Site Selection

At the home-range scale, woodcock females selected early successional cover types and proximity to upland young forests and regenerating agricultural openings. Woodcock occupied diverse forest and wetland compositions, including upland young and deciduous forests, and wetlands. These findings

align with other studies from the northeastern USA that emphasize the value of maintaining diverse habitats that contain dense early successional cover near moist soils which can support nesting woodcock and their young (Pettingill 1936, Mendall and Aldous 1943, Sheldon 1967, Kinsley and Storm 1989, McAuley et al. 1996). Although woodcock nest in forests of mixed species composition that can span various age groups (Dessecker and McAuley 2001), nest sites are most often found in and around forest openings (Bourgeois 1976, Sepik and Derleth 1993, McAuley et al. 1996, Huinker 2020) and align with the patterns of selection we observed in Rhode Island (Figure 2). Nest sites were generally close to upland young forests and agricultural openings, often overlapping with singing grounds, suggesting that male selection of singing sites may align with female selection of nest sites (Dwyer et al. 1988, Dessecker and McAuley 2001).

In the northeast, woodcock typically nest on well-drained upland sites (Mendall and Aldous 1943, Gregg and Hale 1977, McAuley et al. 1996); however, the nest sites located in our study were often near water or in areas with moist soil (Figure 1). At the home-range scale, woodcock was selected for nest sites within wetland deciduous forests, as well as emergent wetlands near streams. In addition, we regularly noticed that nest sites were often close to standing water or near areas where water had inundated the soil for at least some portion of the year (C.R. Slezak, personal observation). Selection for streams is likely occurring at a scale larger than we assessed (i.e., larger than a female's home range), and we hypothesize that females migrating northward prospecting for breeding sites may first settle along riparian corridors before selecting for the home-range scale characteristics described here. In northern New England these low-lying areas are more susceptible to persistent snowpack, making them inaccessible to

early arriving nesting females during some years (Bourgeois 1976, Sepik et al. 1993). This may explain why nest site associations with water have only been observed in regions such as southern New England and areas of the south that experience milder winters (Roboski and Causey 1981).

Local Nest-Site Selection

At the local scale, females selected nest sites that were more concealed visually (Figure 3), possibly representing an antipredator trait that is particularly necessary for ground-nesting species in fragmented landscapes that contain a mosaic of habitats with more edges (Angelstam 1986, Huinker 2020). While there has been extensive research on the vegetation characteristics at woodcock nesting sites (Mendall and Aldous 1943, McAuley et al. 1996, Harris et al. 2009, Miller and Jordan 2011, Huinker 2020), the results are often inconsistent partially because of the broad geographic breeding range (Sepik et al. 1993) and extended breeding season (Slezak et al. 2024a) of woodcock, as well as varied methodological approaches to quantify nest site vegetation (McAuley et al. 2020). However, we identified some commonalities among nest site vegetation measures in Rhode Island and studies from other locations across the breeding range. Woodcock nest sites in Rhode Island had moderate canopy closures (\bar{x} = 35%) similar to those reported in Missouri (\bar{x} = 36%; Murphy and Thompson 1993), although substantially lower than those reported in Michigan (\bar{x} = 62%; Huinker et al. 2020). Nest sites in Rhode Island were composed of relatively equal percentages of woody stems (~17%) and herbaceous plant cover (~24%) similar to nest sites in Pennsylvania (20–29%), although other studies in northern New England did not measure this variable because woodcock nests were initiated before herbaceous plant emergence (McAuley et al. 1996). Nest sites also had moderate grass coverage in Rhode Island (21%) and were slightly lower in Michigan (13%; Huinker 2020). The percentage of bare ground at nests in Rhode Island (38%) was substantially higher than in Michigan (3%; Huinker et al. 2020) and Pennsylvania (4%; Kinsley and Storm 1989). Thus, the relative amount of certain cover types and the total amount of canopy cover at nest sites were broadly similar across studies with a few notable exceptions.

The results of the nest-site selection analyses at the local and the home-range scale suggest that female woodcock select nest sites in early successional cover types that are vegetated, which conceals their ground nest. Management prescriptions for woodcock breeding habitats usually emphasize the need for high stem density with the vegetation structure being more important than species composition (Gregg and Hale 1977, Sepik et al. 1993, Dessecker and McAuley 2001, McAuley et al. 2020). Stem densities at nest sites in Rhode Island were 54,600 stems ha^{-1} and 39,400 stems ha^{-1} for tall (>0.5 m) and short (<0.5 m) woody stems, respectively. Stem densities at nest sites in Alabama were substantially lower (7,002 stems ha^{-1} and 20,630 stems ha^{-1} for woody stems >0.3 m and <0.3 m, respectively; Roboski and Causey 1981). In Pennsylvania, stem densities at nests were 48,550 stems ha^{-1} and 148,175 stems ha^{-1} for woody stems >0.3 m and ≤ 2.5 m and <0.3 m, respectively (Kinsley and Storm 1989). The substantial increase in stem density from south to north, along with the itinerant breeding behavior (i.e., the temporal overlap of migratory and reproductive periods of the annual cycle) of nesting females (Slezak et al. 2024a), makes selection for spe-

cific stem densities or species of vegetation by individual females unlikely. Instead, females select nest sites within their home ranges with more horizontal and vertical structures compared to the available surrounding habitat, which helps to conceal the nest (McAuley et al. 1996, Dessecker and McAuley 2001, Harris et al. 2009). Because woodcock are itinerant breeders and exhibit extreme flexibility in their ability to migrate between nesting attempts (Slezak et al. 2024a), females must respond flexibly to differences in land use patterns and available habitat as they select nest sites across the breeding range. The itinerant breeding behavior of woodcock highlights the importance of maintaining diverse landscapes that contain areas of suitable nesting habitat for woodcock across their breeding range.

Nest and Brood Survival

Studies of woodcock nest and brood survival in the northeastern United States are limited, and most often estimate survival using biased estimators (i.e., apparent survival) that do not account for exposure time (Huinker 2020). The daily survival estimates that we report for Rhode Island are the first in southern New England to assess whether landscape configuration, vegetation, and weather influence woodcock nest and brood survival. Our estimates of nest survival were extremely low compared to other studies, all from the northern part of the breeding range, such as Michigan (33%; Huinker et al. 2020), Minnesota (46–79%; Daly et al. 2019), and Maine (50–75%; McAuley et al. 1990). Brood survival was also higher in Michigan (84% surviving to 32 days; Huinker 2020), Minnesota (75–84% surviving to 15 days; Daly et al. 2015), and Maine (44–83% surviving to 21 days; Dwyer et al. 1988, McAuley et al. 2006). Notably, we did not measure any local-scale habitat characteristics at brood locations, such as woody ground cover or soil moisture that have been shown to influence brood survival in Michigan (Huinker 2020). Common to all such studies, nest-survival estimates were lower than brood survival estimates, suggesting that the former may be more important than the latter for limiting woodcock annual productivity (Derleth and Sepik 1990, Kramer et al. 2019b, Huinker 2020). Similar to other recent studies of woodcock nest survival (Huinker 2020), we found that vegetation characteristics did not influence nest-survival estimates and landscape configuration and percent young forest did not influence brood survival estimates.

Similar to other ground-nesting birds, nest failure for woodcock appears to be predator mediated and we found no direct evidence that any of the monitored nests or broods had failed from exposure to adverse climatic conditions. Adverse effects of weather (e.g., periods of low temperatures and precipitation) on nest and brood survival are more likely to occur at the northern extent of the breeding range rather than at mid-latitudes like Rhode Island (McAuley et al. 2006, Kramer et al. 2019a) or in other areas near the southern terminus of the breeding range (Wiley and Causey 1987). Although there may be range-wide patterns of nest and brood survival, the peculiar life history of woodcock (i.e., prolonged breeding season, high rate of renesting, and itinerant breeding) have evolved as a countermeasure to regularly low nest and brood survival observed in southern New England (Slezak et al. 2024a).

Conservation Implications

Our nest-site selection analysis at 2 spatial scales reinforces past literature highlighting the importance of creating and

maintaining habitat for *S. minor* across their breeding range that includes early successional cover types, mature forests, and wetlands that are beneficial to both nesting females and their young (Dessecker and McAuley 2001, Masse et al. 2014, Slezak et al. 2024b). In disturbed landscapes with high anthropogenic disturbance, such as those found in Rhode Island, we should prioritize habitat structure and configuration that potentially reduces nest detection by predators. Woodcock nests and broods are depredated by a suite of meso- and avian predators (e.g., mink, striped skunks, red foxes, etc.; Kramer et al. 2019b, Daly et al. 2019, Huinker 2020) that have increased in abundance in the northeast U.S. because of land use alteration, fragmentation, and loss (Litvaitis 2001, Zamuda et al. 2022). Remaining natural areas in Rhode Island are severely fragmented and land conversion is one of the most serious threats to forests in the state (Riely et al. 2019). Fragmented landscapes promote “mesopredator release” (*sensu* Crooks and Soulé 1999) and may be one reason for the low-survival estimates observed in our study.

Given these high predation rates in fragmented landscapes, it is possible that woodcocks are susceptible to ecological traps, where perceived habitat quality does not align with actual survival outcomes. Areas that appear suitable due to their availability of cover may inadvertently attract woodcock but result in low recruitment and survival due to elevated predation risk (Battin 2004, Robertson and Hutto 2006).

Low nest survival estimates for woodcock in Rhode Island may have limited our ability to detect the influence of landscape configuration, vegetation, and weather, because predation rates were high enough that discerning differences between successful and unsuccessful nests would be difficult or require a larger sample of nests (Mezquida 2004). In highly disturbed landscapes like Rhode Island, we suggest that wildlife managers create experimentally managed forests and adapt current forestry practices to reflect the forest configurations that best reduce predation rates for ground-nesting birds. Based on the hard forest edges and low survival rates that we observed for *S. minor* in Rhode Island, we suspect that softening edges when creating early successional cover types may help mediate depredation of ground-nesting birds like *S. minor*.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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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.

Conflict of interest statement

The authors declare no conflicts of interest.

Author contributions

Conceptualization: CRS, SRM. Methodology: CRS, IMD, SRM. Investigation: all authors. Visualization: CRS, SRM. Funding acquisition: SRM. Project administration: SRM. Supervision: SRM. Writing—original draft: CRS, IMD, SRM. Writing—review & editing: CRS, IMD, JEK, SRM

Data availability

Analyses reported in this article can be reproduced using the data and code provided by Slezak et al. (2025).

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