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Early Successional Forest Birds and the Effects of Habitat Management in Different Landscapes

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EARLY SUCCESSIONAL FOREST BIRDS AND THE EFFECTS OF HABITAT MANAGEMENT IN DIFFERENT LANDSCAPES

BY

STEPHEN J. BRENNER

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR A MASTER OF SCIENCE
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2018

MASTER OF SCIENCE THESIS

OF

STEPHEN J. BRENNER

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UNIVERSITY OF RHODE ISLAND
2018

ABSTRACT

Early successional forests are a rare and declining forest type in the Northeastern U.S., and active management is required in order to maintain this habitat for the many declining bird populations that inhabit these areas. Studies on the movements, spatial ecology, and habitat selection of declining species of interest within newly created habitats offer opportunities to assess the success of management, and inform future management decisions and practices. Yet the impact of management may be limited by the placement of newly formed habitat within a larger landscape context. I investigated the impact of landscape and management context on the spatial ecology of American woodcock (*Scolopax minor*) and Eastern towhee (*Pipilo erythrophthalmus*) within managed early successional forests in the state of Rhode Island. First, I conducted a reciprocal transplant experiment to test if American woodcock select breeding grounds based on the perceived quality of the surrounding landscape. Second, I investigated the post-fledging and post-breeding ecology of Eastern towhees, a declining early successional forest songbird, in different landscapes managed and maintained for woodcock to test the efficacy of using woodcock as an umbrella species.

I experimentally relocated male woodcock between two types of landscapes that differed in forest composition and relative likelihood of use. Second-year male woodcock that were relocated from high-likelihood of use landscapes into low-likelihood of use landscapes during the breeding season almost always returned to their original high-likelihood landscape of capture (71%), whereas second-year male woodcock that were relocated from low-

likelihood of use landscapes into high-likelihood of use landscapes (8%) seldom returned to their original low-likelihood landscapes of capture. The results from this experiment provide strong evidence that male woodcock can assess landscape-level differences in habitat, and will then settle and attempt to attract a mate(s) based on key landscape features identified by a resource selection function developed for woodcock.

I tracked the movements and post-fledging behaviors of adult Eastern towhees in areas that were initially managed for woodcock. Adult towhees in two woodcock-sized landscapes that differed in forest composition and likelihood of woodcock use averaged similar home range sizes during the post-fledging period (3.09 ± 0.43 ha, and 2.37 ± 0.49 ha, respectively), and the different landscapes had no impact on the number of young that adult birds were able to raise to independence. However, there were differences in the maximum distances adults travelled during the independence stage between the two woodcock landscapes. While there is some evidence that the forest composition of the surrounding landscapes may impact these post-breeding movements, these movements coincided with the abrupt behavioral shift of adults from caring for dependent young, to being largely independent of young and thus focused more on personal maintenance. Given that towhees successfully raised young in areas managed for woodcock in different landscape contexts, woodcock can serve as an effective umbrella species for towhees and other generalist-young forest songbirds.

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DEDICATION

This thesis is dedicated to the memories of:

John and Joan Brenner; loving grandparents and entertainers;

and

Richard C, Louise, and Richard J Vivacqua; unfailing generous and kind

PREFACE

This thesis was prepared according to the Manuscript Format guidelines established by the Graduate School at University of Rhode Island. Manuscript 1, "Landscape context matters when American woodcock *Scolopax minor* select singing-grounds: results from a reciprocal transplant experiment", is formatted for publication in the *Journal of Avian Biology*. Manuscript 2, "Independence Day: Post-fledging movements and behaviors of adult Eastern towhees in landscapes managed for American woodcock", is formatted for publication in the journal *The Condor*.

TABLE OF CONTENTS

LIST OF TABLES

TABLE PAGE

CHAPTER 1

CHAPTER 1, Appendix A

CHAPTER 2

LIST OF FIGURES

FIGURE PAGE

CHAPTER 1

CHAPTER 2

CHAPTER 1

"Landscape context matters when American woodcock *Scolopax minor* select singing-grounds: results from a reciprocal transplant experiment"

by

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Abstract

The multi-scale 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 woodcock at eight actively managed singing ground sites in Rhode Island, USA during the springs of 2016 and 2017 in two types of landscapes that differed in forest composition and relative likelihood of use. Woodcock (n=19) were affixed with radio transmitters, relocated to high- or low-likelihood of use landscapes, and tracked after translocation for the remainder of the breeding season to determine if birds returned to their original site of capture or remained in the landscape to which they were relocated. Male woodcock 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 male woodcock captured in low-likelihood landscapes rarely (1/12, or 8%) returned to their original low-likelihood landscape. The results of our translocation experiment support the hypothesis that woodcock can assess habitat at the 4 km^2 scale and will use this information when deciding where to settle and display in hopes of attracting a mate(s). These results also validate the woodcock-specific resource selection function that what used to develop our landscape

classifications, and thus provides a framework for assessing frequently developed but often untested management tools. Land managers should provide such resources at this landscape scale to benefit woodcock and many other migratory birds that depend on young forest habitat.

Introduction

For animals that migrate, habitat selection and establishment of a breeding territory are critical decisions that impact survival, 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 core use areas of the highest quality habitat available, although as more individuals settle, the best available habitat may become 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 perceived quality or an area and where individuals primarily inhabit (Gutzwiller et al. 1983, Martin 1998, MacFaden and Capen 2002), but the landscape matrix surrounding a given 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). As much effort is expended on new habitat creation to promote use of certain bird species and increase habitat quality at a local scale (Chandler et al. 2009, Boves et al. 2015), landscape-level factors must be taken into account to promote effective management. The underlying assumption of these habitat selection models that is rarely directly tested 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).

Translocations have been used in 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 asses habitat selection is that this forces individuals to essentially choose between a smaller and usually known set of the available habitats (Matthews and Rodewald 2010, Liu and Swanson 2015). The link between habitat selection and habitat quality has been studied extensively in birds (Johnson 2007), but as far as we know there has been no study that has used translocations to investigate the processes of habitat selection in American woodcock (*Scolopax minor*).

We studied habitat selection of the American woodcock (hereafter 'woodcock') in landscapes with different resource abundance and probability of use. Woodcock are a migratory forest-dwelling shorebird that rely upon early successional forest in order to breed (Kelley et al. 2008), yet the steady loss of habitat within the last 40 years has led to population declines across their range (Mcauley et al. 2005, Cooper and Rau 2012). In the northeastern United States, best management practices include clearcutting forest to create young forest habitat to promote woodcock breeding activity (McAuley et al. 1996, Dessecker and McAuley 2001, Williamson 2010). In our study, we used reciprocal translocations between landscapes that differed in forest composition, abundance of resources, and likelihood of use to test if woodcock can assess habitat at a landscape scale and select habitat accordingly. Landscape designations were derived from a species-specific resource selection function for the region, and our experiment also serves as a test of this and similar selection-based management tools. We predicted that male woodcock captured in resource abundant, high-likelihood of use landscapes 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 predicted result would imply that woodcock assess their surroundings relatively rapidly and subsequently make critical settlement decisions based on landscape composition.

Methods

In order to test if woodcock can perceive landscape-level (4 km^2) differences in habitat and select particular singing grounds based on these apparent differences, we reciprocally translocated male woodcock between singing grounds in landscapes predicted to have either high or low-likelihood of use by woodcock.

Study Area

All singing grounds selected for this study were at or near (<300 m) state-managed early successional forest, and all featured male woodcock breeding activity within selected landscapes. These two 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 early successional forests should be focused. All research was conducted within central and southern Rhode Island in Washington and Kent Counties (Fig. 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 sp.*), 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 six state-owned management areas, we delineated 147 landscapes, each a 4 km^2 circle centered on young forest patches that had been recently (<15 years old) 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 northeast U.S. recommend 2-4 km^2 habitat mosaics that can support woodcock at this landscape scale (Williamson 2010, Masse et al. 2014). From a woodcock perspective, 4 km^2 would generally encompass breeding, roosting, and daytime feeding areas (Palmer 2008, Williamson 2010), as been shown for male woodcock inhabiting some of the same management areas used in our study (Masse et al. 2014).

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 10x10 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 model parameters included forest cover type, slope, elevation, distance to existing early successional forest, distance to agricultural openings, distance to hydric soil, and distance to stream (Masse et al. 2014). Using the focal statistics tool in ArcGIS 10.2 (Environmental Systems Research Institute, Redlands CA), we created a new dataset of the average relative probability of use within 4 km^2 for each 10 x 10 m cell, and then extracted these values for 147 landscapes that we delineated within the six state-managed wildlife areas.

Site selection and pairing

We selected four high-likelihood landscapes and four low-likelihood landscapes based on these criteria: a) the probability of use values were distinctly different between the two groups (high-likelihood score $\geq$ 45, low-likelihood score $\leq$ 35); b) no spatial overlap between landscapes in the same likelihood of use rank; c) there was an appropriate distance between paired high-likelihood and low-likelihood landscapes (8.5-22 km); and d) in the past 5 years male woodcock had been observed displaying within that 4 km^2 area. Our four 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 four 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, Fig. 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 km to 22 km (Table 1), and drive time ranged from 25 – 45 minutes. 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 has been recorded up to 2.7 km in Maine (Dwyer et al. 1988), and 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 mistnets to capture male woodcock from 3 April – 12 May in 2016 and 2017 at scouted singing grounds where males were observed performing courtship display flights (Sheldon 1967, McAuley et al. 1993). Age of captured males was determined using plumage characteristics of the wings (Sheldon 1967). After recording morphometric information and ageing, we used cattle tag cement (Nasco, Fort Atkinson, WI) and a crimped wire belly-band to affix Advanced Telemetry Systems A5400 VHF transmitters (4.5 g, <3% body mass) to each male, as previously done in woodcock tracking studies (Masse et. al 2014). All birds were then placed inside modified soft-walled 13.5 x 9 in. pet carriers for transport. Mesh openings were covered with a cloth to provide darkness for each bird during transportation. Carriers were then placed inside motor vehicles and immediately driven to designated release points at the paired landscape (Table 1).

Only second-year (SY) male woodcock (first time breeders) were relocated to landscapes of alternative forest composition. This was done in an effort to eliminate potential site fidelity bias exhibited by older males at singing grounds (Dwyer et al. 1988). To determine the effect of vehicle exposure and transportation protocols, a subset of control birds were exposed to the same treatment procedures as relocated individuals (i.e. captured, transmitter affixed, driven in a vehicle for 25-45 min) but then were released back at the sites they were originally captured in.

We defined the breeding season from the first week of April (1 April) to the second week of May (14 May). Woodcock that display in Rhode Island during March are presumed migrants (9 of 10 males caught in March 2017 left the study region by 7 April, 10 of 12 males caught in March and early April 2011 left the study region by 8 April). We noticed significant declines in male display activity (i.e. peenting calls while on the ground, aerial display flights) at all sites by the first week of May in both years.

Breeding season monitoring

We located birds with transmitters using a three-element Yagi antenna and R2000 series receiver (Advanced Telemetry Systems, Duluth, MI). 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 at its release site. If the bird was not detected anywhere in the release landscape, we then searched the landscape where the bird was original captured. If a bird remained in the same 50 m area for over 3 days (thus suspected of depredation or transmitter slip), we then attempted to flush the bird by walking to its exact location to determine if it was alive or dead. We continued to record the presence of birds at release and/or capture sites every 1-2 days until the end of the breeding season or at least two weeks post translocation. During evening trapping of additional males, we also scanned for all relevant frequencies in order to pick up birds that may stay in unmonitored daytime locations but returned to the singing ground at night. This strategy of locating birds allowed us to determine whether or not a woodcock chose to return 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 during the breeding season back at its original landscape of capture 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, a few birds left the study area completely after translocation. These individuals were also considered ‘not returned’ as they were not detected back where they were originally captured. If a bird was depredated before 14 May, it had to be detected in the same landscape for at least 15 days to be included in this analysis. The longest number of days it took for any bird to return was 14 days.

Post-breeding season monitoring

After 14 May, each of the eight landscapes was thoroughly checked every two weeks for any birds that had subsequently moved. We also used these biweekly checks to scan for any birds that went off radio throughout the season. 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 re-appeared at any study landscape.

To determine diurnal home range size and habitat use of male woodcock from 15 May – 24 August, we tracked all remaining individuals at daytime locations 2-3 times a week. When individuals were found we approached until the bird’s transmitter emitted a signal that was detectable without the use of antenna and at a standardized level of gain per receiver. This method allowed for an approach of $\leq$ 18 - 20 m without flushing the bird as shown in previous work with similar equipment (Masse et al. 2013). We stratified sampling locations per individual throughout daytime hours (0600 – 1800 EST) to ensure that most daytime hours were accounted for.

Statistical Analysis

We used Fisher's Exact Test to test differences in the proportions of woodcock returning to their original site of capture between the two types of landscapes (Agresti 1992, Upton 1992). We estimated diurnal summertime home ranges using kernel density methods (Worton 1989). We used a Guassian kernel with likelihood cross-validation bandwidth estimator in Geospatial Modeling Environment (Beyer 2013) to generate home range (95% contour) and core-use (50% contour) areas. We collected 29-31 locations for individual woodcock diurnal home ranges, and used the likelihood cross-validation bandwidth estimator recommended for small sample sizes (<50 locations per individual, Horne and Garton 2006). We compared the home range size of translocation birds to control birds using Welch's *t*-test for unequal variances. Using a use-availability design for habitat selection (Johnson 1980), we considered the composite home ranges (95% contour) as the available habitat and composite core use areas (50% contours) as used habitat for all woodcock tracked in the summer.

To determine resource selection of relocated woodcock, we followed the methods of Masse et al. (2014) to generate a resource selection function for woodcock in Rhode Island. Briefly, we used logistic regression to derive coefficient values for the exponential of the resource selection function [w(x0=exp(B1x1 + … + Bixp)] (Manley et al., 2002). We generated 14 *a priori* logistic regression models to determine probability of use by woodcock in the state and used the information-theoretic approach based on Akaike's Information Criterion (AIC) and Akaike weights (wi) to select the best model (Anderson et al.

2000). Our highest-ranked regression model was then compared to the highest-ranking model in Masse et al. (2014).

Results

In the springs of 2016 and 2017, we captured and radio-tagged 32 male woodcock (*n* = 16 in 2016, *n* = 16 in 2017). Eleven of these birds were 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, n= 4 SY). Two of the remaining 21 individuals were not included in the translocation analysis. One of these birds was relocated during an unanticipated extended period of military training drills at the 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 or were movements random?

Nineteen male woodcock were moved from high to low or low to high-likelihood landscapes and then were tracked to determine whether they returned to their original landscape of capture. Male woodcock 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 male woodcock captured in low-likelihood landscapes rarely (1/12, or 8%) returned to their original low-likelihood landscape (Fig. 2; significant difference in proportions (p=0.01)).

After exposure to a vehicle ride, all control birds regardless of age (n=11) remained at their landscape of capture for the remainder of the breeding season or until they were depredated (n=2). Given that every control bird remained within the landscape they were caught and continued some degree of breeding behavior post-vehicle ride, we consider the results of our transplant experiment independent of placement in a pet carrier and exposure to a < 1 hour-long trip in a vehicle.

Behavior of translocated woodcock

The behavior of each of the 19 relocated male woodcock is described below, including whether the birds returned to their exact capture sites, performed breeding displays post relocation, and the duration spent at the relocation and/or original capture sites until the end of the breeding season (14 May). 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 less than two weeks to return. The one male that returned to its original low-likelihood landscape of capture took 8 days to return.

We captured seven second-year males in high-likelihood landscapes (Tillinghast (n=2), Great Swamp South (n=5)) and relocated each to low-likelihood landscapes. Five of these birds (from Tillinghast (n=1) and Great Swamp North (n=4)) returned to their original landscape of capture (Fig. 2). Three of these five 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 but departed the study region or went off radio before the end of the breeding season. Of the two birds that 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 went outside the study region or off radio for the remainder of the breeding season

We also captured 12 second-year males in low-likelihood landscapes (Big River East (n=6), Carolina (n=2), Midway (n=2), Arcadia Pine Top (n=2)) and moved each to high-likelihood landscapes (Fig. 2). Only one of these birds (from Arcadia Pine Top) returned to its original landscape of capture and 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 their new high-likelihood landscapes until predated (18 days post relocation) or until the end of the breeding season, but were not observed exhibiting breeding behavior. Two individuals were detected for $\leq$ 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 of all landscape boundaries after the breeding season during summer tracking, closer to its original landscape than its new transplanted area. However, it was not detected in either its original landscape of capture or its new landscape during the breeding season.

Post-breeding home range and habitat selection

The average size of control woodcock (n=7) diurnal kernel home ranges (27.4 ± 10.2 ha, range: 1.2-70.7 ha) and translocation woodcock (n = 5) diurnal kernel home ranges (60.2 ± 40.2 ha, range: 1.61-209.1 ha) did not significantly differ (t=0.79, df= 4.5, p =0.47), further suggesting that exposure to a vehicle ride and experimental translocation did not impact this aspect of their spatial behavior. Of the 14 logistic regression models that we tested, the top-ranked model produced the lowest AIC and accounted for 31% of the Akaike weight. Our highest-ranking model shared 6 of the 7 environmental parameters as the top-ranking model from Masse et al. (2014), with slope being excluded from our best model. Similar to the top-ranked model from Masse et al. (2014), our model suggested that the relative probability of use by woodcock 1) increased with increasing elevation, 2) decreased with increasing distance to hydric soil and agricultural openings, and 3) increased in wetland forest types but decreased in wetland coniferous forest. Our models differed from the top-ranked model from Masse et al. (2014) in that our model showed a) higher probability of use in upland young forest and upland coniferous forest, and b) higher probability of use with increasing distance to stream. Our average low-likelihood composite probability of use score (35) increased by seven points from the Masse et al. (2014) composite probability of use score (28). Our average high-likelihood probability of use score (54) increased by one point from the Masse et al. (2014) model.

Discussion

After translocations of second-year male woodcock, the proportion of woodcock that returned to their original high-likelihood landscape of capture was higher (71%) than the proportion that returned to their original low-likelihood landscape of capture (8%). These results support the hypothesis that woodcock can perceive differences in habitat composition at a landscape scale, and demonstrate that woodcock are able to return at least 8.5 km after relocation to better habitat.

Implications for migratory birds inhabiting seasonal environments

Our results demonstrate that male woodcock are able to assess habitat at the 4km^2 landscape scale and use this information while deciding where to settle and display in hopes of attracting a mate(s). 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. Such a reciprocal translocation experiment indicates that each male made their settlement decision(s) based on the relative quality of at least two 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), and post-breeding commuting behavior by males in our study system has been documented only up to 2.2 km (Masse et al. 2013). If the relocated birds were randomly selecting habitat, we would expect males to settle in any high-likelihood landscape within ~2.7 km. However, we found that the translocated male woodcock that returned to their original capture locations moved much further and were never found in any of the other seven 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.

Another 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 1 April – 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 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. Yet all capture sites featured nearby potential nesting habitat and our experiment confirms landscape-level factors will impact selection decisions made by male woodcock.

Another explanation for the settlement of younger, inexperienced males in landscapes with less resources could be conspecific social cues (Greene and Stamps 2001, Ward and Schlossberg 2004, Ahlering and Faaborg 2006). Migrating woodcock, particularly first-time breeders, may be drawn into singing-grounds where more males are already displaying. 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, yet we lack substantial productivity or fitness data to prove or disprove this idea (Robertson abd Hutto 2006, Chalfoun and Martin 2007). 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 makes it difficult to fully address the impact of conspecific attraction or density-dependent interactions on the woodcock in our study. Yet the results from this translocation experiment signals important connections between landscape composition and breeding-season settlement decisions in woodcock.

Implications for understanding of the woodcock breeding system

The woodcock breeding system has been described as a dispersed lek system (Ellingwood et al. 1993) as well as male-dominated resource defense polygyny (Dwyer et al. 1988). Male woodcock will defend their display areas from other males, often multiple males will display in close proximity to one another, and multiple females will mate with a select few males (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 from a breeding ground (Keppie and Redmond 1985). Once females copulate, they will then usually nest nearby (<150 m) the singing grounds (Palmer 2008) and continue to visit nearby singing males at dusk even while nesting (McAuley et al. 1993). This is the basis of the suggested forest management scheme developed for American woodcock where fields and forest openings used by males as singing grounds are close to high stem density areas used by females for nesting (Gregg and Hale 1977, McAuley et al. 1996, Williamson 2010).

Our results suggest that males are selecting landscapes with more breeding resources (i.e. singing grounds and potential nesting areas) and post-breeding resources (i.e. feeding and roosting areas) (Sepik and Derleth 1993, Masse et al. 2013), and this suggests that the abundance of such resources, and perhaps their defendability, underlies the woodcock breeding system. We observed replacement by some males after we removed males from a given landscape, confirming that sub-dominant males may be present at singing grounds and will take advantage of the disappearance of the singing, presumably dominant males (Keppie and Redmond 1985, Sepik and Derleth 1993). 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). This strategy of being a subordinate male in a singing ground with more females and nearby high quality nesting habitat may be better for some birds compared to becoming a dominant male at a singing ground in a landscape with a lack of quality nesting habitat and few females.

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 in nature and occurs at multiple scales (Johnson 1980), our results are most pertinent to second-order selection at the scale of 4 km^2. Successful habitat management is often measured by occupancy and density. But occupancy and density alone do not always indicate quality (Van Horne 1983, Battin 2004). For example, male woodcock in our study were present at low-likelihood-of-use sites but when moved to higher likelihood-of-use areas, they usually stayed indicating that their presence does not always mean they occur in preferred habitat. Future research to address the impact of landscape quality and management for young forests should investigate the fitness consequences of woodcock settlement and habitat selection in alternative landscapes.

While the primary focus of our experiment was to test the impact of landscape composition on the breeding-site selection of male woodcock, our methodology was also inherently testing the resource-selection and probability of use map that was created for woodcock management in the state (Masse et al.

2014). Given that the birds in our study returned more frequently to areas predicted to be higher-likelihood of use, the results from our experiment also validate the predictive capability of the woodcock-specific resource selection function used to derive the different landscape types. Resource selection functions are an often used to predict animal occurrence or spatial use (Johnson et al. 2006), but these tools are not often tested in field based-experiments. By testing and validating the woodcock-specific resource selection function and subsequent probability of use map in Masse et al. (2014), our study provides a framework for evaluating conservation and land management tools.

The results from this experiment coupled with the resource selection function and case studies from previous research in the region (Masse et al. 2014) can be used to improve site selection by locating new habitat in the best possible landscape. Specifically, land managers should assess the overall habitat quality within at least a 2-4 km^2 area and create patches of new early-successional 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) as specified by the resource selection function. Such forest management is especially needed in southern New England, which is dominated by late-successional forests 60-100 years old and increasing urban/suburban development (Butler et al. 2012), and which is within the eastern migration corridor for woodcock (Sullins et al. 2016). Managing for woodcock and specifically for early successional forest habitat at the landscape scale would also benefit a large swath of other birds (Masse et al. 2015) and mammals that depend on young forests and have populations in decline, including New England cottontail *Sylvilagus transitionalis* (Litvaitis and Villafuerte 1996, DeGraaf and Yamasaki 2003, Schlossberg and King 2007).

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Figure 1

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

Figure 2

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

Table 1. Relative likelihood of use, probability of use scores, habitat characteristics, and basic woodcock breeding demographics for eight landscapes in southern Rhode Island during spring of 2016 and 2017. The eight landscapes are organized by paired high- and low-likelihood of use between which woodcock were reciprocally translocated from 8.5-22 km, depending on pairing. Composite probability of use score was derived from the probability of use map of Masse et al. (2014). Percent habitat characteristics are from statewide land cover data (RIGIS 2012). Female detections include any capture of female, nest discovery, or visual of female with young.

Landscape	Landscape Likelihood of Use	Composite Probability of Use Score (1-100)	% Hydric Soil within landscape (4 km^2)	% Upland young forest within landscape (4 km^2)	%Wetland forest within landscape (4 km^2)	% Upland Coniferous forest within landscape (4 km^2)	Female Detected	Highest number of singing males recorded during migration (March)	Highest number of singing males during breeding (April-May)	Distance to paired site
Great Swamp South (GSS)	High	45	48	6	36.4	2.7	Yes	18	7	8.5 km
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	17.5km
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	15.5km

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	9.5km/ 22km (GSN)
Arcadia: Pine Top (AC)	Low	33	10	3.4	5.4	13.3	No	11	3	
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**	**-**

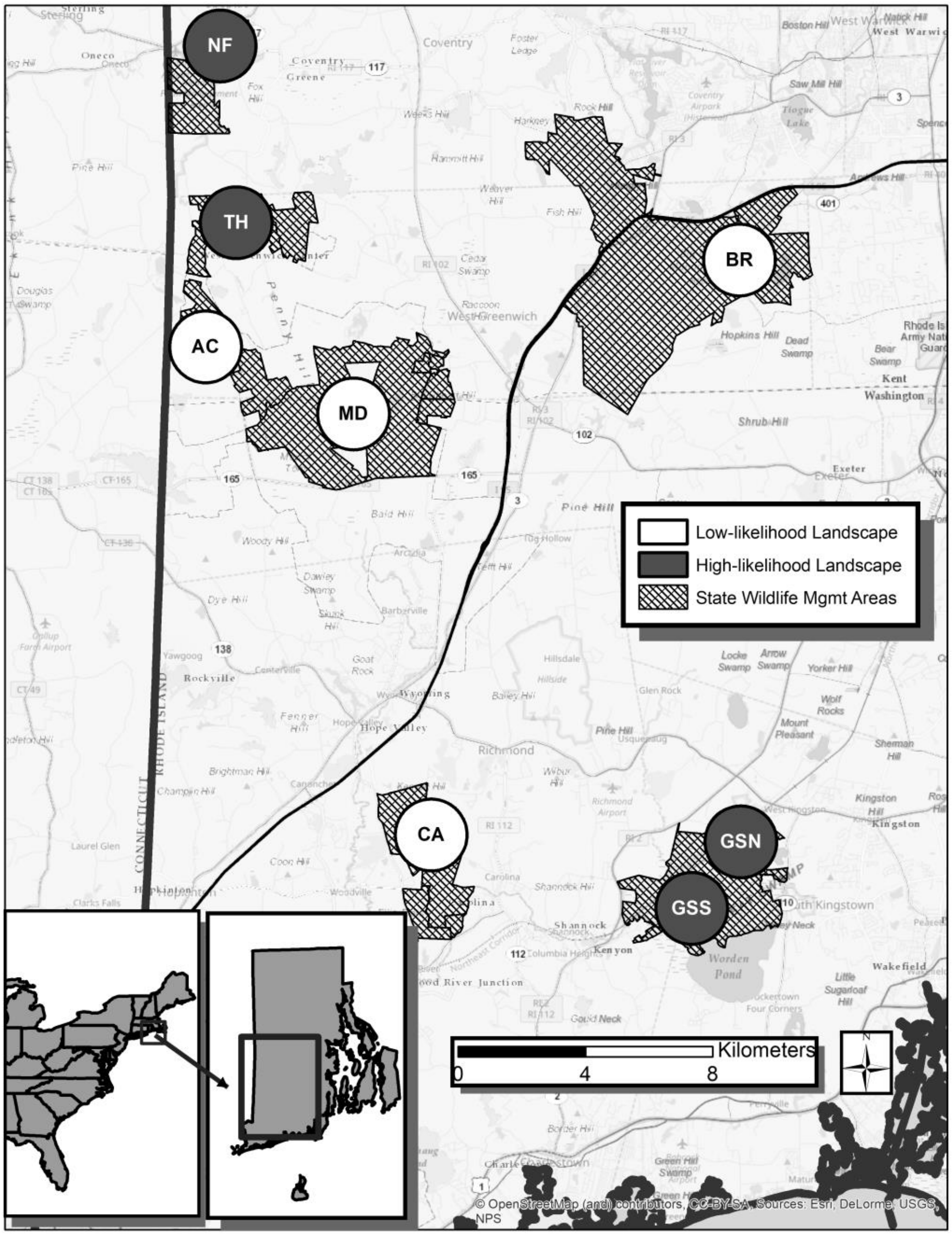

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Fig. 1

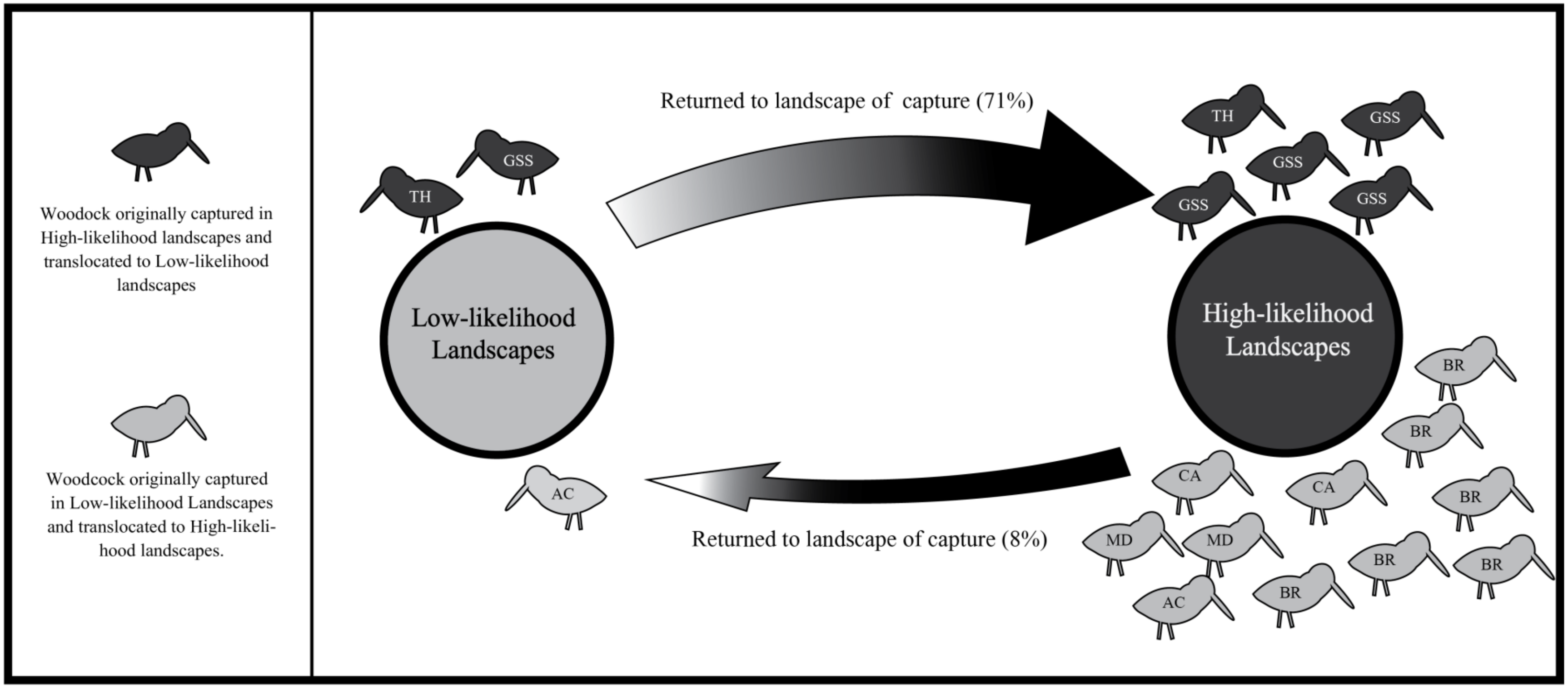
Woodock originally captured in High-likelihood landscapes and translocated to Low-likelihood landscapes
Woodcock originally captured in Low-likelihood Landscapes and translocated to High-likelihood landscapes.
Returned to landscape of capture (71%)
Returned to landscape of capture (8%)
Low-likelihood Landscapes
High-likelihood Landscapes
TH
GSS
AC
GSS
GSS
GSS
GSS
TH
BR
BR
CA
CA
BR
MD
MD
BR
BR
AC
BR

Fig. 2

Appendix A. Supplementary material.

Table A1. Comparison of top-ranking logistic regression models for resource selection and coefficient values (β) between current study and Masse et al. (2014). Model variables include elevation (E), slope (SL), forest type (For), and distance to nearest stream (DST), agricultural opening (DAG), upland young forest/scrub (DYF), and moist soil (DSOIL). Coefficients include upland coniferous forest (CF), upland deciduous forest (DF), upland young forest/scrub (UYF), coniferous wetland forest (CWF), deciduous wetland forest (DWF), wetland young forest (WYF), and mixed wetland forest (MWF). "*" indicates coefficients that were both a) different in direction from the Masse model and b) significant in our model

	Highest model fromMasse et al. (2014)	**Highest model, current study**
	E, SL, For, DST, DAG, DYF, DSOIL	E, For, DST, DAG, DYF, DSOIL
β		
Elevation	0.00210	0.00302
Slope	-0.01870	-
Forest Type		
CF	-0.31110	0.57600*
DF	0.09060	0.70310
UYF	-0.22690	1.08500*
CWF	-0.02730	-0.91570
DWF	0.68390	0.56140
MWF	0.19930	0.21560
WYF	0.39340	1.5510
DST	-0.00080	0.00023*
DAG	-0.00162	-0.00018
DYF	-0.00025	0.00002
DSOIL	-0.00117	-0.00028

CHAPTER 2

"Independence Day: Post-fledging movements and behaviors of adult Eastern towhees in landscapes managed for American woodcock"

by

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Abstract

Umbrella species management offers a potential solution to the financial and logistical challenges of managing for the many declining species in early successional forests, a habitat that is also critical for many mature and young forest songbird species during the post-fledging and post-breeding period. We investigated the movements of adult Eastern Towhees (*Pipilo erythrophthalmus*) during the post-fledging period in 4 km^2 landscapes managed for American Woodcock (*Scolopax minor*), a popular umbrella species candidate for young forest management. Home range size (mean = 2.8 ± 0.33 ha) and the number of young raised to independence (range 1-3) did not differ during the post-fledging period between adult towhees inhabiting either high- or –low likelihood of woodcock use landscapes. Adults covered distances of ca. 65 – 100 m during the early stages of the post-fledging period and this did not differ between the two landscapes. In contrast, once their young became independent, adults moved across longer distances in high-likelihood of use woodcock landscapes compared to low-likelihood of use landscapes (149.2 ± 10.9 m and 111.2 ± 14 m, respectively). These movements were best explained by general breeding characteristics and landscape factors at a much smaller spatial scale than the 4 km^2 woodcock-sized management. These results combined with the fact that young forest habitat was the predominate forest type used by adult towhees caring for fledglings, and that this same young forest habitat was created in the region to promote woodcock use, suggests that early successional forest management for woodcock can provide effective breeding habitat for towhees.

Introduction

Land managers and conservationists frequently face the challenge of using limited resources while having to manage for multiple species. Umbrella species management can offer an efficient solution to such challenges because land management focused on a single ‘umbrella’ species can simultaneously benefit many co-occurring species (Lambeck 1997, Simberloff 1998, Fleishman et al. 2001) while also elevating the funding potential and resource allocation for the focal species of interest (Andelman and Fagan 2000, Kellert 2012, Fourcade et al. 2016). Game bird species are popular candidates for umbrella species status because they are usually charismatic species that attract opportunities for financial gains through hunting revenues, there are often established management histories and prescriptions, and there are usually potential benefits of this management for non-game species (Suter et al. 2002, Masse et al. 2015).

Most bird studies that assess habitat quality in areas principally managed for game species focus on songbird occupancy and density during the breeding period when males are territorial (Suter et al. 2002, Roberge and Angelstam 2004, Johnson 2007). Other studies on non-target songbirds also measure nest success and survival of young (Herkert et al. 2003, Campbell et al. 2007, Chandler et al. 2009). Although the results of such studies can help determine whether certain land management techniques benefit these non-target songbird species, the territory establishment and nesting period constitute an important but relatively small portion of a migratory songbird’s breeding cycle. Recent work has focused on the post-fledging period because survival during this period often strongly influences population dynamics (Vega Rivera et al. 1998, Streby and Andersen 2011, Cox et al. 2014, Vernasco et al. 2018), and because movements and habitat use during the post-fledging period are often different than at other times of the annual cycle (Chandler et al. 2012, Burke et al. 2017).

Landscape-level factors may affect spatial movement, habitat use, and nest success in songbirds (Saab 1999, MacFaden and Capen 2002, Okada et al. 2017) and landscape-level features could lead to the different patterns of use or avoidance of certain managed areas at different life stages (Ahlering and Faaborg 2006, Fahrig 2013, Chapter 1). Few studies of non-target songbird species have characterized the spatial movements of adults during the post-fledging stage (Bayne and Hobson 2001, Vitz and Rodewald 2006). Even though adult survival rate is usually high during this time (Krementz et al. 2000, Sillett and Holmes 2002), there are potential changes in habitat use as young become more mobile and independent. This multi-week periods constitutes a large portion of time that many migratory birds will spend in management areas and may influence predation risk or habitat selection (Vitz and Rodewald 2007, Streby 2016). During the post-fledging stage, adults are not anchored to a nest with immobile young that require frequent feedings, protection, and thermoregulation (van Overveld et al. 2017), and thus the effect of landscape-level factors on adult movement patterns and space use may be especially prominent during this stage with more independence (Bayne and Hobson 2001).

We studied the movement patterns and habitat use of adult Eastern towhees (*Pipilo erythrophthalmus*) during the post-fledging period while they inhabited areas actively managed for American woodcock (*Scolopax minor*). The loss of early successional forests throughout southern New England (Schlossberg and King 2007, Buffum et al. 2011) has been associated with the declines of popular upland gamebird species such as Ruffed grouse (*Bonasa umbellus*) and American woodcock, as well as many non-game bird species (Askins 2001, King and Byers 2002). Early successional forests have been shown to be important for songbirds that inhabit mature forests during the nesting period, such as Ovenbird (*Seiurus aurocapilla*) and Wood thrush (*Hylocichla mustelina*) which move to early successional forests during the post-fledging stage (Vega Rivera et al. 1998, Vitz and Rodewald 2010, Chandler et al. 2012). Early successional forest management in New England has focused on creating singing-grounds, roosting fields, and nesting habitat for American woodcock (hereafter, 'woodcock') via forest clearcuts and active brush-thinning and mowing operations (Williamson 2010, Masse et al. 2014). Previous research has identified woodcock as a good umbrella species candidate for other early successional forest species (Bakermans et al. 2015, Masse et al. 2015), but little work has explored the impacts of this land management on the spatial ecology of songbirds within landscapes managed for woodcock.

The Eastern towhee is a common but declining songbird in the northeast that inhabits scrub, edge, and young forest habitats (Greenlaw 2015, RI Wildlife Action Plan). Eastern towhees (hereafter, 'towhee') are an excellent species to study in habitat managed for woodcock as they are found during the breeding season predominately in early successional and young forests (Greenlaw 2015), occur simultaneously in the region with woodcock (Fleishman et al. 2001), and have demonstrated quick responses to management in previous studies (Yahner 2003). Towhee occurrence in managed shrublands in southern New England was influenced by certain landscape-level features in previous studies (Askins et al. 2007). However, no previous study has investigated the movement behavior of adult towhees during the post-fledging period when adults with fledglings are no longer tethered to their nest. Our primary objective was to compare home range size, habitat use, and movement patterns of adult towhees during the post-fledging period in state-managed landscapes that differed in their likelihood of use by woodcock. If woodcock serve as an effective umbrella species for towhees and other scrub-generalist songbirds, then we would expect towhees to positively respond to forest management targeted for woodcock. We predicted that towhees in higher-likelihood of woodcock-use areas would successfully raise more young to independence than towhees in low-likelihood of woodcock-use areas, and we predicted that adult towhee spatial ecology would depend on the likelihood of use of an area by woodcock.

Methods

Study Area

All research was conducted within central and southern Rhode Island in Washington and Kent Counties. Early successional forest management in these state-owned areas has focused in part on creating singing grounds, roosting fields, and nesting habitat for woodcock via forest clearcuts (Masse et al. 2014). Given that one of the goals of this study was to determine how such clearcuts created for woodcock were used by towhees during the post-fledging stage, the sites where we searched for and eventually tracked eastern towhees were the same state-managed young forests that were selected for a separate, simultaneous study on American woodcock habitat selection (Chapter 1). Briefly, we identified six woodcock-sized landscapes (4 km^2) of two types: high- and low-likelihood of use by woodcock. Each of these landscapes was centered on an area of managed early successional forest and had to contain evidence of woodcock breeding activity. In high-likelihood of woodcock use landscapes (hereafter, 'HL landscapes'), there was more early successional forest/upland shrub, more hydric soils, and generally more mature deciduous or mixed forest (Masse et al. 2014, Chapter 1). In low-likelihood of woodcock use landscapes (hereafter, 'LL Landscapes'), there was more mature coniferous forest and relatively less early successional forest/upland shrub. This landscape size (4 km^2) was chosen to match the recommended sizes for woodcock management in the northeast (Williamson 2010, Masse et al. 2014). Our three HL landscapes were Great Swamp North (41°28'24"N, 71°34'19"W), Great Swamp South (41°27'10"N, 71°35'27"W), and Tillinghast Pond (41°38'55"N, 71°45'40"W). Our three LL landscapes were Big River East (41°38'19"N, 71°34'40"W), Arcadia: Midway (41°38'20"N, 71°34'39"W), and Arcadia: Pine Top (41°36'50"N, 71°46'26"W).

Towhee trapping and tracking

We searched for territorial towhees from 25 May – 5 August 2016 and 2017 and limited our search to areas within the six focal landscapes that were previously managed young forest and upland scrub, including recent (<15 years) forest clearcuts, powerline right-of-ways, and areas with active brush thinning or mowing to maintain woodcock singing-grounds. We opportunistically searched for towhee territories by walking within and along the edge (<50 m) of these managed young forest patches and looked for evidence of breeding activity (carrying nest material, carrying food, or caring for recently fledged young). When possible, we would locate nests and monitor nests until fledge or failure (Martin and Geupel 1993).

We used conspecific audio playback and mist nets to attract and capture territorial adult towhees or adults with nests or fledglings from 25 May – 5 August (Kramer et al. 2017). We captured and tracked only one of the two adults that were caring for the same brood and did not target any particular sex during capture. After ageing, sexing, and gathering basic morphometric measurements (Pyle 1997), we gave each individual a unique plastic color-band combination in addition to a standard USFWS aluminum band (BBL permit #22923). We used an elastic modified leg-loop harness design (Rappole and Tipton 1991), with size of harness based on the body mass of the bird (Naef-Daenzer 2007), to affix an Advanced Telemetry Systems (Duluth, MI) model A2400 VHF radio transmitter (weight = 0.71g, <2% body mass) to adult towhees with accompanying fledglings.

We used a three-element Yagi antenna and ATS R2000 series receiver to track radiomarked adult towhees. Adults were located by first tracking individual signals with receivers to within 5-15 meters of a bird. Observers would then visually search for and record each individual’s color bands and record the GPS location of each individual. Once located, a 20-minute observation period followed to determine breeding stage, the number of accompanying fledged young, and degree of parental care activity (Table 1). Some birds (n=3) lost their transmitters before the end of the breeding season but were still raising young. These birds were tracked using vocalizations and resights, with the same 20-minute observation protocol as if tracking by VHF.

We tracked adults from the first week after their young fledged from the nest (0-6 days after fledge) until at least three weeks after fledge or as long as the bird was on radio (23 days – 54 days). We attempted to track each individual at least three times a week in order to gather 15 or more locations throughout the post-fledging period. We gathered one location per day for each individual to use in home range and movement analysis to reduce autocorrelation (Avgar et al. 2016, Calabrese et al. 2016), and we stratified our sampling times each day to capture a majority of the active daytime hours for songbirds (0530 EDT – 1500 EDT, Anich et al. 2009). Only adults that were able to successfully fledge and raise at least one towhee fledgling to independence (21 days post fledge) were included in the statistical analysis of home range and movement patterns.

Determining age of recently fledged young

In cases where we discovered adults with young after the nestling period and during the first week (0-6 days) of fledge (14 of 31 individuals), we visually estimated the age of fledglings using plumage, locomotive, and behavioral cues (Table 1). These age estimates were based on the characteristics of known-age fledglings and previous work with fledgling songbirds (Sullivan 1988, Kershner et al. 2004, White and Faaborg 2008, Burke et al. 2017). Adults that we began tracking with young that were older than one week after fledge (7+ days) or for which were unable to obtain 15+ GPS locations were not used in home range or movement analysis. To determine changes in movement patterns over time, we categorized the age of fledglings into 4 broad stages: early-fledge (0-6 days), mid-fledge (7-13 days), late-fledge (14-20 days), and independence (21+ days, Table 1). Any adults we captured and began tracking with young that did not clearly fit within these four stages were excluded from home range and movement analysis (n=2).

Statistical Analysis

We used kernel density methods (Worton 1989) within Geospatial Modeling Environment (Beyer 2013) to calculate diurnal post-fledging home ranges (95% contour) for adult towhees. We specified a Gaussian kernel with likelihood bandwidth estimator as recommended studies such as ours with a small number (<50) of locations per individual (Horne and Garton 2006). We gathered on average 21 points per individual (range: 16-31 points) for 31 adult towhees with accompanying fledgling(s). We estimated forest composition within a given area (% young forest/scrub, mature coniferous forest, mature deciduous forest, mixed forest, and grassland/agriculture) as well as young forest patch size using statewide land cover data (RIGIS 2012) in ArcGis 10.2 (Environmental Systems Research Institute, Redlands CA).

We used general linear models to test the effects of landscape type, number of young, sex, and young forest patch size on post-fledging home range size. We also used general linear models to determine the effect of the surrounding forest composition on home range size at four different landscape scales: the original 4 km^2 woodcock-landscapes (1,120 m from the edge of the home range), at 500 m from edge of home range, at 250 m from the edge of the home range, and 100 m from edge of home range. We used Fisher's exact test to assess whether number of young raised to independence differed by landscape types.

To determine the maximum distance moved during the four different stages of fledgling development, we plotted all locations in ArcGis and measured the longest distance recorded between any two points that occurred within the same stage. To control for the longer time span of the independence stage over the other three stages, the points between which the max distance was measured had to occur within seven days of each other. We considered this measurement an indicator of the extent of space use during the different stages of the post-fledging period. This measurement was not intended as direct measurement of maximum daily distance travelled or total movement distances within each stage.

We then used linear mixed-effects models to determine if maximum distance traveled by adults during each of the four fledgling development stages depended on landscape type, number of young, sex, site, and year. We used the ID of each individual bird as a random effect to control for repeated measures, and Tukey post hoc testing using least-squared means to determine significance at *alpha*=0.05 between groups at different stages. After determining that maximum distance traveled during independence stage differed between the two landscape types, we conducted two additional statistical analyses to discern what general breeding and what landscape variables influenced the maximum distance moved during this stage. We used general linear models to test the effect of woodcock landscape type and all combinations of the number of young, sex, young forest patch size, and home range size on maximum distance travelled during the independence stage. We also used general linear models to test the effects of surrounding forest composition at four different landscape scales on the distance moved during the independence stage. All of these habitat models also included woodcock landscape type (i.e. HL or LL) as a fixed effect.

Given that that the predominate habitat used by adults with fledglings was young forest/scrub, we used Chi squared test (χ^2) to compare proportions of adult locations in young forest between the two types of woodcock landscapes at each of the four fledgling development stages. All statistical testing was completed using R open-source software (Version 3.3.2, www.r-project.org). Values are reported as means ± SE. We used Akaike's Information Criteria (AIC) and Akaike weights (ω_i) to select the best model among competing models (Anderson et al. 2000).

Results

From 25 May – 5 August in 2016 and 2017, we captured, color banded, and affixed transmitters to 60 adult towhees. Of these, 31 adults (21 male, 10 female) provided a sufficient number of locations to be used in our analysis of home range size and habitat use during the post-fledging stage, and maximum distance travelled during each of the four stages of fledgling development. Nineteen of these birds were tracked in HL landscapes, and 12 birds were tracked in LL landscapes. Twelve of these adults (39%) successfully raised one fledgling to independence (7 in HL, 5 in LL), 16 adults (52%) raised two fledglings (9 in

HL, 7 in LL), and three adults (9%) raised three fledglings to independence (3 in HL). Of the 29 adults captured but not used for home range and habitat use analysis, 10 adults successfully raised fledglings, but we either began tracking them after the first week of fledge, or we did not gather 15+ points throughout the season. Three of these adults successfully raised one fledgling to independence (2 in HL, 1 in LL), six adults raised two fledglings to independence (3 in HL, 3 in LL), and one adult raised three fledglings to independence (LL). The number of successfully raised young during the post-fledging period was independent of landscape type (p=0.735). Of the other 19 adults not used for home range or habitat use analysis, 10 adults were tracked but we could not confirm whether they successfully brought young to fledge or successfully nested at all, eight adults attempted to raise young but failed (sometimes in multiple attempts) during incubation, nestling, or right before fledging, and one individual was depredated within a week of tracking.

Home range and maximum distance travelled in different woodcock landscapes

Home range size of the 31 adults during the post-fledging period averaged 2.8 ± 0.33 ha (range: 0.78 - 8.06 ha). There was no difference in post-fledging home range size for towhees in HL landscape (3.09 ± 0.43 ha) compared to LL landscapes (2.37 ± 0.49 ha, R^2=0.04, F=1.18, $p = 0.285$, Fig 1). All 11 models to explain home range size had poor fit ($R^2 \leq 0.122$) and none of these models were significant ($p \geq 0.134$).

The best model to explain maximum distance moved by adults across the post-fledging period included fledgling development stage (F=11.3, $p \leq 0.001$) and landscape type. During the first three stages of fledgling development, there was no difference in maximum distance travelled by adults in different woodcock landscapes (early fledge: 68.9 ± 10.9 m in HL, 70.7 ± 14.7 m in LL, $t = 0.1$, p = 0.925; mid fledge: 98.1m ± 10.7 in HL, 89.8 ± 13.4 m in LL, $t = 0.5$, p = 0.635, late fledge: 96.8 ± 10.9 m in HL, 73.3 ± 13.4 m in LL, $t = 1.4$, p = 0.184, Fig 2). However, during the independence stage, adult towhees in HL landscapes had a higher maximum distance travelled than adults in LL landscapes (149.2 ± 10.9 m in HL and 111.2 ± 14 m LL, respectively, $t = 2.2$, p = 0.039; Fig 2.). The overall highest ranked model to explain differences in maximum distance travelled during the independence stage of fledgling development included home range size, landscape type, sex, and patch size ($R^2 = 0.709$, $F = 18.7$, $p \leq 0.001$, Table 2A). Distance traveled was further in HL compared to LL landscapes, increased with home range size and patch size, and was further for males. The highest ranked model that incorporated landscape composition was landscape type and forest composition at the 100 m scale ($R^2 = 0.293$, $F = 3.0$, p = 0.026, Table 2B).

Most (54.5%) of the adult towhee locations collected throughout the post-fledging period occurred within young forest/scrub, with mature upland forest types (26.2%) and grasslands/fields (14.6%) accounting for the majority of the remaining habitat types. Adult towhees in HL landscapes compared to LL landscapes used marginally less young forest/scrub during the early-fledge stage (51.7% in HL and 69.3% in LL, χ^2=2.9, df=1, p = 0.086) and mid-fledge stage (43% in HL and 60% in LL, χ^2=3.4, df=1, p = 0.063). There was no difference in young forest/scrub use between adults in different landscape types during the late-fledge (55% in HL and 60% in LL, $\chi^2 = 0.1$, df=1, $p = 0.705$) or independence stage (55.4% in HL and 60% in LL, $\chi^2 = 0.5$, df = 1, $p = 0.467$).

Discussion

Potential impact of umbrella species management on adult towhees during the post-fledging period

Overall, home range size of adult towhees during post-fledging and the number of young raised by these birds were similar across landscapes that differed in their suitability for woodcock. These results combined with the fact that young forest habitat was the predominate forest type used by adult towhees caring for fledglings, and that this same young forest habitat was created in the region to promote woodcock use, suggests that early successional forest management for woodcock can provide effective breeding and post-breeding habitat for towhees.

Woodcock require several different forest types and habitats during the breeding and post-breeding period in order to thrive. Woodcock require clearcuts and open fields for displaying and roosting, young forest and scrub for nesting, and moist soils with enough vegetative cover for safe diurnal feeding (Dessecker and McAuley 2001, Masse et al. 2014). Some aspects of the movements and habitat use of woodcock may differ from that of towhees, although they clearly both require early successional forest during the breeding season. Recommended minimum patch size for young forest songbirds such as towhees in the northeast is 0.6 – 1 ha (Askins et al. 2007, Schlossberg and King 2007), and the smallest patch size used by breeding towhees in our study was 0.76 ha. Thus, both the size and type of habitat needed for breeding towhees was available in the state-owned management areas we studied. Adequate vegetation to provide nesting cover, protection for fledged young from predators, and adequate forage (Greenlaw 2015, Stoleson 2013) are necessary for scrub-generalist towhees to successfully raise young, and this vegetation was available in the landscapes managed for woodcock. However, we need better information about how such land management affects productivity (i.e. nest success, clutch and brood size, fledging success), recruitment, and survival of towhees before we can determine if management for woodcock enhances towhee populations.

Behavioral shift for adult towhees once young reached independence

We would expect adults to travel further distances as their young develop; however, we did not observe significant changes in adult movement distance at earlier stages while they were still caring for their fledglings, even as young became more mobile in the mid- and late-fledge stage (Fig 2). Only when parental care ceased during the independence stage did we observe a behavioral shift where adults traveled significantly greater distances. Studies on the movements of recently independent fledglings of other songbird species observed similar increases in distances traveled once the young became independent (Vega Rivera et al. 1998, White and Faaborg 2008). This behavioral shift likely signals an important period for adult birds that have successfully raised young, as this independence or post-breeding stage has been associated with individual maintenance and recovery of condition before migration (Vitz and Rodewald 2007). We observed multiple instances of adults foraging on berries during this time, potentially to capitalize on the increased abundance of food and fruit in young forest habitat (Vitz and Rodewald 2007, Stoleson 2013), and potentially signaling a dietary shift towards increased frugivory that many eastern songbirds experience during autumn migration (Parrish 1997, Alan et al. 2013).

Habitat use of adult towhees during the post-fledging period did not change over time or between adults in different landscapes. Previous studies have shown that fledglings from mature forest habitats shift to early successional habitats during the post-fledgling period (Vega Rivera et al. 1998, Chandler et al. 2012, Burke et al. 2017). In contrast, fledgling Golden-winged warblers (*Vermivora chrysoptera*) shift from inhabiting young forests to using more mature forest when they become independent of their parents during the post-fledging period (Streby 2016). While we observed large groups of fledglings moving and foraging together without adults during the independence stage, we were not explicitly tracking young and we are unable to report specific habitat use of juvenile birds. However, our observations of recently independent young towhees from different broods forming small flocks is similar to grouping behavior that has been noted in other songbird species (Sullivan 1988).

Adult towhees that inhabited higher likelihood of woodcock use landscapes moved further during the independence stage (21+ days after fledge) than those inhabiting lower likelihood of woodcock use landscapes. These more extensive movements during the independence stage was most related to forest composition within 100-250 m of towhee home ranges, which is a much smaller scale than the $4km^2$ area recommended for woodcock (Williamson 2010). Previous research on shrubland bird communities in the state also noted the positive impact of certain habitat features within 100 m of territorial males (Buffum and McKinney 2014), further indicating that landscape impacts on the movement of songbirds in young forest habitat likely occurs at a smaller scale than $4km^2$ landscape impacts on woodcock movements (Chapter 1).

Ultimately, it appears that caring for fledged young has the largest impact on the distances adults travel during the post-fledging period based on the spatial and behavioral shifts we noted in adults once their young became independent. Interestingly, the number of young did not significantly impact the distances travelled or size of home ranges during the post-fledging period. Considering the average clutch size for towhees (Greenlaw 2015) is relatively small compared to cavity nesters (Martin 1992), the differences in overall distance travelled while raising young likely would not be very dramatic between brood sizes. However, differences in energy expenditure or foraging time are likely to be different for adults based on the number of fledglings to care for (Drent and Daan 1980).

Woodcock as an umbrella species

Our results suggest that management for woodcock singing and nesting grounds in forested landscapes can provide breeding habitat for towhees. Towhees are part of a particular guild of generalist shrubland songbirds that forage primarily on the ground and rely upon forest understory (Langlois 2017, Greenlaw 2015). However, other declining early successional forest/shrubland songbirds have more specific habitat requirements than the relatively ubiquitous towhee (DeGraaf and Yamasaki 2003, Leuenberger et al. 2017) and have been shown to respond differently to landscape and local scale features than the towhee (Askins et al.

2007, 2012). A particular management strategy that fits for some early successional species in one region may not apply to other early successional species in a different region, and thus it is critical that the objectives, ecology, and requirements of non-target species are well understood before broad management recommendations are applied across taxa (Hale and Swearer 2017). With continued studies that combine occupancy, reproductive, and spatial information, umbrella species management can be used as an effective conservation tool when attempting to manage for the highest number of species.

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Figure 1.

Home range size for adult towhees during the post-fledging stage. Circles represent individual home range sizes for 19 towhees in high-likelihood of woodcock use landscapes. Triangles represent individual home range sizes for 12 towhees in low-likelihood of woodcock use landscapes.

Figure 2.

Maximum distance travelled by adult towhees during four different fledgling development stages. Solid lines and circles represent towhees in high-likelihood of woodcock use landscapes. Dashed lines and triangles represent towhees in low-likelihood of woodcock use landscapes.

Table 1. General characteristics (i.e. appearance, mobility) of young and Eastern towhees the parental care behavior of adult towhees during the four stages of the post-fledging period.

Fledgling Stage	Appearance of young	Mobility of young	Parental care by adult towhees
Early-fledge (0-6 days)	Plumage is part downy, spotted on chest, drab colors. Minimal tail visible. Large, soft yellow bill	Big legs with developing flight feathers. Cannot fly above 2-3 meters, mostly limited to ground or short jumps,	Adults very attentive. Feeding frequently, become very agitated when observer near fledgling(s)
Mid-fledge (7-13 days)	Plumage is developing, but still mostly spotted appearance with some richer brown tones developing. Some tail visible. Outer bill edges still noticeably yellow	Able to make decent lateral flights to escape (5-15 meters). Movement is more fluid. Not able to reach canopy or high perches	Adults still feed regularly and remain near young. Less agitation when observers near, but still will call frequently.
Late-fledge (14-20 days)	Spotting mostly limited to face and replaced by streaking on body. Wings and tail developing adult colors (brown or black). Full tail.	Sustained flights and confident movers on the ground. Able to reach high perches and canopy	Adults will still travel with young, but limited feedings and limited agitation when observers are near.
Independence (21+ days)	Body plumage buff with faint streaks, but wings and tail fully adult in color. Head usually buff color.	Fully capable in all movements. Begins to call like adult after week 4	Little to no parental care. Adults will occasionally move with young.

Table 2. **(A)** Highest ranked general breeding models to explain the maximum distance moved by adult towhees during the independence stage of the post-fledging period. Variables included woodcock likelihood of use landscape (amwoLand), number of young (young), young forest patch size (patch), sex, and overall home range size (HR) during post-fledging period. **(B)** Highest ranked landscape composition models to explain the maximum distance moved by adult towhees during the independence stage of the post-fledging period. Variables included percent young forest/shrub (PctShrub), percent mature coniferous forest (PctCon), percent mature deciduous forest (PctDec), percent mixed forest (PctMix), and percent grassland/agriculture (PctGrass) at four different landscape scales.

(A) General Breeding Models	Variables	AIC	**Δ** AIC	ω_i
1	amwoLand, HR, Sex, patch	302.48	0	0.59
2	amwoLand, HR, Sex	303.74	1.7	0.31
3	amwoLand, HR, patch	307.27	5.3	0.05
4	amwoLand, HR	307.74	27.6	0.04
5	amwoLand	335.26	32.8	<0.001
6	amwoLand, Sex	336.33	33.8	<0.001
7	amwoLand, Patch	337.25	34.8	<0.001

(B) Landscape Composition models				
Hab1	amwoLand, PctScrub, PctCon, PctDec, PctMix, PctGrass @ 100 m	330.66	0.00	0.70
Hab2	amwoLand, PctScrub, PctCon, PctDec, PctMix, PctGrass @ 250 m	332.60	1.94	0.27
Hab3	amwoLand, PctScrub, PctCon, PctDec, PctMix, PctGrass @ 500 m	336.93	6.27	0.03
Hab4	amwoLand, PctScrub, PctCon, PctDec, PctMix, PctGrass @ 1,120 m	342.64	11.98	<0.01

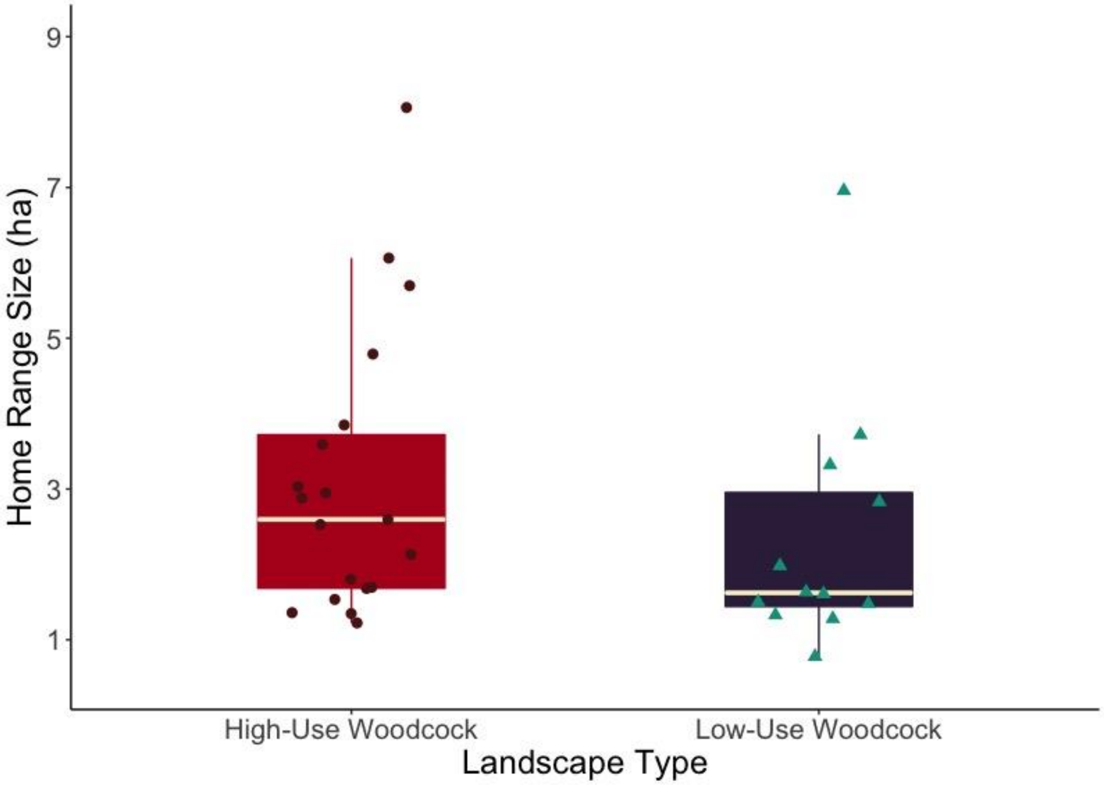
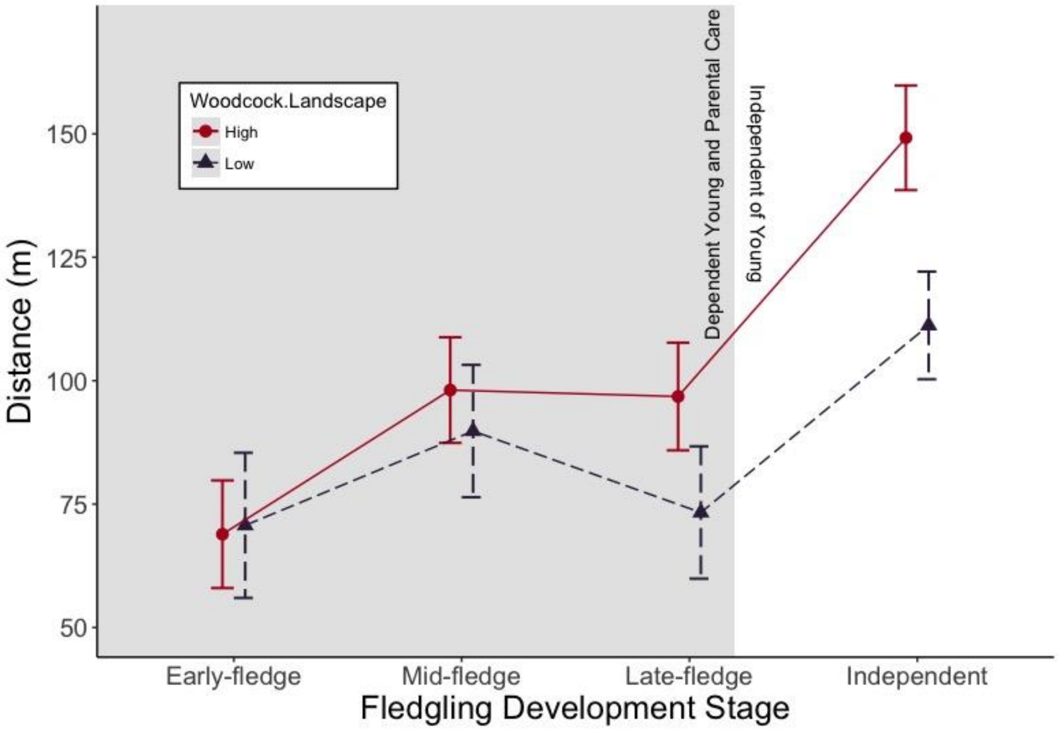

9
7
5
3
1
Home Range Size (ha)
High-Use Woodcock
Low-Use Woodcock
Landscape Type

Fig 1.



Woodcock.Landscape
High
Low
Dependent Young and Parental Care
Independent of Young
Distance (m)
150
125
100
75
50
Early-fledge
Mid-fledge
Late-fledge
Independent
Fledgling Development Stage

Fig 2.