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RESEARCH ARTICLE

Landscape context matters when American Woodcock select singing grounds: Results from a reciprocal transplant experiment

Stephen J. Brenner,[1] Bill Buffum,[1] Brian C. Tefft,[2] and Scott R. McWilliams[1*]

[1] Department of Natural Resources Science, University of Rhode Island, Kingston, Rhode Island, USA
[2] Rhode Island Department of Environmental Management, Division of Fish and Wildlife, West Kingston, Rhode Island, USA
* Corresponding author: srmcwilliams@uri.edu

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ABSTRACT

The multiscale nature of habitat selection during the breeding season for migratory birds means that core-use areas (e.g., breeding territories) are selected based on their local habitat features, but these may also be influenced in some way by features within a larger-scale landscape. We conducted a reciprocal transplant experiment to test the hypothesis that habitat selection and movements of male American Woodcock (*Scolopax minor*) in core-use areas during the breeding season depend on the perceived quality of the surrounding landscape. We captured second-year male woodcocks ($n = 19$) at high- or low-likelihood of use landscapes in Rhode Island, USA, affixed each with a radio transmitter, relocated them to the opposite type of landscape, and then determined if they returned to their original site of capture or remained in the landscape to which they were relocated. Birds captured in high-likelihood landscapes and moved to low-likelihood landscapes generally returned to their original high-likelihood landscape (5/7, 71%), but birds captured in low-likelihood landscapes and moved to high-likelihood landscapes rarely returned to their original low-likelihood landscape (1/12, 8%). These results support the hypothesis that woodcock assess their surroundings relatively rapidly and subsequently make critical settlement decisions based on landscape composition. Given that woodcock choice is predicted by the woodcock-specific resource selection function, these results also provide support for the use of this tool to guide forest management for woodcock.

Keywords: American Woodcock, habitat selection, landscape, *Scolopax minor*, translocation, young forest management

El contexto del paisaje importa cuando *Scolopax minor* elige los terrenos de canto: Resultados de un experimento de trasplante recíproco

RESUMEN

La naturaleza multi-escalar de la selección de hábitat de las aves migratorias durante la estación reproductiva significa que las áreas núcleo usadas (e.g. territorios reproductivos) son seleccionadas en base a sus características locales del hábitat, pero éstas pueden también estar influenciadas de algún modo por las características adentro de una escala más amplia de paisaje. Realizamos un experimento de trasplante recíproco para evaluar la hipótesis que la selección de hábitat y los movimientos de los machos de *Scolopax minor* en las áreas núcleo usadas durante la estación reproductiva dependen de la calidad percibida del paisaje circundante. Capturamos machos del segundo año ($n = 19$) en paisajes con alta y baja probabilidad de uso en Rhode Island, EEUU, les colocamos a cada uno un radio transmisor, los relocalizamos en el tipo de paisaje opuesto y luego determinamos si regresaron al sitio original de captura en el paisaje desde el cual fueron relocalizados. Las aves capturadas en los paisajes de alta probabilidad y llevadas a los paisajes de baja probabilidad generalmente regresaron a sus paisajes originales de alta probabilidad (5/7, 71%), pero las aves capturadas en los paisajes de baja probabilidad y llevadas a paisajes de alta probabilidad raramente represaron a sus paisajes originales de baja probabilidad (1/12, 8%). Estos resultados apoyan la hipótesis que *S. minor* evalúa los alrededores relativamente rápido y subsecuentemente toma decisiones críticas de asentamiento basado en la composición del paisaje. Dado que la elección de *S. minor* es predicha por la función de selección de recursos específica para la especie, estos resultados también apoyan el uso de esta herramienta para guiar el manejo forestal para *S. minor*.

Palabras clave: manejo de bosque joven, paisaje, *Scolopax minor*, selección de hábitat, traslocación

INTRODUCTION

For animals that migrate, habitat selection and establishment of a breeding territory are critical decisions that impact survival and breeding success, and potentially create links between breeding, wintering, and stopover sites during migration (Martin 1998, Gunnarsson et al. 2005, Norris and Marra 2007). Upon arrival at a given breeding area, individuals presumably occupy the highest-quality habitat available, although as more individuals settle, the best available habitat may be lower in quality leading to occupation of a range of quality habitats (Fretwell and Lucas 1970, Rosenzweig 1981, Pulliam and Danielson 1991). Microhabitat factors influence the perceived quality of an area where individuals settle (Gutzwiller et al. 1983, Martin 1998, MacFaden and Capen 2002), but the landscape surrounding a given territory or core-use area can also influence habitat selection and subsequent daily movements and resource availability (Saab 1999, Webb et al. 2010, Kennedy et al. 2011). The spatial arrangement, amount, or isolation of habitat at the landscape scale has been shown to influence individual occupancy, dispersal, and habitat use (Paradis et al. 1998, Kennedy et al. 2011, Fahrig 2013). Much management effort focuses on creation or modification of habitat to promote use by certain bird species and increase habitat quality at a local scale (Chandler et al. 2009, Boves et al. 2015), but landscape-level factors must be taken into account to promote effective management. A rarely tested assumption of these habitat selection models is that individuals can assess available habitat quality at some broader scale and then select the best available habitat at a given time (Johnson 2007, Chudzinska et al. 2015).

We studied habitat selection of the American Woodcock (*Scolopax minor*, hereafter "woodcock") in landscapes with different resource abundance and probability of use. Woodcock are migratory, forest-dwelling shorebirds that rely upon early successional (hereafter "young") forest to breed (Kelley et al. 2008). Loss of habitat within the last 40 yr has led to population declines across their range (McAuley et al. 2005, Cooper and Rau 2012). In the northeastern United States, best management practices (BMPs) include clearcutting forest to create young forest habitat to promote woodcock breeding (McAuley et al. 1996, Dessecker and McAuley 2001, Williamson 2010). The location of newly created habitat within a larger landscape context could influence the selection, habitat use, and behavior of woodcock within these areas, and this in turn will determine the effectiveness of the management action.

In our study, we used reciprocal translocations of woodcock between landscapes that differed in forest composition, abundance of resources, and likelihood of use to determine if woodcock can assess habitat at a landscape scale and select habitat accordingly. Translocations have been used in other avian studies to determine territorial establishment, movement barriers, stopover duration, and site fidelity across landscapes (Komdeur et al. 1995, Villard and Haché 2012, Liu and Swanson 2015, Krištín and Kaňuch 2017). The advantage of experimentally moving birds between different landscapes to assess habitat selection is that this forces individuals to essentially choose between a restricted set of available habitats (Matthews and Rodewald 2010, Liu and Swanson 2015). Such a reciprocal transplant experiment also allows us to confirm that habitat selection of relocated woodcock is consistent with that predicted from a woodcock-specific resource selection function (RSF; Masse et al. 2014). We predicted that male woodcock captured in resource-abundant, high-likelihood of use landscapes (as predicted by the RSF) and moved to limited-resource, low-likelihood of use landscapes would return more often than male woodcock captured in low-likelihood of use landscapes and moved to high-likelihood of use landscapes. Such a pattern would imply that woodcock assess their surroundings relatively rapidly and subsequently make critical settlement decisions based on landscape composition.

METHODS

Study Area

All singing grounds selected for this study were at or near (<300 m) state-managed young forest, and all featured male woodcock breeding activity within selected landscapes. These 2 criteria ensured that the results from our experiment could inform best management practices on state-owned lands, most importantly the decision of where creation or expansion of young forests should be focused. All research was conducted within central and southern Rhode Island in Washington and Kent counties (Figure 1). The state-owned management areas that were used in our study within this region included Great Swamp Management Area (41°27′30″N, 71°34′60″W), Carolina Management Area (41°28′30″N, 71°28′50″W), Arcadia Management Area (41°35′50″N, 71°41′55″W), Big River Management Area (41°38′10″N, 71°35′50″W), Nicholas Farm Management Area (41°41′05″N, 71°46′35″W), and Tillinghast Pond Management Area (41°38′40″N, 71°45′25″W). Much of this region is dominated by red maple (*Acer rubrum*), oak (*Quercus* spp.), and white pine (*Pinus strobus*) forest, with upland shrubland/young forest accounting for <3% of non-coastal areas in the state (Buffum et al. 2011).

Landscape Size and Likelihood of Use by Woodcock

Within these 6 state-owned management areas, we delineated 147 landscapes, each a 4 km^2 circle centered on young forest patches that had been recently (<15 yr ago) created by selective clearcuts (1–10 ha) or were being actively maintained by brush thinning and mowing. Defining a landscape size depends on a variety of factors, including daily movements of the focal organism, management objectives, and size of study area (Bird and Lenore 2012). Current management practices for the northeastern

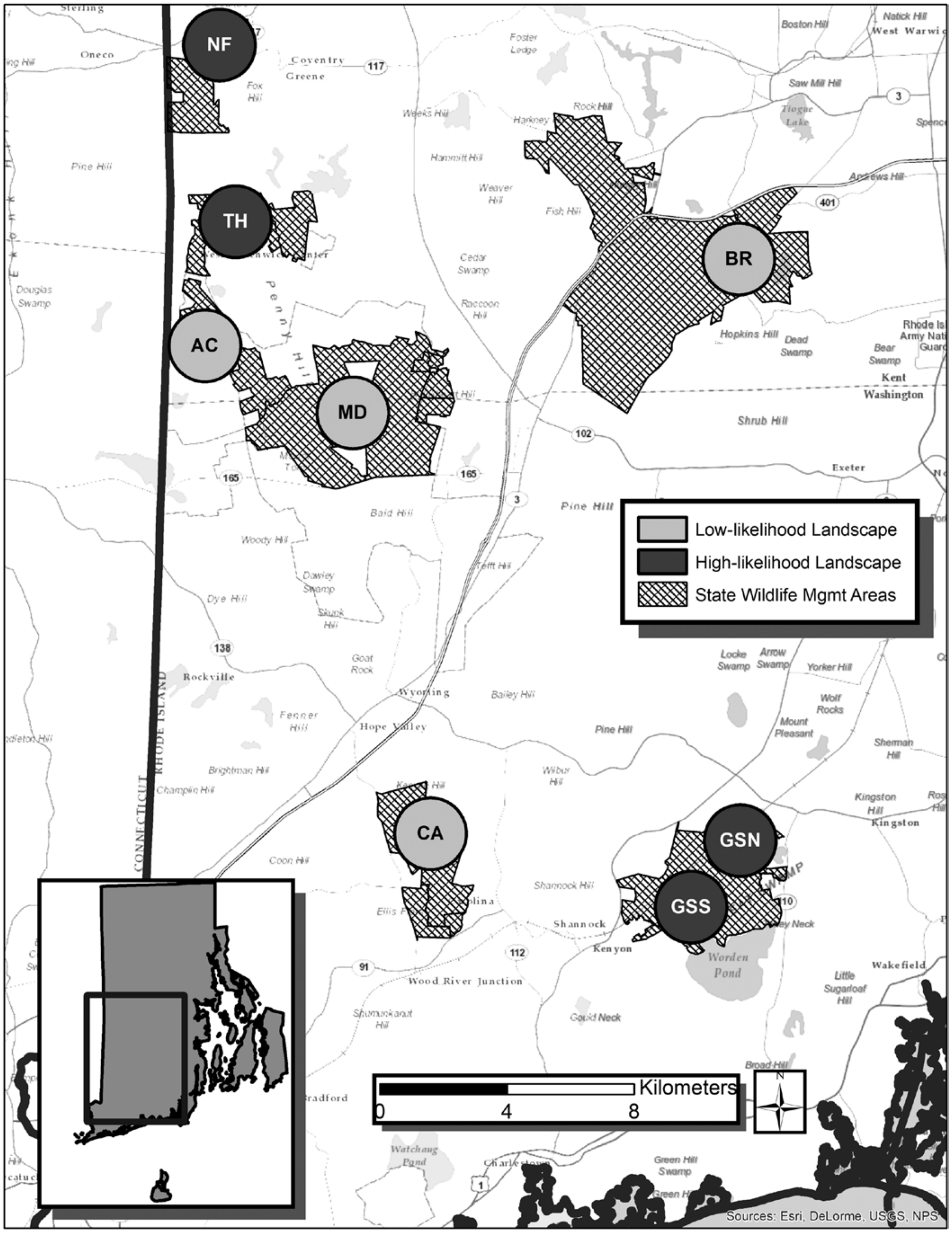

FIGURE 1. Map of study region and location of 8 landscapes used for American Woodcock reciprocal transplant experiment in southern Rhode Island, USA. AC = Arcadia Pine Top, BR = Big River East, CA = Carolina, GSN = Great Swamp North, MD = Midway, GSS = Great Swamp South, NF = Nicholas Farm, TH = Tillinghast Pond. All landscapes were 4 km^2 and centered on state-managed young forest patches.

U.S. recommend 2–4 km^2 habitat mosaics that can support woodcock at this landscape scale (Williamson 2010, Masse et al. 2019). From a woodcock perspective, 4 km^2 would generally encompass several core-use areas used for breeding, roosting, and daytime feeding (Palmer 2008, Williamson 2010), as has been shown for male woodcock inhabiting some of the same management areas used in our study (Masse et al. 2014). We recognize that the term "landscape" can imply a much larger area than 4 km^2 for other animals in other contexts. However, we feel justified in referring to the 4 km^2 area as a "landscape" for woodcock given that (1) this size area is larger than the mean home range of woodcock over the entire summer period (0.51 ± 0.14 km^2; range: 0.10–4.7 km^2), which includes the core-use areas used by woodcock for breeding, roosting, and feeding (Masse et al. 2014); and (2) habitat management for woodcock is typically focused on a 2–4 km^2 area that provides herbaceous forest openings and old fields for breeding, courtship, and roosting, and young forest for nesting and feeding.

To determine the resource composition and likelihood of use of the landscapes by woodcock, we used a probability of use map developed specifically for male woodcock in the state of Rhode Island (Masse et al. 2014). The output of the model assigned a woodcock relative probability of use to each 10 × 10 m cell within the study region. The probability of use was developed from a resource selection function based on diurnal radiotracking of 52 male woodcock during May–August 2011 and 2012 in the same region we used for our study. The best-performing model included the following parameters: forest cover type, slope, elevation, distance to existing young forest, distance to agricultural openings, distance to hydric soil, and distance to streams (Masse et al. 2014). Using the focal statistics tool in ArcGIS 10.2 (Environmental Systems Research Institute, Redlands, California, USA) and the output from this best-performing resource selection function model (Masse et al. 2014), we estimated the average relative probability of use score for the 147 landscapes (each 4 km^2) that fit within the 6 state-managed wildlife areas. For each of these 4 km^2 landscapes, the average relative probability of use was calculated across each of the 10 × 10 m cells within each 4 km^2 area.

Site Selection and Pairing

We selected 4 high-likelihood landscapes and 4 low-likelihood landscapes based on these criteria: (1) the average relative probability of use values were distinctly different between the 2 landscape groups (high-likelihood score ≥45, low-likelihood score ≤35); (2) there was no spatial overlap between landscapes in the same likelihood of use rank; (3) there was an appropriate distance between paired high-likelihood and low-likelihood landscapes (8.5–22 km); and (4) in the past 5 yr male woodcock had been observed displaying within that 4 km^2 area. Our 4 high-likelihood landscapes were Great Swamp South (41°27′29″N, 71°35′27″W), Great Swamp North (41°28′26″N, 71°34′18″W), Tillinghast Pond (41°38′54″N, 71°45′48″W), and Nicholas Farm (41°41′58″N 71°46′08″W), and our 4 low-likelihood landscapes were Carolina (41°28′32″N, 71°41′18″W), Midway (41°35′38″N, 71°43′05″W), Big River East (41°38′19″N, 71°34′21″W), and Arcadia: Pine Top (41°36′58″N, 71°46′28″W) (Table 1, Figure 1).

Each high-likelihood site was paired with a low-likelihood site for the translocation experiment based primarily on distance and drive time between sites. Distances between paired sites ranged from 8.5 to 22 km (Table 1), and drive time ranged from 25 to 45 min. We kept enough distance between paired sites so that returning to a given bird's capture site would require active habitat selection and not normal dispersal movements. Within–breeding season dispersal of young males averaged 1.3 km and was recorded as up to 2.7 km in Maine (Dwyer et al. 1988), with one exceptional record of an unknown-aged male moving up to 7 km within the same breeding season (McAuley et al. 1993). Given our shortest pairing distance was 8.5 km, we likely eliminated site selection based on simple dispersal behavior. It was harder to assess what constituted too large a distance for a woodcock to return to any given site regardless of habitat quality. However, given that woodcock in southern New England are migratory, we assumed most potential translocations within the state that did not cross major barriers (such as Narragansett Bay and nearby islands) were a reasonable distance for woodcock to travel.

Woodcock Trapping and Transportation

We used mist-nets to capture male woodcock April 3–May 12 in 2016 and 2017 at singing grounds where males were observed performing courtship display flights (Sheldon 1967, McAuley et al. 1993). This timing allowed us to avoid capturing woodcock that display during migration. We noticed significant declines in male display activity (i.e. peenting calls while on the ground, aerial display flights) at all sites by the second week of May in both years.

Age of captured males was determined using plumage characteristics of the wings (Sheldon 1967). We used cattle tag cement (Nasco, Fort Atkinson, Wisconsin, USA) and a crimped wire belly-band to affix transmitters (4.5 g, <3% body mass; Advanced Telemetry Systems A5400 VHF, Isanti, Michigan, USA) to each captured male (detailed methods in McAuley et al. 1993, Masse et al. 2014). All birds were then placed inside modified soft-walled 34 × 23 cm pet carriers for transport. Mesh openings were covered with a cloth to provide darkness for birds during transportation to designated release points at the paired landscape (Table 1).

Only second-year (SY) male woodcock (first-time breeders) were relocated. This was done in an effort to eliminate potential site fidelity bias exhibited by older males (after second-year, ASY) at singing grounds (Dwyer et al. 1988). To determine the effect of vehicle exposure

TABLE 1. Relative likelihood of use, probability of use scores, habitat characteristics, and basic American Woodcock breeding demographics for 8 landscapes in southern Rhode Island during spring of 2016 and 2017. The 8 landscapes are organized by paired high- and low-likelihood of use between which woodcock were reciprocally translocated from 8.5 to 22 km, depending on pairing. Average probability of use score was derived from the probability of use map of Masse et al. (2014). Percent habitat characteristics are from state-wide land cover data (RIGIS 2012).

			Within landscape (4 km^2)					Number of singing males		
Landscape	Landscape likelihood of use	Average probability of use score (1–100)	Percentage of hydric soil	Percentage of upland young forest	Percentage of wetland forest	Percentage of upland coniferous forest	Female detected[a]	During migration (March)[b]	During breeding (April–May)[c]	Distance to paired site
Great Swamp South (GSS)	High	45	48	6	36.4	2.7	Yes	18	7	8.5 km (CA)
Carolina (CA)	Low	26	9	0.3	5.8	41.9	Yes	3	2	
Great Swamp North (GSN)	High	63	48	5	10	6	No	14	2	17.5 km (MD)
Midway (MD)	Low	30	5	2.3	2.4	66.7	No	2	2	
Tillinghast (TH)	High	51	16	5.1	12.2	22.5	Yes	12	4	15.5 km (BR)
Big River East (BR)	Low	23	13	1.6	8	35.2	Yes	8	6	
Nicholas Farm (NF)	High	55	20	0.5	2	30	No	0	0	9.5 km (AC)
Arcadia: Pine Top (AC)	Low	33	10	3.4	5.4	13.3	No	11	3	22 km (GSN)
High-likelihood averages	–	53.5	33	4.2	15.2	15.3	–	11	3.3	–
Low-likelihood averages	–	28	9.3	1.9	5.4	39.3	–	6	3.3	–

[a] Female detections at a given site included any capture of females while catching males, as well as any observations of woodcock nests or females with young.
[b] Highest single-night count of displaying males during surveys at singing grounds during migration.
[c] Highest single-night count of displaying males during trapping and surveys at singing grounds during the breeding period.

and transportation protocols on male behavior and movements, we also captured control birds and exposed them to the same treatment procedures as relocated individuals (i.e. captured, transmitter affixed, driven in a vehicle for 25–45 min) but they were then released back at the sites they were originally captured. Median date of capture for relocated birds was April 22 (range: April 3–May 7) and for "control" birds was April 29 (range: April 18–May 12).

Breeding Season Monitoring

We located reciprocally transplanted birds with transmitters using a 3-element Yagi antenna and R2000 series receiver (Advanced Telemetry Systems). On the day following capture and marking, we first determined if the bird remained at the release site. If the bird was detected, we recorded the bird as present. If the bird was not detected anywhere in the release landscape, we then searched the landscape where the bird was originally captured. If a bird remained in the same 50 m^2 area for >3 days, suggesting mortality or a dropped transmitter, we attempted to flush the bird to determine if it was alive. We continued to record the presence of birds at release or capture sites every 1–2 days until the end of the breeding season or at least 2 weeks post-translocation. During evening trapping of additional males, we also scanned for all radiotagged birds that may have used unmonitored daytime locations but returned to the singing ground at night. During this evening fieldwork we also recorded whether focal birds exhibited any breeding behavior (e.g., peent calls, aerial displays; Sheldon 1967). This strategy of locating birds allowed us to determine whether or not a woodcock returned to its original landscape of capture, but not the exact timing or movement paths of the returning birds.

We considered a bird to have "returned" if it was detected back at its original landscape of capture during the breeding season and if it was not detected again at the paired landscape of release. We considered a bird to have "not returned" if it never returned to its original landscape. During the breeding season, 3 birds left the study area completely within 2 days of translocation. These individuals were also considered "not returned" as they were not detected where they were originally captured, nor were they depredated within the study area. If a bird was depredated before May 14, it had to be detected in the same landscape for at least 15 days to be included in this analysis. The longest time it took for any bird to return was 14 days.

Post–Breeding Season Monitoring

After May 14, each landscape was thoroughly checked every 2 weeks for any birds that could have moved between paired landscapes. These checks included scanning for tagged birds at display grounds, potential roosting sites, and possible and known diurnal feeding areas within each 4 km^2 landscape. We found no evidence of post-breeding birds that were previously considered outside the study area by the end of the breeding season to have returned to any study landscape.

Statistical Analysis

We first used Fisher's exact test to test differences in the proportions of woodcock returning to their original site of capture between the 2 types of landscapes (Agresti 1992, Upton 1992). We used generalized linear models (GLMs, logit link function) to determine if landscape type, date of capture, site, relocation distance, and presence of a female (or females) at the capture site affected the return behavior of woodcock (binary response variable: 1 = return or 0 = not return). An intercept-only null model was also included for model comparison. Each independent variable was tested as a single-factor model due to the relatively low sample size. We used Akaike's Information Criteria corrected for small sample size (AIC_c) and Akaike weights (w_i) to rank the competing single-factor models (Anderson et al. 2000). All statistical testing was completed using R 3.3.2 open-source software (www.r-project.org) and model selection was completed using the BBMLE package (Bolker and R Development Core Team 2016).

RESULTS

In the springs of 2016 and 2017, we captured and radiotagged 32 male woodcock (n = 16 in 2016, n = 16 in 2017). Eleven of these birds were used as "control" birds that were radiotagged, driven in pet carriers for similar durations as treatment birds but then returned to their capture location and thus not relocated (n = 7 ASY, 3 in low- and 4 in high-likelihood landscapes, and n = 4 SY, 2 in low- and 2 in high-likelihood landscapes). All control birds regardless of age or landscape type of origin remained at their landscape of capture for the remainder of the breeding season, thus demonstrating no direct negative effect of the capture, transmitter attachment, and vehicle ride. Two of the remaining 21 SY individuals were not included in the translocation analysis. One of these birds was relocated during an unanticipated extended period of military training drills at a release site, and so was subjected to a high amount of disturbance from the training exercises. The other individual was depredated within 2 days of relocation at its new site.

Did Reciprocally Transplanted Woodcock Assess Landscapes?

Nineteen woodcock were moved between landscapes. Birds captured in high-likelihood landscapes and moved to low-likelihood landscapes almost always (5/7, or 71%) returned to their original high-likelihood landscape, whereas

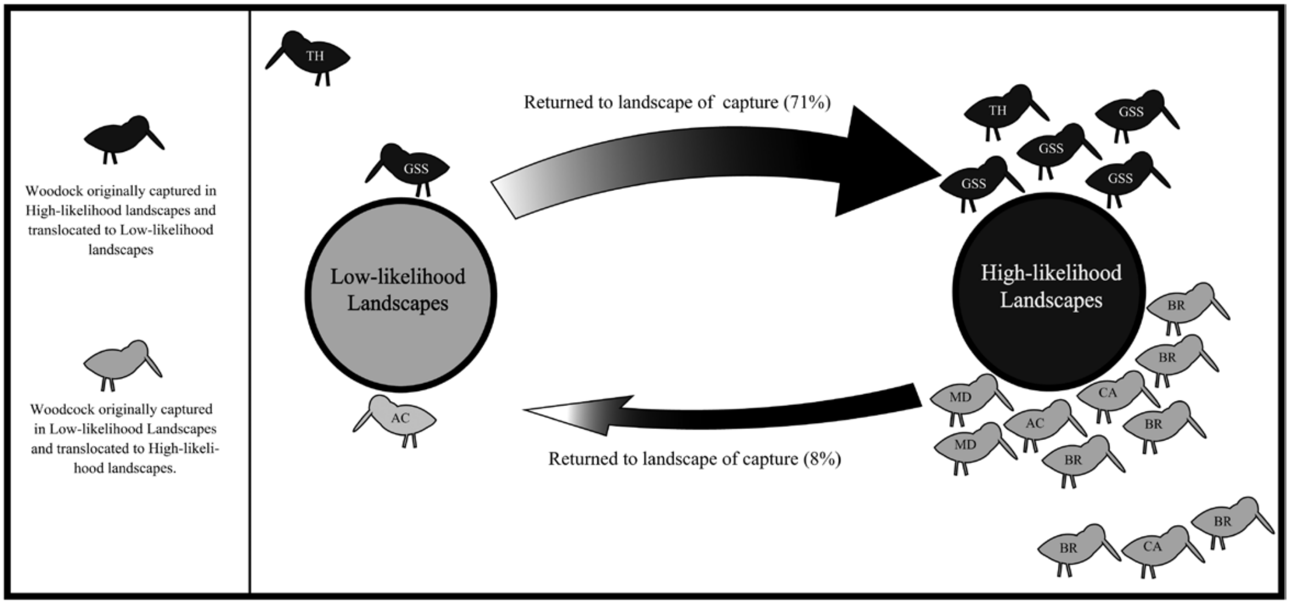

FIGURE 2. Return behavior of 19 translocated second-year male American Woodcock. Abbreviations correspond to specific landscape of origin for each individual bird: AC = Arcadia Pine Top, BR = Big River East, CA = Carolina, GSS = Great Swamp South, MD = Midway, TH = Tillinghast Pond.

birds captured in low-likelihood landscapes rarely (1/12, or 8%) returned to their original low-likelihood landscape (Figure 2; significant difference in proportions, $P = 0.01$). Landscape type and relocation distance models were the only models that were most highly ranked ($\Delta AIC_c < 3$, combined $w_i = 0.93$; Table 2), explained the return behavior of woodcock significantly better than the null model (likelihood ratio test, $P < 0.02$), and had the highest model fit (log-likelihood estimates closest to zero; Table 2). However, the model with only landscape type was much better supported than the relocation distance model (Table 2).

TABLE 2. Model, number of parameters (K), log-likelihood estimate (Logl), difference in Akaike information criteria (ΔAIC_c), and Akaike weights (w_i) for competing single-factor GLMs assessing return behavior of translocated second-year male American Woodcock.

Model	K	Logl	ΔAIC_c	w_i
Landscape type	2	−7.63	0.0	0.75
Relocation distance	2	−9.04	2.8	0.18
Null	1	−11.85	6.4	0.04
Presence of female	2	−11.74	8.2	0.01
Date of capture	2	−11.79	8.3	0.01
Site	6	−5.27	9.5	<0.01

Behavior of Translocated Woodcock

Relocated woodcock took on average 7 days (range: 3–14 days) to return to their original capture sites. The individual that took 14 days to return dropped its transmitter upon release and was later recaptured and identified by band number at its original high-likelihood site, so it is possible that it took this bird <2 weeks to return. The one male that returned to its original low-likelihood landscape of capture took 8 days to return.

We captured 7 birds in high-likelihood landscapes (Tillinghast [$n = 2$] and Great Swamp South [$n = 5$]). Five of these birds (from Tillinghast [$n = 1$] and Great Swamp North [$n = 4$]) returned to their original landscape of capture (Figure 2). Three of these 5 birds continued to display within 100 m of their capture sites for the remainder of the breeding season, one returned to within 200 m of its capture site for the remainder of the breeding season but did not display, and one returned to within 200 m of its capture site, displayed, but then departed the study region (or its radio failed) before the end of the breeding season. Two birds did not return to their original high-likelihood landscape of capture. One remained in the paired low-likelihood landscape for the remainder of the breeding season. The other individual displayed for an evening in its new low-likelihood landscape but then left the study region (or its radio failed). This bird was initially captured relatively early in the breeding season (April 7) and was potentially a migrant.

We also captured 12 SY males in low-likelihood landscapes (Big River East [$n = 6$], Carolina [$n = 2$], Midway [$n = 2$], Arcadia Pine Top [$n = 2$]; Figure 2). Only one of these birds (from Arcadia Pine Top) returned to its original landscape of capture, where it continued to display within 100 m of where it was initially caught. Six individuals stayed in their new high-likelihood landscapes for the remainder of the breeding season and exhibited breeding behavior (i.e. display flights) at these new locations. Two birds remained in the new landscape but did not display; one remained for the entire breeding season, the other was depredated 18 days after relocation. Two individuals were detected for ≤2 nights in their new landscapes but were not detected in the study region for the remainder of the breeding season. One individual was found outside both paired landscapes after the breeding season, but was never detected in its original landscape of capture.

DISCUSSION

The proportion of SY male woodcock (first-time breeders) that returned to their original high-likelihood landscape after translocation was higher (71%) than the proportion that returned to their original low-likelihood landscape (8%). These results support our hypothesis that woodcock can perceive differences in landscape composition, and demonstrate that woodcock are able to return at least 8.5 km to better habitat after relocation.

Implications for Migratory Birds Inhabiting Seasonal Environments

Our results demonstrate that male woodcock are able to assess habitat at the landscape scale and use this information while deciding where to settle and display. We found that most relocated woodcock returned from low-likelihood landscapes to within 200 m of their original capture location in high-likelihood landscapes, a particularly strong demonstration of homing ability (in this case 8.5–15.5 km) to environments with more resources (Krištín and Kaňuch 2017). In contrast, woodcock that were moved from low-likelihood landscapes into high-likelihood landscapes rarely returned to their original capture locations in the low-resource landscapes despite being moved similar distances across the same landscapes. This result indicates that each male made his settlement decision(s) based on the relative quality of at least 2 landscapes: the capture location where the male was initially displaying as well as the landscape to which he was subsequently moved.

We can reject several alternative hypothesis for the patterns observed from this reciprocal translocation experiment. One possible explanation for the return behavior we observed was that study birds were normally dispersing back to sites of capture. Second-year male woodcock in the northeastern U.S. typically disperse within the breeding season no more than 2.6–2.7 km (Hudgins et al. 1985, Dwyer et al. 1988). If the relocated birds were randomly selecting habitat, we would expect males to settle in any high-likelihood landscape within ~3 km. However, we found that the translocated male woodcock that returned to their original capture locations moved much farther and were never found in any of the other 7 landscapes that we carefully monitored, even though in some cases these other landscapes were closer than the original capture location or site pairing. Thus, normal dispersal behavior during the breeding season cannot sufficiently explain our results.

A possible explanation for the patterns observed from this reciprocal transplant experiment is that density of males at release sites may have influenced settlement decisions of translocated males. During April 1 to mid-May, we detected and captured more young males in low-likelihood landscapes (n = 12) than in high-likelihood landscapes (n = 7), although during March, when many male woodcock were passing through the area on migration, we detected more males overall during surveys of singing ground in the high-likelihood landscapes (Table 1). This pattern of settlement and habitat selection could suggest a saturation of our high-resource landscapes, forcing the individuals we caught in the low-resource landscapes to initially settle there. However, when we added individuals into these high-resource landscapes, 8 of the 11 remained at release landscapes for the rest of the breeding season, indicating these high-resource landscapes were not saturated and could support more males.

More young males may have been caught in low-likelihood landscapes simply because they were selecting any singing ground near potential nesting habitat with adequate stem density (Gregg and Hale 1977, McAuley et al. 1996), regardless of landscape context. However, the reciprocal nature of our study design repeated across multiple site pairings suggests that local habitat features cannot fully explain the behaviors of the woodcock, and that woodcock do in fact select and settle in areas based on landscape context. In general, under a hierarchical framework for habitat selection, individuals initially select habitat at a larger landscape scale before then considering smaller-scale habitat features (Johnson 1980).

Another pattern we observed was that more SY male woodcock inhabited low-likelihood landscapes by April–May after migrants had departed. Such settlement patterns of younger, inexperienced males in landscapes with fewer resources could be the result of conspecific social cues (Greene and Stamps 2001, Ward and Schlossberg 2004, Ahlering and Faaborg 2006). Male woodcock will defend their display areas from other males, and often multiple males will display in close proximity to one another (Pitelka 1943). There is also a dominance structure between males, with subordinate males present at breeding grounds that will replace a dominant male if it is removed (Keppie and Redmond 1985). For subordinate males, this clustering could be particularly important, as hanging around the periphery of a high-quality breeding ground controlled by a more dominant bird may provide opportunities to gain copulations or replace the dominant male if he disappears

(Keppie and Redmond 1985, Dwyer et al. 1988). Thus, male woodcock, especially SY, first-time breeders, may be attracted to sites with other singing males even when in low-quality landscapes. If this is the case, the isolated patches of habitat surrounded by limited resources on a landscape may serve as an ecological trap for younger birds, although we lack productivity or fitness data to support or refute this idea (Robertson and Hutto 2006, Chalfoun and Martin 2007). These data could also address the relationship between bird density and habitat quality (Battin 2004).

We acknowledge that the dynamic changes in density of displaying males during spring, moving birds between locations throughout the breeding season, and the lack of information on reproductive success across all of our sites, make it difficult to fully address the effect of conspecific attraction or density-dependent interactions on the woodcock in our study. Yet the results from this translocation experiment reveal important connections between landscape composition and breeding-season settlement decisions in woodcock. Landscape features have been shown to impact breeding behavior and movements in other game birds such as in lek-mating prairie-grouse (*Tympanuchus* spp.) indicating that this ability of individuals to assess habitat at multiple scales may be of broader relevance (Winder et al. 2015, Lautenbach et al. 2017).

Implications for Woodcock and Young Forest Management

Our results confirm the importance of landscape-level management for American Woodcock and for investigating species-specific habitat selection within contrasting landscapes (Hoodless and Hirons 2007, Kennedy et al. 2011). Given that habitat selection is hierarchical and occurs at multiple scales (Johnson 1980), our results are most pertinent to second-order selection at the scale of ~4 km^2.

Resource selection functions are often used to predict animal occurrence or spatial use (Johnson 2007), but these tools are seldom tested using field-based experiments. Given that our experiment showed use of areas predicted by the woodcock-specific resource selection function, we believe this resource selection function can be used to guide land managers (Masse et al. 2014, 2019). Specifically, the resource selection function predicts that woodcock would more likely choose to settle in patches of young forest habitat that are within ~1 km of abandoned fields or forest openings (singing grounds), young forest and upland shrub (quality nesting habitat), and forested areas with hydric soils (safe feeding areas). Such forest management is especially needed in southern New England, which is dominated by late-successional forests 60–100 yr old and increasing urban/suburban development (Butler et al. 2012), and where it would also benefit woodcock migrating within the eastern corridor (Sullins et al. 2016). Managing for woodcock and specifically for young forest habitat at the landscape scale would also benefit a large suite of other birds and mammals that depend on young forests and have populations in decline, such as New England cottontail (*Sylvilagus transitionalis*; Litvaitis and Villafuerte 1996, DeGraaf and Yamasaki 2003, Schlossberg and King 2007, Masse et al. 2015).

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