

Nonbreeding and Migratory Ecology of Golden-Winged Warblers and Effects of
Landscape Composition and Configuration on American Woodcock Productivity

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Dedication

My work is dedicated to my parents who are a source of constant love, support, and encouragement in my life.

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Chapter 1

Nonbreeding Isolation and Population-Specific Migration Patterns Among Three Populations of Golden-Winged Warblers

Overview: Golden-winged Warblers (*Vermivora chrysoptera*) are Nearctic-Neotropical migrants experiencing varied regional population trends not fully explained by breeding-grounds factors (e.g., nest success). No detailed information exists on the nonbreeding distributions, migration routes, or timing of migration among populations of this species, and factors outside the breeding period may influence population trends. I tracked annual movements of 21 Golden-winged Warblers from three North American breeding locations experiencing varying population trends using geolocators from 2013-2015 to investigate the potential for nonbreeding site factors to influence breeding populations. I used the template-fit method to analyze light data collected with geolocators and estimate locations of individual warblers throughout the year. Geocator-marked warblers exhibited significant isolation among populations during migration and the nonbreeding period. During the nonbreeding period, Golden-winged Warblers from Minnesota, USA ($n = 12$) occurred in Central America from southern Mexico to central Nicaragua; warblers from Tennessee, USA ($n = 7$) occurred along the border of northern Colombia and Venezuela; and warblers from Pennsylvania, USA ($n = 2$) occurred in north-central Venezuela. Golden-winged Warblers I monitored from these three breeding populations exhibited essentially no effective overlap ($<0.001\%$) outside the breeding period. Warblers travelled at slower rates over more days in fall migration than spring migration. Fall migration routes at the Gulf of Mexico were population-specific, whereas spring routes were more varied and overlapped among populations. Geocator-marked Golden-

winged Warblers from Pennsylvania migrated 4,000 and 5,000 km yr⁻¹ farther than Tennessee and Minnesota warblers and spent almost twice as long migrating in the fall compared to Minnesota warblers. My results reveal nearly complete temporal and geographic isolation among three populations of Golden-winged Warblers throughout the annual cycle resulting in opportunities for population- and site-specific factors to differentially influence populations outside the breeding period. My findings highlight the need for monitoring multiple populations of migratory species to understand and better inform conservation strategies.

Key Words: geolocators, isolation, migration, nonbreeding period, template-fit method, *Vermivora chrysoptera*

INTRODUCTION

Conserving and managing migratory species is inherently complicated due largely to their reliance on multiple landscapes at different stages of their annual cycle. The combination and degree to which each life stage (e.g., nascence through independence from adult care), geographical location (e.g., a large estuarine stopover site), or portion of the annual cycle (e.g., the nonbreeding period) influence a population is often unknown; thus, resulting conservation strategies are often built with information representing a limited portion of a migratory species' annual range (e.g., Roth et al. unpublished report). This trend is concerning as recent studies demonstrate the influence of poorly studied life stages (e.g., the post-fledging period; Cohen and Lindell 2004, Streby and Andersen 2011) and carryover effects (e.g., habitat quality and food availability influencing subsequent productivity; Norris et al. 2004, Legagneux et al. 2012) on population dynamics of migratory species. Previous research suggests that like other migratory taxa, global populations of many migratory birds are declining at alarming rates (Robbins et al. 1989, Sauer et al. 1996, Sanderson et al. 2006), presenting an important and time-sensitive opportunity to develop full life-cycle conservation and management plans and identify and mitigate key factors driving population declines.

The value of identifying migration routes, nonbreeding sites, and habitats used by migratory birds outside of the breeding period is not a new frontier in ornithology (e.g., Lincoln 1921, Hanson and Smith 1950), but one that is only recently being considered across taxa beyond waterfowl and shorebirds. The recent increase in efforts to develop informed, full life-cycle management and conservation plans is likely explained by

technological advances that allow for tracking and monitoring most migrant bird species throughout the annual cycle (Webster et al. 2002, Holmes 2007, Stutchbury et al. 2009, Faaborg et al. 2010, Streby et al. 2015b). These technologies provide avenues to identify nonbreeding sites, migratory pathways and connectivity, and population overlap away from the breeding grounds with finer spatial and temporal resolution than previously attainable using other methods (e.g., stable isotope analysis and/or band recoveries; Dunn et al. 2006, Macdonald et al. 2012, Hobson et al. 2016), though tradeoffs exist among available methods.

Golden-winged Warblers (*Vermivora chrysoptera*) are small (~9-g) Nearctic-Neotropical migrants currently experiencing one of the most dramatic declines of any North American songbird (Buehler et al. 2007). Trajectories for breeding populations of Golden-winged Warblers vary by region with sustained severe declines in southern Appalachian states such as Tennessee, USA (-7.88% annually from 1966-2013, 95% CI [-11.62, -4.70]), severe and recently accelerating declines in northern Appalachian states such as Pennsylvania, USA (-7.08% annually from 1966-2003, 95% CI [-9.1, -4.78]; -8.36% annually from 2003-2013, 95% CI [-15.27, -2.15]), and stable trends for populations in western Great Lakes states such as Minnesota, USA (0.81% annually from 1966-2013, 95% CI [-0.52, 2.18]; Sauer et al. 2014). Most studies attribute these declines to breeding-grounds factors; namely, the loss or lack of available nesting habitat and low productivity (i.e., nest success) often in combination with competition and the effects of hybridization with a closely related sister species, the Blue-winged Warbler (*Vermivora cyanoptera*; Gill 1980, 1997; Confer and Knapp 1981; Confer et al. 2010; Buehler et al.

2007; Bulluck and Buehler 2008). Despite extensive prior research on the breeding grounds including recent genomics work suggesting Golden- and Blue-winged Warblers comprise a single, polymorphic species (Toews et al. 2016), there is no consistent evidence that any single factor, or combination of factors from the breeding grounds provides a complete and parsimonious explanation for the differential population trends observed in this species across its breeding distribution (Confer and Knapp 1981, Klaus and Buehler 2001, Gill 2004, Vallender et al. 2007, Bulluck et al. 2013).

Because breeding-grounds factors fail to fully explain the variation in local and regional population trends throughout the breeding distribution, it is logical that these trends may be linked to factors outside the breeding period along migration routes, at nonbreeding sites, or both. Little is known about Golden-winged Warblers away from North American breeding sites (Chandler and King 2011, Bennett 2012, Chandler et al. 2016) and although the distribution of Golden-winged Warblers at sites outside the breeding period is approximately delineated, no detailed information exists on the assortment and distribution of breeding populations away from the breeding grounds (Buehler et al. 2007). Recent evidence from the stable isotope analysis of feathers collected from Golden-winged Warblers at nonbreeding sites indicates nonbreeding warblers in South America likely breed in the Appalachian region and nonbreeding warblers sampled in Central America likely breed at more northern latitudes in the Great Lakes region; however, these data suggest possible population overlap as some Central American warblers sampled in Honduras may have Appalachian breeding origins (Hobson et al. 2016). The extent to which Golden-winged Warbler breeding populations

segregate on nonbreeding sites, use different migratory pathways, or use the same pathways but at different times of the year (or any combination of the above), affects the likelihood of site-specific factors (e.g., land-cover change, chemical exposure, anthropogenic factors, etc.) to influence populations independently of each other and contribute to the trends observed in regional populations on the breeding grounds.

I set out to identify migration routes and connectivity, nonbreeding sites, and distribution of breeding populations away from the breeding grounds in three breeding populations of Golden-winged Warblers, and quantify nonbreeding population overlap among populations to determine whether trends of local breeding populations may be caused by factors outside the breeding period. I predicted that population-level differences in migration routes, timing, and distribution outside the breeding period exist among three populations of Golden-winged Warblers (Tennessee, Pennsylvania, and Minnesota) with Appalachian breeding populations (i.e., Tennessee and Pennsylvania) likely occurring in South America, and Great Lakes populations likely occurring in Central America during the nonbreeding period (Hobson et al. 2016). I discuss how observed differences in spatial-use patterns outside the breeding period among these three breeding populations may contribute toward local breeding-population trends and how future conservation strategies may use this information to focus efforts on declining populations.

METHODS

Study Area and Field Methods

I attached 84 geolocators (model ML6240, 2-min light-sampling regime; 0.40 g stalkless and 0.47 g with 5-mm light-stalk; Biotrak, Wareham, UK; see Streby et al. [2015b] for detailed attachment methods and Peterson et al. [2015] for discussion of geocator effects) to adult male Golden-winged Warblers at three sites in the eastern USA during April-May of 2013 and 2014. I marked 43 individuals ($n = 20$, 2013; $n = 23$, 2014) at Rice Lake National Wildlife Refuge, Aitkin County, Minnesota (hereafter Rice Lake; 46.5° N, 93.3° W), 21 individuals ($n = 20$, 2013; $n = 1$, 2014) at North Cumberland Wildlife Management Area, Campbell County, Tennessee (hereafter Cumberland Mountains; 36.2° N, 84.2° W), and 20 individuals ($n = 20$, 2014) at Delaware State Forest, Monroe County, Pennsylvania (hereafter Delaware Forest; 41.3° N, 75.1° W). I marked all warblers within ~15 km of one another at each site.

I captured territorial male Golden-winged Warblers in mist nets using broadcasts of conspecific and congeneric songs and calls. I observed Blue-winged Warblers and phenotypic hybrids at or near all of my sites but only marked phenotypically pure Golden-winged Warblers, although it is possible that some birds were cryptic hybrids (Vallender et al. 2007). I banded each geocator-marked individual with a standard U.S. Geological Survey band and 1-3 plastic color bands. In 2014 and 2015 I systematically and opportunistically searched for returning geocator-marked Golden-winged Warblers within 500 m of their original capture location (see Peterson et al. [2015] for details on recapture methods and analysis of geocator effects). At Rice Lake I expanded the 2015 search radius to 2.5 km after forest management caused abandonment by Golden-winged Warblers of my primary study area and an outward redistribution of birds.

Sites in the Cumberland Mountains were composed of mixed hardwood forests at an average elevation of 780 m; some sites were managed for timber production and others were reclaimed mountaintop-mining sites (Bulluck and Buehler 2008). Rice Lake is in east-central Minnesota in the northern hardwood forest transition zone at an average elevation of ~350 m. Land cover consisted of a mosaic of upland and wetland forest, shrubland, and grassland surrounded by small amounts of agriculture (Ford et al. 2006). Delaware Forest is in Pennsylvania on the Pocono Plateau and land cover was composed of forested hills and valleys with swamps and peat bogs at an average elevation of ~300 m (Bakermans et al. 2015). Rice Lake is ~1,300 km north-northwest of the Cumberland Mountain site and ~1,600 km northwest of the Delaware Forest site. The Delaware Forest site is ~1,000 km northeast of my Cumberland Mountain site.

Statistical and Geolocator Data Analysis

I extracted and unpacked data from recovered geolocators using BASTrak software (Biotrak, Wareham, UK). I performed subsequent geolocator data analysis in R (v. 3.3.0, R Core Team, 2016). I used the BASTag package (Wotherspoon et al. 2013) to automatically identify transition periods (i.e., sunrises and sunsets) using a light threshold value of 2. I calibrated my data in FLIGHTR (v. 0.3.6; Rakhimberdiev and Saveliev 2015) using transitions recorded for geolocator-marked warblers known to be on breeding sites (i.e., 1-2 days following deployment through 1 July of the deployment year, and from the date of first resighting to the date of recovery in the following spring). I used FLIGHTR to estimate the spatial likelihood of occurrence for all twilights using the template-fit method (Ekstrom 2004, Rakhimberdiev et al. 2015). I chose a program using the

template-fit method over the more commonly employed threshold method (Hill and Braun 2001) because it has been demonstrated to be more accurate and less sensitive to potential shading error than currently available threshold models (Ekstrom 2007, Rakhimberdiev et al. 2016). The template-fit method of light-level analysis also provides an inherent estimate of uncertainty with each location estimate unlike the threshold method (Ekstrom 2007).

FLightR estimates the tracks of migratory animals equipped with geolocators by combining two component models: (1) a physical model that estimates the geographic location of the geocator on the globe for each transition (i.e., sunrise or sunset) using light data analyzed with the template-fit method, and (2) a movement model employing a hidden Markov chain model constrained by predetermined spatial and behavioral masks (Rakhimberdiev et al. 2015). I used the physical, template-fit model in FLightR with a land mask to estimate location likelihoods for each transition but did not use the movement model to link location estimates together because FLightR failed to estimate biologically reasonable migration tracks using my data (e.g., location tracks never approached South or Central America, warblers apparently began migrating while they were known to be on the breeding grounds, warblers constantly changed locations throughout the breeding and nonbreeding period, etc.; G.R. Kramer, personal observation, E. Rakhimberdiev, personal communication).

I used FLightR to create likelihood surfaces for each transition throughout the year. I multiplied the likelihood surface derived from an individual transition by the likelihood surfaces of the five subsequent transitions to produce a joint likelihood surface

reflecting the most likely location of the geolocator at the third transition (i.e., the approximate midpoint) of the six-transition product string. The joint likelihood surface for any given transition is therefore informed by the two preceding, and three subsequent transitions and has a pixel size $\sim 0.5^\circ$. Multiplying likelihood surfaces together is necessary to achieve location estimates because a likelihood surface derived from a single sunrise or sunset is curvilinear and does not provide enough information to estimate a location by itself (Rakhimberdiev et al. 2015). Likelihood surfaces estimated from single transitions produce swaths of likelihoods across the hemisphere at nearly perpendicular angles depending on whether the transition is a sunrise or a sunset thus necessitating the multiplication of multiple likelihood surfaces to identify areas of high likelihood of location during both sunrise and sunset.

I assumed geolocator-marked warblers did not move between these six-transition periods (i.e. three sets of consecutive sunrises and sunsets), though there are likely times that geolocator-marked birds in my study spent <3 days at a particular site. I chose a six-transition window to balance the smoothing effect of multiplying likelihood surfaces together with a relatively short period to identify movements. The lack of certainty around any particular point is reflected in the overall probability of occurrence over those six twilights; therefore, individuals that remained stationary during a particular period should produce point estimates with higher probabilities and smaller core areas of the highest probabilities than moving or migrating individuals. Notably, Golden-winged Warblers are primarily nocturnal migrants and therefore most likely to make long-distance migratory flights from sunset to sunrise (i.e., a maximum of three movements

per three-day, six-transition, period). I transformed each joint likelihood surface into a utilization distribution (i.e., probability distribution function) by dividing the likelihood in each cell of a given joint likelihood surface by the sum of the likelihoods across all cells of the surface. This allowed me to directly compare utilization distributions between and among individuals and populations. I extracted the coordinates of the cell with the highest probability of utilization and assigned those coordinates and the associated probability to the third transition (i.e., sunrise or sunset) of the multiplication string used to calculate that utilization distribution. Following the extraction of coordinates and associated maximum probabilities for each transition in the dataset, I plotted the coordinates as points and reviewed them in QGIS (QGIS Development Team, 2015). I averaged points when there was a location estimate from a sunrise transition and a sunset transition on the same date resulting in only one location estimate per date. If there was only one estimate for any given date (e.g., if one of the twilights was excluded as an outlier during processing in FLIGHTR), I used that estimate as the location point estimate.

Identification of Migration Routes

I treated my template-derived points as previous studies treated threshold-derived location estimates (e.g., Delmore et al. 2012). To delineate general fall migratory routes, I used points from 2 July to 31 October and deleted points arbitrarily north of the breeding site and >150 km from land (i.e., outside the range of expected location error). I defined the onset of fall migration as the first point in a string of ≥ 5 that were $> \pm 1^\circ$ longitude from the breeding site (i.e., east or west), and > -3 to -5° latitude from the breeding site (i.e., south). Longitude estimates are highly accurate using the template-fit method

whereas latitude estimates are less accurate (Rakhimberdiev et al. 2016). I developed these criteria based on the ability of FLIGHTR to place geolocator-marked warblers at their breeding sites when they were known to be there and I adjusted these criteria depending on the characteristics of the individual geolocator (e.g., if locations during the period of known location were consistently biased north or south). I relied primarily on longitudinal movements to identify the beginning of migratory periods as my method allows for a bird to travel straight south for ~300-500 km within a 100-km buffer east and west of the study site before being characterized as a migrant. For this reason, I acknowledge that my estimates of the onset of fall migration may be later than when warblers initiated migration. I marked the end of fall migration as the date an individual crossed an imaginary plane $\pm 1^\circ$ longitude and $\pm 4^\circ$ latitude from its estimated nonbreeding site (calculated below).

To delineate general spring migration routes, I selected points from 1 March to the end of a geolocator's tracking period and defined the onset of spring migration as the first point in a string of ≥ 5 consecutive points for which the longitude of the bird was $> 1^\circ$ west of its estimated nonbreeding site (calculated below). I marked breeding-site arrival as the first point in the spring period $< \pm 1^\circ$ longitude (i.e., east or west) from the study site and < -3 to -5° latitude (i.e., south) from the breeding site and confirmed breeding-site arrival with field observations (Peterson et al. 2015). I recreated spring and fall migratory pathways by linking single points, or clusters of points (i.e., > 2 consecutive points separated by < 150 km), together chronologically. I disregarded nonsensical, low probability points at this stage, which were rare (i.e., usually < 5 points per bird per

migration; for example, if an individual appeared to move back and forth across the Gulf of Mexico, I considered the first movement to be the true movement and assumed the bird did not traverse the Gulf of Mexico twice in two consecutive days). Migration routes are to be interpreted as general migratory trajectories and not as exact paths.

I investigated migration-route directness by dividing the great circle (i.e., direct) route distance directly linking an individual's breeding site to its estimated nonbreeding site by the distance travelled along generalized spring and fall migration routes. A perfect value of one would occur if an individual migrated along the great circle route from its breeding site to its nonbreeding site (and vice versa). Warblers deviating from a great circle route travel a greater distance than is required (assuming no physiological or physical barriers) and receive a lower, less efficient estimate of directness. I acknowledge that there are likely energetic advantages to not migrating along direct routes, so my estimates of directness are simply an aid to compare migration pathways among breeding populations. I characterized spring and fall migration routes as crossing the Gulf of Mexico (i.e., overwater routes crossing the Gulf of Mexico directly in one flight), island hopping (i.e., routes with stopover sites associated with islands in the western Caribbean), or circumventing the Gulf of Mexico (i.e., primarily overland movements with stopovers along the eastern coast of Mexico). I tested for population-level differences in broad-scale migration-route characteristics using a Fisher's exact test.

Identifying Nonbreeding Sites of Warblers

I estimated the nonbreeding sites of individual warblers by deriving a utilization distribution for the entire period during which Golden-winged Warblers are resident in

Central and northern South America. I multiplied each likelihood surface for transitions (i.e., sunrises and sunsets) spanning 1 January – 28 February together and divided the likelihood in each cell in the resulting surface by the sum of likelihood across the entire surface to derive a utilization distribution representing the probability of residency during the nonbreeding period. I selected these dates to avoid location-error issues known to occur in some cover types and species during the tropical wet-season (McKinnon et al. 2013) and because Golden-winged Warblers defend a single territory between fall and spring migration (Chandler and King 2011).

I estimated the effective overlap between populations at nonbreeding sites by averaging nonbreeding utilization distributions for all warblers of a given population. The resulting utilization distribution represents the probability of a warbler from that population occupying any cell during the nonbreeding period. I then quantified overlap among populations during the nonbreeding period by multiplying their nonbreeding utilization distribution (as calculated, above) together. The sum of the product surface is the probability that sampled warblers from both populations occupied the same cells during the nonbreeding period. This process does not measure geographic or area overlap, but instead results in a statistical representation of overlap. The probability of an individual from a population occupying any given cell during the period 1 January – 28 February is multiplied by the probability of an individual from a different population occupying the same cell over the same period providing a scaled estimate of overlap.

I produced a single point estimate for the nonbreeding site of each warbler by averaging the latitude and longitude of a subset of point estimates from 1 November – 28

February occurring within 250 km of the delineated nonbreeding range of Golden-winged Warblers (U.S. Geological Survey Gap Analysis Program) to limit the effect of outliers while allowing geocator-marked warblers to occur outside their predetermined range.

I evaluated differences between populations using one-way ANOVA and post hoc Tukey HSD tests in R (R Core Team 2016) unless noted otherwise. I used multiple linear regression to evaluate relationships between variables and used *t*-tests to determine if regression coefficients were significantly different from zero. Results of all tests were considered statistically significant at $\alpha = 0.05$. All means are presented \pm SD.

RESULTS

I recovered geolocators from 15 Golden-winged Warblers in 2014 ($n = 9$, Rice Lake; $n = 6$, Cumberland Mountains). Three of 15 (20%) geolocators recovered in 2014 at Rice Lake collected data for only a portion of the year. Two of these geolocators malfunctioned (one in January, one in February), and one functional geocator was recovered with mud caked on the light sensor and stopped recording reliable data in early November 2013. In all three cases, I recovered enough data to estimate fall migration and nonbreeding sites; however, it was not possible to estimate initiation of spring migration or arrival at breeding areas from those geolocators. In 2015, I recaptured and recovered geolocators from 8 Golden-winged Warblers marked in 2014 ($n = 3$, Rice Lake; $n = 1$, Cumberland Mountains; $n = 4$, Delaware Forest). Two geolocators (50%) recovered at the Delaware Forest in 2015 malfunctioned and failed to record data after ~two months following deployment, and I censored those units from all analyses. Consequently, I

analyzed light-level data from 21 geolocators deployed on 20 individual Golden-winged Warblers (I recovered a geocator from one individual at Cumberland Mountains in both 2014 and 2015). Eighteen of 21 (86%) geolocators contained data for the full year whereas the remaining three geolocators (14%) contained data for fall migration and a portion of the nonbreeding period (Appendix A, Appendix B). I recovered fewer geolocators in 2015 than in 2014 due to vegetation management efforts resulting in cover-type changes that caused Golden-winged Warblers to occupy breeding territories outside of the core of my Rice Lake study site (G.R. Kramer, personal observation).

Nonbreeding Sites and Population Overlap

Golden-winged Warblers marked at Cumberland Mountains ($n = 7$) occurred at sites on the border region of northern Colombia and Venezuela during the nonbreeding period (Figure 1, Table 1). Warblers breeding at Rice Lake ($n = 12$) occurred at sites in Central America ranging from southern Mexico to south-central Nicaragua during the nonbreeding period (Figure 1, Table 1) and were on average >200 km farther apart from each other than Cumberland Mountain warblers (397 ± 288 km vs. 166 ± 69 km, $n = 66$ and $n = 21$, respectively, one-way ANOVA, $F_{2,86} = 9.5$, $P = 0.001$). Golden-winged Warblers marked at Delaware Forest ($n = 2$) occurred at sites in Venezuela during the nonbreeding period (Figure 1, Table 1). All three populations used areas during the nonbreeding period at significantly different longitudes (Table 1, Figure 1) but latitude of these areas only differed between Rice Lake and both Delaware Forest and Cumberland Mountain populations ($P < 0.001$ for both comparisons, post hoc Tukey test; Table 1,

Figure 1). The three breeding populations I marked exhibited no effective range overlap (<0.01% for all comparisons; Figure 1) during the nonbreeding period.

Migration Routes and Timing

The average fall departure date from the breeding grounds did not differ among the three breeding populations I marked (Table 1, Figure 2), although there were differences in characteristics of fall migration routes among these populations (Fisher's exact test, $P < 0.001$). All 12 (100%) Golden-winged Warblers migrating from Rice Lake traversed the Gulf of Mexico, whereas only 29% (2/7) of warblers from Cumberland Mountains and 0% (0/2) of warblers from Delaware Forest crossed the Gulf of Mexico during fall migration (Figure 3). Golden-winged Warblers migrating from Cumberland Mountains and Delaware Forest "island hopped" through the western Caribbean (5/7 [71%], Cumberland Mountains; 1/2 [50%], Delaware Forest) or circumvented the Gulf of Mexico to the west (0/7 [0%], Cumberland Mountains; 1/2 [50%], Delaware Forest; Figure 3). Golden-winged Warblers that crossed the Gulf of Mexico arrived at nonbreeding sites 19 ± 7 days earlier than warblers that island hopped, and 38 ± 7 days earlier than warblers circumnavigating the Gulf of Mexico, controlling for breeding population and fall departure date ($F_{3,17} = 17.2$, $P < 0.001$). Golden-winged Warblers from Delaware Forest migrated along routes >2,000 km longer than Rice Lake and Cumberland Mountain warblers during fall migration (Table 1, Figure 1).

Warblers from all three breeding populations migrated at similar average daily rates during fall migration (Table 1), regardless of migration route ($F_{3,17} = 0.5$, $P = 0.7$), but warblers that left their breeding sites later in the season migrated faster with the

average daily rate of migration increasing by $2.5 \pm 0.4 \text{ km day}^{-1}$ for each day that a bird deferred the onset of fall migration (two-tailed t -test, $t_{16} = 5.8$, $P < 0.001$), controlling for breeding population and migration route ($F_{4,16} = 9.4$, $P < 0.001$). The duration of fall migration differed among the Golden-winged Warbler breeding populations I monitored with Delaware Forest warblers migrating over a longer period than Rice Lake warblers (Table 1, Figure 2). Rice Lake warblers arrived at nonbreeding sites one month earlier than warblers from Delaware Forest (Table 1, Figure 2) and also initiated spring migration 20 and 25 days after both Delaware Forest and Cumberland Mountain warblers, respectively (Table 1, Figure 2). As a result, Rice Lake warblers spent 20% and 29% more days at nonbreeding sites than Cumberland Mountain and Delaware Forest warblers, respectively (Table 1, Figure 2).

Golden-winged Warblers from Cumberland Mountains arrived at their breeding areas 22 ± 4 days before Rice Lake warblers (Table 1). Date of onset of spring migration was not a significant predictor of arrival date on breeding areas after controlling for breeding population (two-tailed t -test, $t = 1.7$, $P = 0.11$). The duration of spring migration did not differ among the three breeding populations I monitored (Table 1, Figure 2) and showed no relationship to the type of route used to navigate the Gulf of Mexico (i.e., crossing, island hopping, or circumnavigating) when I controlled for breeding population effects ($F_{3,14} = 1.0$, $P = 0.41$); however, warblers that migrated longer distances did so at a faster rate ($\bar{x} = 0.03 \pm 0.01 \text{ km day}^{-1}$ for each km travelled along their spring migration route, $t = 2.2$, $P = 0.04$) after controlling for breeding population effects. The type of route used by individual warblers to navigate the Gulf of Mexico during fall migration

did not predict the type of route used during spring migration when controlling for breeding population ($F_{3,17} = 1.3$, $P = 0.29$) and I found no evidence of population-level differences in the frequencies of routes used by individuals during spring migration (Fisher's exact test, $P = 0.14$). The Cumberland Mountains warbler with two years of tracking data took the same general route during both fall migrations (island hopping route) but used different routes each year during spring migration (circumventing route, spring 2014; crossing route, spring 2015).

I found no difference in the average daily rate of spring migration among breeding populations (Table 1). The date of onset of spring migration did not predict the daily average rate of migration in spring ($R = 0.14$, $F_{3,14} = 2.0$, $P = 0.17$) nor did the type of route used to navigate the Gulf of Mexico when controlling for breeding population ($F_{3,14} = 0.5$, $P = 0.70$). Spring-migrating Golden-winged Warblers from Delaware Forest took routes >2,600 km longer than warblers migrating to Rice Lake and >1,900 km longer than warblers migrating to Cumberland Mountains (Table 1, Figure 3). Golden-winged Warblers from Cumberland Mountains travelled farther than Rice Lake warblers during spring migration although this difference was not statistically significant (Table 1).

Migration-route directness varied among breeding populations during both fall and spring migrations (Table 1, Figure 3). The most extreme differences in migration-route directness occurred between Rice Lake warblers and warblers from both Delaware Forest and Cumberland Mountains (Table 1, Figure 3). Routes taken by Rice Lake warblers during spring migration were more direct than routes taken by warblers from

Delaware Forest and Cumberland Mountains (Table 1, Figure 3). I found no differences in fall migration-route length compared to spring migration-route length when I controlled for breeding population effects (two-tailed t -test, $\bar{x} = -467 \pm 164$ km, $t_{14} = 1.2$, $P = 0.27$). Golden-winged warblers travelled at an average daily rate 77% faster in the spring than during fall migration controlling for breeding population effects (two-tailed t -test, $\bar{x} = 0.77 \pm 0.29$, $t_{14} = 2.6$, $P = 0.008$; Table 1).

DISCUSSION

I describe previously unknown aspects of migration and nonbreeding distribution of three breeding populations of Golden-winged Warblers, including evidence for extensive spatial and temporal isolation among these populations throughout their annual cycle. Different migratory patterns and nonbreeding distribution among these breeding populations suggest that factors outside the breeding period could differentially influence population ecology and trends. Golden-winged Warblers exhibited low migration-route diversity during fall migration with individuals from the western Great Lakes region (Rice Lake) exclusively crossing the Gulf of Mexico, individuals from the southern extent of their breeding distribution (Cumberland Mountains) largely using an eastern route crossing the Caribbean Sea, and individuals from the northern part of the Appalachian Mountains (Delaware Forest) using similar eastern routes to Cumberland Mountain warblers, or completely circumventing the Gulf of Mexico. Fraser et al. (2013) found low levels of route diversity among populations of Purple Martins (*Progne subis*) during fall migration with populations showing similar trends to Golden-winged

Warblers in their use of routes around the Gulf of Mexico with eastern breeding birds more likely to use eastern routes crossing the Caribbean Sea, central breeding birds using direct trans-Gulf-of-Mexico routes, and western populations circumventing the Gulf of Mexico with primarily overland routes. Golden-winged Warbler breeding populations used a variety of routes to traverse or circumnavigate the Gulf of Mexico in the spring (Figure 3). Eastern and western Veeries (*Catharus fuscescens*) and Barn Swallows (*Hirundo rustica*) showed similarly high variation in spring vs. fall migration routes (Hecksher et al. 2011, Hobson and Kardynal 2015, Hobson et al. 2015) but Red-eyed Vireos (*Vireo olivaceus*) exhibited a reversed trend in which fall migration routes were more variable than spring routes (Callo et al. 2013). Interestingly, Wood Thrushes (*Hylocichla mustelina*) tracked for multiple seasons showed individual annual variation in migration routes, especially during spring, suggesting seasonal variation in routes may be related to a combination of individual experience, weather, and/or energetic condition during migration (Stanley et al. 2012). I failed to detect any effect of route type on arrival time or rate of migration during both fall and spring suggesting that whether a Golden-winged Warbler crosses the Gulf of Mexico directly, island hops, or circumnavigates the Gulf of Mexico, they do so at no noticeable expense to their migratory schedule and such decisions may result from exogenous influences (e.g., weather). Higher variation in spring migration routes may also be explained by the shorter duration of spring vs. fall migration periods. In fall, migrating warblers may have more flexibility and be able to wait for favorable conditions to undertake their preferred route. In spring, the migration period is shorter and warblers may be more likely to take variable routes depending on

the conditions at the time they reach the Gulf of Mexico. I also note that the single individual I monitored during two years used different migration routes in each of those years, suggesting that exogenous factors (e.g., weather, physiological condition, etc.) may influence migration, although additional information is necessary to understand how widespread this phenomenon is, and its implications for Golden-winged Warbler conservation.

Golden-winged Warblers in my study all travelled at daily average rates that were similar among breeding populations during both fall and spring migrations with the general trend of travelling faster during spring than during fall. Golden-crowned Sparrows (*Zonotrichia atricapilla*; Seavy et al. 2012) and Northern Wheatears (*Oenanthe oenanthe*; Schmaljohann et al. 2012) exhibited similar accelerated migration rates in spring vs. fall. When I controlled for the effects of breeding population on migration rate, individuals travelling longer routes did so faster. Northern Wheatears demonstrated similar patterns with populations migrating >14,000 km (one-way) doing so twice as fast as individuals from populations migrating ~4,100 km (Bairlein et al. 2012). Moreover, I failed to detect any relationship between spring departure and arrival on breeding areas when I controlled for breeding-population effects. Although my sample sizes are relatively small, this finding warrants further investigation as it contradicts other research suggesting birds leaving nonbreeding sites earlier also arrive on the breeding grounds earlier and that early arrival confers some fitness benefit over late arrival and identifies high-quality individuals (e.g., Norris et al. 2004, Spottiswoode et al. 2006).

Golden-winged Warblers exhibited variation in migration-route lengths and directness. Delaware Forest warblers took the longest and least direct routes compared to Rice Lake and Cumberland Mountain warblers. Shorter, more direct routes may be more efficient in that birds travel less distance, but a tradeoff may exist when those routes are more dangerous, or more energetically demanding than longer, primarily overland routes. Golden-winged Warblers from the Delaware Forest population successfully migrated 4,000-5,000 km yr⁻¹ farther than Cumberland Mountain and Rice Lake populations suggesting that, at least, Cumberland Mountain and Rice Lake populations are not approaching limits of their physiology during migration. Additional evidence from Golden-winged Warblers suggests that Cumberland Mountain warblers are capable of undertaking ~1,500-km facultative migrations to avoid large, long-lasting tornadic storms immediately after completing a ~5,200 km obligate migration (Streby et al. 2015a). Migration is purported to be among the most dangerous periods for migratory species (Sillett and Holmes 2002) and therefore may be a factor influencing population trends in Golden-winged Warblers populations, which must travel longer periods or greater distances relative to other populations. However, declines in abundance in recent decades could only be explained by migration-route distance if that distance has changed from periods of stable population numbers or a change in the birds' ability to complete the route.

I found complete isolation during the nonbreeding period among these three breeding populations as they used sites along a general east-west gradient that reflected arrangement on the breeding grounds (Figure 1). My findings generally confirm results of

a recent isotopic analysis of nonbreeding Golden-winged Warblers, although I found no evidence of Appalachian Mountain warblers occurring in Central America suggesting more significant isolation among populations (Hobson et al. 2016). I acknowledge that sampling more individuals may result in greater population overlap; however, considering Delaware Forest and Cumberland Mountain warblers as a single Appalachian population still suggests complete population isolation among western Great Lakes breeding warblers and Appalachian Mountain breeding warblers. My findings are similar to those reported in western-breeding populations of Swainson's Thrushes (*Catharus ustulatus*; Delmore et al. 2012, Cormier et al. 2013), eastern- and central-breeding Gray Catbirds (*Dumetella carolinensis*; Ryder et al. 2011), and Ovenbirds (*Seiurus aurocapilla*; Hallworth et al. 2015) and unlike patterns observed in Wood Thrushes (Stanley et al. 2015) and Purple Martins (Fraser et al. 2012) in which breeding populations showed moderate to extensive overlap during the nonbreeding period, excluding migration. Unlike several other species of Nearctic-Neotropical migrant songbirds (e.g., Hecksher et al. 2011, Cormier et al. 2013) Golden-winged Warblers in my study showed no evidence of long-distance movements within the nonbreeding period corroborating evidence from radio-telemetry studies of Golden-winged Warblers in Costa Rica (Chandler and King 2011) and Nicaragua (Chandler et al. 2016). Smaller-scale, nonbreeding-grounds efforts may therefore be effective in conserving individual populations of this species. Conversely, the use of a relatively small area throughout the nonbreeding period implies a reliance on that location and the availability and quality of

appropriate land cover in that region potentially suggesting sensitivity to moderate- or large-scale changes in land-cover types and composition in Golden-winged Warblers.

European migratory bird species that disperse more broadly during the nonbreeding period are less likely to be declining than species with restricted distributions during the nonbreeding period compared to their breeding distributions (Fuller 2016, Gilroy et al. 2016). Golden-winged Warblers in my study demonstrated this trend at the population level with greater nonbreeding dispersion among populations with stationary trends (e.g., Rice Lake) compared to breeding populations in decline (e.g., Cumberland Mountains) suggesting that migratory diversity (i.e., within-population variation in migratory routes and/or destinations) may be related to population dynamics. Accordingly, conservation efforts targeting Golden-winged Warblers breeding in the western Great Lakes region might be most effective if focused on protecting appropriate nonbreeding sites throughout Central America. Such efforts would help conserve nonbreeding-site diversity of Golden-winged Warblers breeding within the western Great Lakes region. Conservation efforts targeting Golden-winged Warblers breeding in the Appalachian Mountains region might be most effective if focused on targeting appropriate nonbreeding sites in northern South America (i.e., Colombia and Venezuela). Targeted conservation efforts for Golden-winged Warblers breeding in the Appalachian Mountain region may be especially effective at appropriate sites along the border of Colombia and Venezuela where a high proportion of my sample of geolocator-marked Golden-winged Warblers that bred in the Appalachian Mountains region spent the nonbreeding period.

I documented spatial segregation among three populations of Golden-winged Warblers in their nonbreeding distribution and differences among breeding populations in migration routes and behavior highlighting the importance of identifying the full life-cycle movements of multiple populations of the same species. I found no evidence of Appalachian-breeding warblers occurring in Central America during the nonbreeding period, outside of migration, suggesting that sampling of additional Appalachian populations may be required to determine if any nonbreeding population overlap exists among Appalachian and Great Lakes Golden-winged Warbler populations in Central America (Hobson et al. 2016). Additionally, future efforts may benefit from sampling both Golden- and Blue-winged Warblers from additional populations across their respective distributions as the two likely constitute phenotypic morphs of the same species and a species-wide study focused on a single morph would be incomplete (Toews et al. 2016). Moreover, as many passerine populations are female-limited (i.e., some males are unpaired; Habib et al. 2007, Streby and Andersen 2011), it is critical that female migration and nonbreeding ecology are addressed by future studies of species of conservation concern. Finally, the nonbreeding population structure I describe suggests breeding population trajectories may be driven by population- or site-specific factors experienced by populations independently during the nonbreeding period or migration. Identifying those environmental factors associated with individual survival across the nonbreeding distribution and during migration might aid in the development of robust conservation strategies. My findings suggest a need for a more comprehensive evaluation

of the ecology and distribution of Golden-winged Warblers outside the relatively well-studied breeding period.

Table 1. Mean values (SD) of migration and nonbreeding period characteristics of Golden-winged Warblers from breeding populations in Minnesota (Rice Lake National Wildlife Refuge; RL), Tennessee (Cumberland Mountains; CM), and Pennsylvania (Delaware Forest; DF), USA derived from geolocator data. *P*-values are given for one-way ANOVA, and superscript letters indicate a significant difference between breeding populations for Tukey's HSD post hoc test using *P* < 0.05. See text for definitions of terms.

	Population			<i>P</i>
	RL	CM	DF	
Nonbreeding-period factor	(<i>n</i> = 12)	(<i>n</i> = 7)	(<i>n</i> = 2)	
Nonbreeding-period longitude	84.41°W ^a (2.07)	71.95°W ^b (0.70)	65.82°W ^c (3.87)	<0.001
Nonbreeding-period latitude	15.31°N ^a (2.07)	8.71°N ^b (0.90)	9.99°N ^b (0.49)	<0.001
Migration factor				
Fall departure date	Jul 24 (8)	Jul 22 (10)	Jul 16 (2)	0.39
Fall migration termination date	Sep 21 ^a (14)	Oct 5 (20)	Oct 28 ^b (12)	0.02
Spring migration departure date	Apr 10 ^a	Mar 16 ^b	Mar 21 ^b	<0.001

	(10)	(3)	(2)	
Breeding-site arrival date	May 16 ^{a,1}	Apr 24 ^b	May 6	<0.001
	(6)	(9)	(8)	
Fall migration duration (d)	59 ^a	75	104 ^b	0.03
	(20)	(28)	(10)	
Nonbreeding (resident) period duration (d)	200 ^a	169 ^b	143 ^b	<0.001
	(20)	(20)	(14)	
Spring migration duration (d)	36 ¹	38	46	0.26
	(8)	(8)	(6)	
Fall migration distance (km)	4,144 ^b	4,710 ^b	6,748 ^a	<0.001
	(369)	(277)	(1,808)	
Spring migration distance (km)	4,575 ^{b,1}	5,228 ^b	7,212 ^a	<0.001
	(616)	(513)	(216)	
Total migration distance (km)	8,702 ^{a,1}	9,938 ^b	13,959 ^c	<0.001
	(963)	(604)	(1,592)	
Fall migration average daily rate (km day ⁻¹)	76	73	64	0.83
	(18)	(35)	(11)	
Spring migration average daily rate (km day ⁻¹)	132 ¹	141	158	0.64
	(12)	(40)	(15)	

Fall migration-route directness	0.86 ^a (0.04)	0.68 ^b (0.04)	0.57 ^b (0.15)	<0.001
Spring migration-route directness	0.78 ^{a,1} (0.07)	0.61 ^b (0.06)	0.52 ^b (0.02)	<0.001
Great circle distance between breeding and nonbreeding period location (km)	3,552 ^b (263)	3,172 ^a (105)	3,742 ^b (40)	0.002

¹ $n = 9$

Figure 1. Estimated location during the nonbreeding period for 21 male Golden-winged Warblers from three breeding populations derived from light-level geolocators. Gray shading represents Golden-winged Warbler distribution. Inset shows breeding distribution and deployment/breeding sites. Squares ($n = 12$) represent Golden-winged Warblers breeding at Rice Lake National Wildlife Refuge, Minnesota, USA; triangles ($n = 7$) represent Golden-winged Warblers breeding at North Cumberland Wildlife Management Area, Tennessee, USA; and circles ($n = 2$) represent Golden-winged Warblers breeding at Delaware State Forest, Pennsylvania, USA. Range maps provided by U.S. Geological Survey Gap Analysis Program.

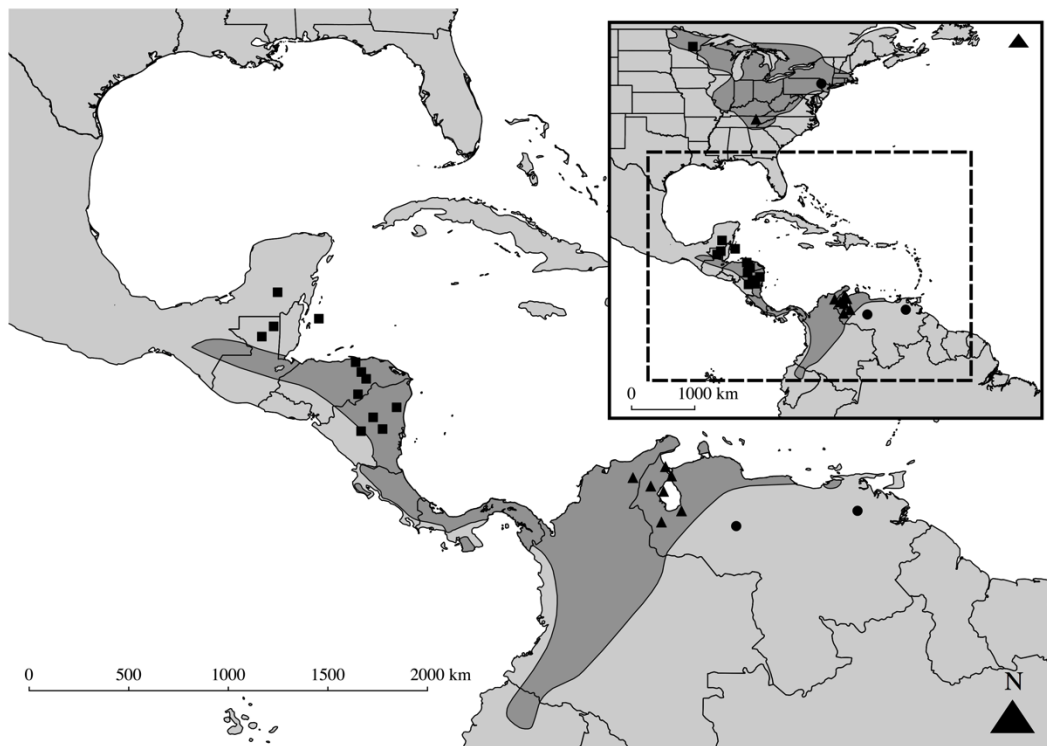


Figure 2. Estimated annual schedules ($n=21$) by month for individual male Golden-winged Warblers ($n=20$; CM13 and CM21 are the same individual marked in consecutive years) marked with geolocators at three breeding sites during 2013-2015. The color of each segment of a horizontal bar represents the status of an individual Golden-winged Warbler from geolocator deployment through recovery for warblers marked at Rice Lake National Wildlife Refuge, Minnesota, USA ($n=12$; labeled 'RL'), Delaware Forest, Pennsylvania, USA ($n=2$; labeled 'DF'), and Cumberland Mountains, Tennessee, USA ($n=7$; labeled 'CM'). Shading represents warblers at breeding areas (green), in fall migration (orange), at stationary nonbreeding areas (blue), and in spring migration (yellow). Periods without geolocator data are shaded in gray.

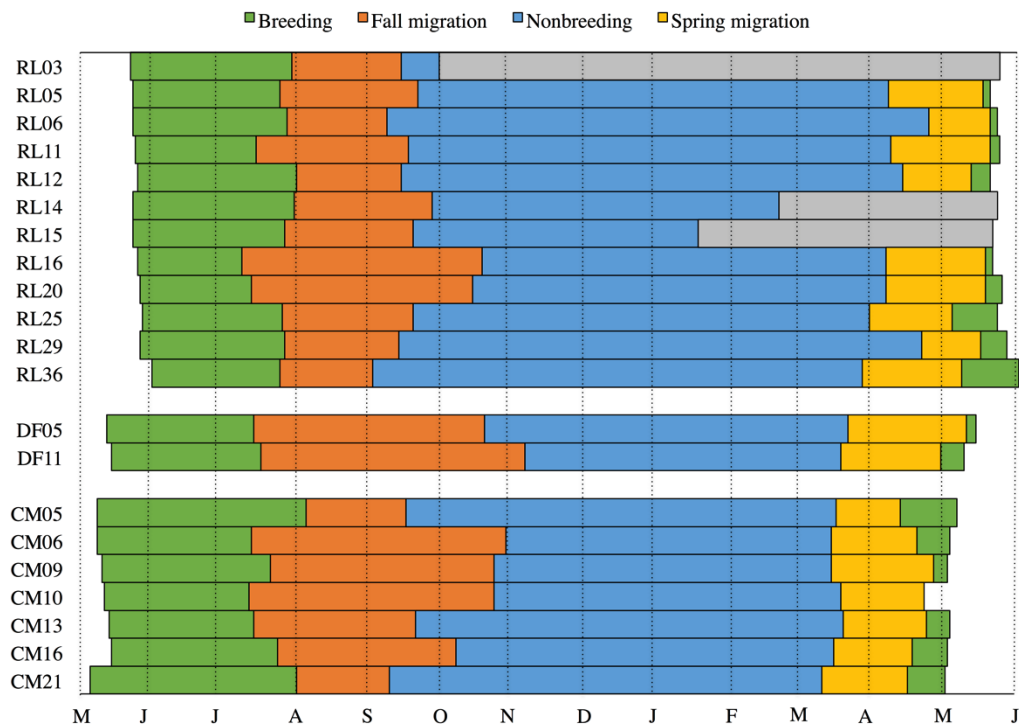
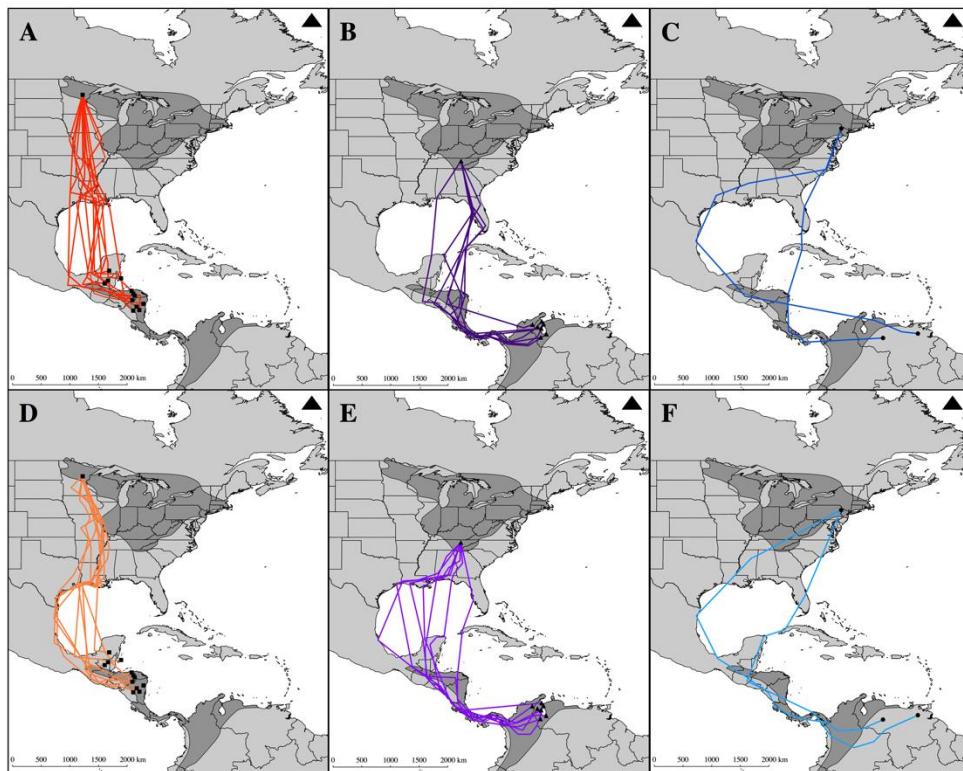


Figure 3. Estimated general migration routes for male Golden-winged Warblers marked at three breeding populations during 2013-2015. Orange tracks represent warblers marked at Rice Lake National Wildlife Refuge, Minnesota, USA (RL; $n = 12$ for fall migration [A]; $n = 9$ for spring migration [D]), purple tracks represent warblers marked at North Cumberland Wildlife Management Area, Tennessee, USA (CM; $n = 7$ for fall [B] and spring migration [E]), and blue tracks represent warblers marked at Delaware State Forest, Pennsylvania, USA (DF; $n = 2$ for fall [C] and spring migration [F]). Range maps provided by the U.S. Geological Survey Gap Analysis Program.



Chapter 2

Effects of Landscape Composition and Configuration on Full-Season Productivity of American Woodcock in Minnesota

Overview: The effects of landscape composition and configuration on the full-season productivity (i.e., juveniles raised to independence from adult care) of most bird species, including American Woodcock (*Scolopax minor*), is largely unknown. Understanding landscape components and cover-type configurations associated with high full-season productivity can be useful in developing more effective management strategies that increase recruitment. I used data on nest and juvenile survival rates of American Woodcock in northern Minnesota from 2011 to 2012 to inform logistic exposure models of survival and predict full-season productivity. I used those models to link landscape features with nest survival rate and juvenile survival rate; predict spatially explicit, full-season productivity across my study area; and identify areas of high productivity within my study landscape. Finally, I used simulations to explore the impact of potential management actions aimed at improving productivity and the effects of long-term succession of young-forest cover types. I found that associations between land-cover composition and different components of productivity (i.e., nest and juvenile survival rates) were scale-specific. Generally, my models suggested stand-level composition (i.e., the amount of cover types within 500 m of the nest) influenced nest survival rate with mature forest having a small, but mostly positive association with nest survival rate in most landscape contexts. Conversely, my models predicted lower nest survival rates in landscapes with greater amounts of grassland and upland shrubland. The amount of

wetland shrubland and upland shrubland at stand (i.e., <500 m) and landscape-level (i.e., 1,000 m) scales was positively associated with juvenile survival rate. My methods demonstrate that the effects of management actions depend on the context of the surrounding landscape mosaic and may be useful for informing local management strategies. Finally, my results suggest that relationships between survival and specific land-cover types may change throughout the reproductive cycle in American Woodcock.

Key Words: juvenile survival, landscape composition, landscape structure, nest success, productivity surface, *Scolopax minor*.

INTRODUCTION

Productivity (i.e., juveniles raised to independence from adult care) is a crucial component of population dynamics and a key element in models of population growth. Estimating the effects of landscape variables on productivity is important for informing and implementing successful management plans. For example, a primary goal of land managers is to manipulate landscapes in a way that minimizes features comprising sink habitats or ecological traps to increase population growth rate (Leopold 1933, Battin 2004). Many models of bird species' population dynamics use estimates of density combined with estimates of nest success but fail to consider juvenile survival, which can result in estimates of population productivity that are at best incomplete and potentially misleading (Streby and Andersen 2011, Shipley et al. 2013). Including both nest and fledgling survival rate in predictive models of full-season productivity is important because the relationships among survival and landscape components may be stage-specific and/or change over time (Streby et al. 2014b). Additionally, many bird species require or select different cover types for rearing juveniles than for nesting (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2007, Streby and Andersen 2011).

Previous studies outline species-specific relationships between edge (Askins 1995, Benson et al. 2010), forest fragmentation (Robinson and Wilcove 1994, Faaborg et al. 1995, Bayne and Hobson 1997, Lloyd et al. 2005), and urban development (Ausprey and Rodewald 2011) and individual aspects of productivity such as nest success, juvenile survival rate, or observed population growth. Until recently (see Peterson et al. 2016), few studies attempted to model the relationships among landscape structure and

productivity across multiple life stages (Streby and Andersen 2011). Juvenile mortality and nest failure are primarily driven by predation in most avian systems (Martin 1993); thus, landscape composition may substantially influence the composition of the predator community, which may affect bird productivity (Hoover et al. 1995, Brawn and Robinson 1996, Chalfoun et al. 2002). Furthermore, predators may respond to landscape variation at different spatial scales than breeding birds and consequently, some aspects of the landscape may influence productivity more than others (Stephens et al. 2005). Therefore, consideration of the entire landscape is required to accurately predict productivity across a spatial extent relevant for population-level management.

American Woodcock (*Scolopax minor*; hereafter “woodcock”) are a migratory, upland-breeding shorebird game-species that breed in diverse forest cover types throughout the eastern U.S. and southeastern Canada. Woodcock populations have declined range-wide based on standardized breeding-ground surveys conducted since the mid-1960s (Seamans and Rau 2012). Additionally, juvenile/adult female ratios measured from wing-collection surveys of hunters imply declines in recruitment (Seamans and Rau 2016). These declines in apparent abundance and productivity are purportedly linked to habitat loss and alteration of landscapes critical to woodcock reproduction (Dwyer et al. 1988, Gregg 1984, Sauer and Bortner 1991, Kelley et al. 2008). In an attempt to stabilize and ultimately increase woodcock populations, efforts have been made to develop and apply regional Best Management Practices (hereafter BMPs; Kelley et al. 2008, Wildlife Management Institute 2010) across regional landscapes.

The implementation of woodcock BMPs is intended to increase the availability of high-quality habitat at a landscape scale (~200-800 ha), thus increasing woodcock population growth rates and population size. Specifically, woodcock BMPs call for creation or maintenance of young-forest cover through clear-cutting, timber harvest, shearing of brush and small trees, and prescribed burning to create patchy and diverse forests (Wildlife Management Institute 2009). The application of woodcock BMPs on a stand- or landscape-scale aims to create a mosaic of diverse forest cover types including young regenerating forested areas for breeding, nesting, brood-rearing, and diurnal feeding habitat for woodcock. Additionally, woodcock BMPs call for the maintenance or creation of open grassy or cleared areas used for courtship displays and nocturnal foraging (Wildlife Management Institute 2009). Woodcock populations are known to respond numerically to vegetation management (Dwyer et al. 1988, McAuley et al. 1996) and previous research suggests microhabitat structure and composition have small, or nonexistent effects on the survival of woodcock nests and juveniles (Daly 2014); however, the influence of large-scale landscape components and their configuration on woodcock productivity is largely unknown.

Herein, I used the methods outlined by Peterson et al. (2016) to assess relationships between landscape structure and composition and productivity of woodcock breeding in northwestern Minnesota to predict full-season productivity at a landscape scale. I used landscape structure and composition to create spatially explicit models of full-season productivity and predicted full-season productivity over the landscape of my study area. These models combine estimates of nest survival rate and juvenile survival

rate, each as a function of landscape structure and composition to predict productivity. Finally, I investigated whether common management strategies for woodcock are effective in increasing productivity.

METHODS

Study Area

I relied on data from a study of woodcock population ecology (Daly 2014) at Tamarac National Wildlife Refuge (NWR), Becker County, Minnesota, USA (47.0°N, 95.6°W) from 2011-2012. Tamarac NWR encompassed >17,000 ha dominated by forested cover types with interspersed lakes, rivers, marshes, swamps, and tallgrass prairie. Tamarac NWR falls in the transition zone between three major biomes: the northern boreal forest, eastern hardwood forest, and western tallgrass prairie. Forests covered 60% of Tamarac NWR and dominant tree species included aspen (*Populus* spp.), jack pine (*Pinus banksiana*), red pine (*P. resinosa*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), red oak (*Quercus rubra*), white oak (*Q. alba*), sugar maple (*Acer saccharum*), and basswood (*Tilia americana*). Portions of the refuge were harvested (i.e., logged) and burned to create and maintain early successional forest and provide breeding, nesting, and brood-rearing habitat for woodcock and associated species.

Demographic Data Collection

Nest and survival data were derived from adult female and juvenile woodcock captured and marked from April-June during 2011-2012 (Daly 2014). Daly (2014)

captured adult female woodcock using mistnets and attached radio-transmitters using a glue-on backpack-style harness ($\leq 3\%$ of their total body mass; ~ 4.8 g, model A5410, Advanced Telemetry Systems, Isanti, MN; McAuley et al. 1993a, 1993b). Radio-marked female woodcock were tracked to nests and nest locations were recorded using handheld Global Positioning System (GPS) units (GPSMAP 76 or eTrex Venture HC Global Positioning System, Garmin Ltd., Schaffhausen, Switzerland), averaging 100 points to ensure <5 m accuracy. Nests were monitored at 2-3 day intervals until they failed (i.e., depredation or abandonment) or succeeded (i.e., evidence that ≥ 1 egg hatched; see Daly [2014] for detailed descriptions of nest-fate determination). I derived estimates of juvenile survival rate (i.e., post-hatching, pre-fledged young) based on the status of juveniles in broods of radio-marked adult females and from data resulting from radiomarking and tracking a subset of juveniles within the broods of radio-marked females. Daly (2014) also found broods of unmarked adult female woodcock using trained pointing dogs and captured and radio-marked juveniles in these broods. Juvenile woodcock were outfitted with a custom-fit micro-transmitter (BD-2NC or BD-2C, Holohil Systems Std., Carp, ON; Blackburn Transmitters, Nacodoches, TX) using an elastic collar that expanded as juvenile woodcock grew. Daly et al. (2015) did not detect an effect of transmitters on the survival of juvenile woodcock in their study, and all transmitter and harness packages were $\leq 3\%$ of the marked individual's mass. Daly (2014) randomly selected 1-4 juveniles per brood to which were attached radio-transmitters and were subsequently monitored to evaluate survival of both marked and unmarked juveniles within the same brood. Daly (2014) tracked broods 4-7 days per

week by tracking either radio-marked adult females or juveniles and noted status (i.e., alive or dead) of juveniles and counted both marked and unmarked juveniles to document brood size.

Landscape Attributes

Following the methods and definitions of Peterson (2014) and Peterson et al. (2016), I categorized six cover types at Tamarac NWR using 1-m resolution digital aerial photographs (2009; Minnesota Department of Natural Resources) in Arc 10.1 Geographic Information System (GIS) software (Environmental Systems Research Institute, Redlands, CA). I confirmed the cover types I classified from aerial photographs using >2,500 locations visited at my study sites. I chose to generally classify cover types into five broad categories (deciduous forest, upland shrubland, forested wetland, grassland, and wetland shrubland) based primarily on vegetation structure that I believed influenced the predator community most likely to depredate woodcock nests and juveniles (e.g., mesopredator mammals and raptors). I defined “mature forest” as stands with canopies >20 m and average canopy closure >60% (Brohman and Bryant 2005). Most mature stands in my study area contained a patchy and dense shrub layer (vegetation <2 m tall) and understory (vegetation between 2 m and ~15 m tall) of a variety of species.

I classified areas dominated by vegetation from 1 – 3 m tall as “shrublands”. In my study area, these stands ranged from 5 – 15 years post-harvest, were 1 – 30 ha in extent, and were composed of shrubs, forbs, grasses and patches of saplings. I differentiated between wetland and upland shrublands in my study because previous research in the same system found that wetland and upland shrublands affected Golden-

winged Warbler (*Vermivora chrysoptera*) productivity differently (Peterson 2014, Peterson et al. 2016). Wetland shrublands were similar in structure to upland shrublands, but were dominated by willow (*Salix* spp.), alder (*Alnus* spp.), sedges, grasses, and hazel (*Corylus* spp.) shrubs. I classified less common cover types including “forested wetlands” of tamarack (*Larix laricina*) or black ash (*Fraxinus nigra*), “grasslands” (without differentiating between wetland or upland), and roads and other small areas of human occupation (e.g., houses, buildings, lawns). Tamarac NWR had open water (i.e., lakes and rivers) that I did not consider as an important cover type for breeding woodcock in my study.

I investigated the importance of an additional component for edge density (i.e., length of edge within a specified area) by identifying edges between mature forest (i.e., deciduous forest and forested wetland) and shrubland (i.e., upland shrubland and wetland shrubland) as the edges between these cover types are reported to be important to woodcock and edges are known to influence avian nest survival (Rudnický et al. 1993, Manolis et al. 2002 et al. 2002, Meunier et al. 2006) and juvenile survival (Peterson et al. 2016). As a result, I investigated six landscape components as potential variables in my models predicting the relationship between each landscape component and nest survival rate and juvenile survival rate using >600 exposure days for each period (Table 1).

I explored the relationship between cover type and survival at different spatial scales by modeling the impact radius for each of the six model covariates described above following the methods described in Peterson (2014) and Peterson et al. (2016). The impact radius allowed me to identify the scale at which each landscape variable was most

strongly associated with survival of nests and juveniles. I determined the impact radius for each landscape variable by buffering each nest location with circles with different radii (Figure 1). I used the landscape composition and configuration surrounding nests to inform my models of both nest survival and juvenile survival because adaptive nest-site selection (i.e., selection of nest sites that maximize full-season productivity) needs to account for survival during both the nesting stage and the juvenile stage (Refsnider and Janzen 2010, Streby et al. 2014a). I explored the relationships between cover types and nest survival at radii of 25, 50, 100, 250, and 500 m. I tested larger radii (i.e., 100, 250, 500, 750, and 1,000 m) in my exploration of factors influencing juvenile survival to account for the mobility of juveniles during this stage (K. Daly and D. Andersen, unpubl. data).

I summed the total area (ha) for each cover type and the total linear distance of edge (km) contained within each buffer zone around each nest location and modeled the relationships between landscape variables and survival at each scale (i.e., impact radii). I constructed linear models and explored potential nonlinear (i.e., quadratic, and cubic) relationships between landscape components and survival using a logistic exposure function (Shaffer 2004) and the “glm” function in the “lme4” package in R (R Core Team 2016). I did not attempt to predict what relationships might occur between cover type and survival at this stage of analysis but instead used this exercise to identify the general scale at which each landscape component most strongly related to survival during nesting and juvenile stages. I ranked models of nest survival rate and juvenile survival rate using Akaike’s Information Criterion corrected for small sample size (AIC_c ; Burnham and

Anderson 2002). I used a combination of AIC_c rankings, the consistency of model rankings (i.e., whether stand- or landscape-scale radii [>250 m] consistently outperformed micro-scale radii and vice versa), and biologically informed predictions to select statistically and biologically meaningful cover types and impact radii to include as covariates in productivity models (Appendix C; Peterson 2014, Peterson et al. 2016).

Following the selection of model covariates, I built logistic exposure survival rate models (Shaffer 2004) for each potential combination of important landscape components at their determined impact radius. I applied these models to each pixel on my digitized landscape such that the survival at any pixel was informed by the specific landscape composition and configuration within the previously determined impact radii specific to each landscape component. Following the methods of Peterson (2014) and Peterson et al. (2016), I estimated daily survival rate (S) within each period for each observed combination of landscape structure and composition (i) and survival period (p) as:

$$S_{ip} = \exp(\alpha_{ip} + \beta_{1ip}x_{1ip} + \beta_{2ip}x_{2ip} + \beta_{3ip}x_{3ip} \dots) / (1 + \exp(\alpha_{ip} + \beta_{1ip}x_{1ip} + \beta_{2ip}x_{2ip} + \beta_{3ip}x_{3ip} \dots))$$

where α is the estimated intercept and β_i is the estimated coefficient for the landscape variable x_i .

To estimate survival rate over the entire period (i.e., nest success and juvenile survival) I raised my daily survival rate estimate to a power equal to the number of days in the period (i.e., 25 days for the nesting period, 15 days for the juvenile period). I applied this logistic exposure survival rate equation to the landscape for each survival period (i.e., nest, juvenile; [p]) based on the surrounding landscape composition and

structure (i). At each pixel on the landscape, I used the amount of each landscape variable surrounding that pixel at the predetermined impact radius and the β -coefficients for the logistic exposure survival rate equations for the appropriate landscape model to predict nest success (i.e., survival from laying to hatching) and juvenile survival rate (i.e., from hatch day to day 15) of woodcock.

I predicted nest productivity (i.e., number of juveniles hatching; NP) given the assumed ability for one re-nesting attempt (i.e., one additional nesting attempt following previous nest failure; McAuley et al. 1990), using a mean hatched brood of four juveniles,

$$NP = (NS + (1 - NS) * NS) * 4$$

where NS is nest success. I calculated full-season productivity (i.e., the number of young raised to day 15; FSP) as,

$$FSP = NP * JS$$

where JS is juvenile survival rate (from hatch day to day 15). I applied these equations to my digitized landscape and produced landscapes containing values for NP, JS, and FSP of theoretical woodcock nests placed within each pixel (1 m²) of my study area. I used these models to identify areas of high and low productivity on my landscape and predict the effects of management actions on the full-season productivity of woodcock breeding at Tamarac NWR. These types of models have been shown to be better at predicting productivity than null models for Golden-winged Warblers breeding at Tamarac NWR (Peterson 2014, Peterson et al. 2016). Like all statistical models of complex biological processes, my models should be interpreted considering their limitations and be validated

and augmented with demographic data collected in future field studies of woodcock in the same, and other portions of the breeding distribution. My relatively small sample sizes and relatively data-driven method of arriving at final models prevented me from reasonably subsetting my data as required for the k -fold cross-validation techniques used by others to test these and similar models (Boyce et al. 2002, Peterson 2014, Peterson et al. 2016). However, for the purposes of my study, these models provide a means of evaluating relative productivity across my study area.

Application of Spatially-Explicit Models of Full-Season Productivity

I simulated the effects of three realistic land-cover management scenarios on the full -season productivity of woodcock at Tamarac NWR to investigate the relationships among cover types and period-specific survival rate and resulting full-season productivity. Within ArcGIS, I applied hypothetical management on landscapes within my study area to illustrate (1) the effect of grassland succession into upland and wetland shrubland, (2) the effects of creating a ~16 ha (i.e., 40-acre) upland shrubland clear-cut surrounded by mature forest, and (3) the effects of succession without further management or disturbance on a heterogeneous landscape containing patches of shrubland, grassland, and mature forest. I constrained my models to areas I expected woodcock might use for nesting based on field observations of woodcock nest locations. Thus, I considered roads, open water, grassland, and any cover types >300 m from upland or wetland shrubland to be areas unused by woodcock and omitted those areas from my analysis. My assessment of used and unused nesting areas is not biased by searching methods because I identified nest locations by tracking radio-marked females, which

minimizes potential bias from standard nest searching methods (Powell et al. 2005, Peterson et al. 2015). I averaged each pixel in my productivity surface with all pixels within a 25-m radius to smooth visualizations of landscape productivity.

I selected three distinct areas of my study site to test the effects of simulated management on the productivity of woodcock. First, I evaluated the change in productivity following the conversion of non-nesting habitat (grassland) into upland shrubland and wetland shrubland. This scenario investigated the relative productivity of woodcock in upland and wetland shrubland cover types while controlling for the surrounding landscape structure and composition. I included woodcock nests in both upland and wetland shrublands, but Daly (2014) did not find any woodcock nests in grasslands. The effects of grassland on nest and juvenile productivity of woodcock is not well understood although grasslands are purported to be a crucial landscape component for breeding woodcock as males use open areas to display and attract females. I used ArcGIS 10.1 to simulate the succession of a grassland into upland shrubland and wetland shrubland within the same surrounding landscape. I investigated the difference between productivity in wetland and upland shrubland cover types by averaging productivity across all potential nesting sites in the study area. I also accounted for the change in available nesting cover types by multiplying the area available for nesting in each scenario by the mean productivity of the area as the succession of grassland to shrubland increases the area available to woodcock for nesting.

Second, I investigated the effects of clear-cutting a section of extensive, mature forest to create a 16-ha (40 acre) patch of upland shrubland surrounded by mature forest.

Woodcock in my study area nested in mature forest up to 300 m from the nearest substantial edge or distinct cover type; however, woodcock tend to nest more densely in more heterogeneous landscapes containing shrublands (Daly 2014). I compared the productivity of the each surface (pre-simulated management and post-simulated management) directly (i.e., not accounting for changes in nesting density following the creation of shrubland cover) and also compared productivity assuming the creation of shrubland cover resulted in an increase in suitable nesting area for woodcock.

Finally, I investigated how productivity of a heterogeneous landscape changes over time by simulating succession of all cover types (i.e., grassland to shrubland, shrubland to mature forest) in the absence of further disturbance or the maintenance of disturbed areas. I chose an area with a patchy and irregular distribution of diverse cover types that reasonably represented a non-managed landscape. I accounted for changes in the amount of nesting cover types as in my first simulation by multiplying the mean productivity by the amount of pixels in appropriate nesting cover types for each landscape.

RESULTS

Daly (2014) monitored 48 nests and 90 juveniles at Tamarac NWR from 2011-2012. Of the 48 nests and 90 juveniles monitored, 21 nests (44%) and 25 juveniles (28%) were depredated. I created 14 logistic exposure models (Table 2, Appendix D) predicting survival rate across two periods (nesting and juvenile survival from hatching to day 15). My spatially-explicit models explained more variation in full-season productivity (nest

survival, ΔAIC_c from null = -4.69; juvenile survival, ΔAIC_c from null = -9.66; Figure 2, Appendix D) than the null (i.e., intercept-only) models. Nest survival rate was negatively correlated with juvenile survival rate ($r = -0.09$) and nest survival rate explained more variation in full-season productivity than juvenile survival rate ($R^2 = 0.67$ and $R^2 = 0.15$, respectively).

Simulation of Cover Type Management

Altering the landscape of my study area resulted in biologically significant changes in full-season productivity of woodcock. My simulations of converting a large grassland to upland and wetland shrubland increased the area available for nesting by 8% (4.5 ha). Converting grassland to upland shrubland increased the predicted full-season mean productivity (i.e., the mean number of juveniles surviving 15 days post-hatching from breeding attempts at a random pixel [1 m²]) by 128% from 0.59 juveniles/breeding female (SD = 0.23) to 1.35 juveniles/breeding female (SD = 0.28; Figure 2C). After accounting for the increase of available nesting cover, the estimated full-season productivity of the upland-shrubland landscape increased by 147%. When I simulated converting the grassland to wetland shrubland, the predicted mean full-season productivity increased by 190% from 0.59 juveniles/breeding female (SD = 0.23) to 1.71 juveniles/breeding female (SD = 0.54; Figure 2D). After accounting for the increase of appropriate nesting cover, the simulated conversion of grassland to wetland shrubland increased the productivity of woodcock on this landscape by 213%.

Following the simulated clear-cutting and subsequent succession of a 16-ha mature deciduous forest stand to upland shrubland, predicted mean full-season

productivity increased 52% from 0.88 juveniles/breeding female to 1.34 juveniles/breeding female (Figure 3). I assumed that woodcock would nest throughout the intact patch of mature forest prior to management in this simulation, and therefore my estimate of productivity is not dependent on the available amount of nesting cover type. Only ~10% of female woodcock Daly (2014) monitored nested in expansive stands of mature forest >200 m from other cover types. Therefore, if I assume only 10% of the unmanaged mature forest in my simulation (6.2 ha) was appropriate for nesting woodcock then the amount of available nesting habitat following clear-cutting increased by 90% and productivity of the landscape increased by 1,430%.

Finally, simulation of forest succession of a diverse and patchy forest matrix of upland shrubland, mature forest, and grassland resulted in an estimated 19% decline in woodcock full-season productivity from 1.01 juveniles/breeding female (SD = 0.56) to 0.81 juveniles/breeding female (SD = 0.23; Figure 4). When I accounted for the change in available nesting habitat following succession of grasslands to shrublands, and shrublands to mature forest, I found the area available for nesting on the landscape increased by 3.8% (3.5 ha) following management, which slightly mitigated declines in the productivity of the entire landscape that I estimated to be -16%.

DISCUSSION

I constructed spatially explicit models that I used to predict full-season productivity (i.e., number of juveniles surviving to 15 days after hatching) of American Woodcock across a diverse landscape in northwestern Minnesota, following the methods outlined by

Peterson (2014) and Peterson et al.(2016). My models related structural and composition characteristics of cover types across a varied and complex landscape to survival of woodcock nests and juveniles. These models allow for identification of areas of high- and low-production and the simulation of effects of potential management scenarios across this and similar landscapes. Because the results of any management action are dependent on the existing landscape mosaic, these models do not provide generalized rules for managers, but instead offer a tool to (1) assess the predicted, spatially explicit productivity of existing landscapes to aid in determining whether management is warranted, (2) identify low-production areas (i.e., sinks), and (3) test different management scenarios to optimize the resulting productivity of the managed area given the unique abundance and distribution of site-specific landscape components.

Overall, my models generally corroborated the findings of other studies reporting no relationship between woodcock nests and the cover type or vegetation structure immediately surrounding the nest (e.g., McAuley et al. 1996). Daly (2014) reported no differences in stem density at woodcock nests over his two-year study period suggesting female woodcock selected nest-sites with similar micro-scale features regardless of the composition of the greater landscape. I found that composition and configuration of cover types influenced woodcock nest survival at the landscape-scale (i.e., within 500-m radius of the nest). Based on the observed nesting behaviors of woodcock in my study and the available evidence from this, and other portions of the species' range, woodcock appear to be capable of finding structurally similar nest sites with relatively low basal area (i.e., ~9 m²/ha) and high stem densities (i.e., >12,000 stems/ha) in a variety of landscape

contexts (e.g., mature forest, upland shrubland, wetland shrubland; McAuley et al. 1996, Daly 2014). If female woodcock tend to choose sites with similar micro-scale characteristics, it is logical that the greater surrounding landscape (and predator community associated with that landscape) may be more likely to influence the survival of nests and juveniles and females may select nest sites that are nearer to cover types and landscape components that confer greater juvenile survival rates (Streby et al. 2014a).

I did not account for weather variables in my models although other studies suggest links between inclement weather and the timing of nest initiation (Roboski and Causey 1981, Dwyer et al. 1988, Whiting 2006), precipitation and survival of juvenile woodcock (Sheldon 1971, Owen 1977, Daly et al. 2015), weather-related stress and juvenile woodcock growth rates (Rabe et al. 2003), and overall woodcock recruitment (Sepik et al. 2000). Weather may influence reproductive success of woodcock, especially at northern breeding latitudes or relatively high elevations (McAuley et al. 2010, Daly 2014), but my primary goal was determining the effects of different landscape compositions and configurations on the full-season productivity of woodcock at my site. Determining the proximate cause of death (e.g., predation versus exposure and subsequent consumption by a predator) was challenging for radio-marked juveniles in Daly's (2014) study; therefore, it is unclear how weather and predation may have interacted to influence juvenile survival rate. Additionally, some land cover types may be more or less suitable to woodcock during inclement weather events and my models may include some effect of the interaction between weather and cover type. Fruitful future research may be to continue to investigate the effects of weather on populations of

woodcock with long-term telemetry studies as changes in climate and weather patterns may lead to more precipitation and severe weather especially during the spring when woodcock nest (International Panel on Climate Change 2014).

Overall, my models and predictions of full-season productivity generally align with the BMPs developed for woodcock in the upper Great Lakes region (Wildlife Management Institute 2010). The BMPs for the upper Great Lakes region recommend a landscape-level approach to managing woodcock in stands 200-400 ha. The impact radii of my models reflect this landscape scale (a 500-m impact radius includes ~78.5 ha) and therefore could be useful for predicting the effects of management prior to its implementation and planning the most effective management strategy for unique landscapes. The woodcock BMPs also call for management units centered around shrubby or forested wetlands with surrounding upland shrubland (Wildlife Management Institute 2010). My models generally suggest these wetlands may confer greater full-season productivity by increasing juvenile survival rate in woodcock nesting within 250 m of these wetlands. The BMPs call for the creation of roosting fields and singing grounds (i.e., grasslands) that amount to $\leq 20\%$ of the overall landscape. My models demonstrated a negative relationship between grassland and survival rate of woodcock nests and therefore, an upper limit closer to 5% of the landscape (e.g., 2 ha for every 40 ha managed) might lead to greater nest productivity in the population I modeled. To maintain a diverse landscape, the BMPs call for a 40-year rotation (depending on soil type and regeneration rates) of stands such that 25% of the landscape is comprised of forest in each of four age classes: 0-10, 11-20, 21-30, and 31-40 years post-harvest. As

such, my models may be used to assess the geometry and configuration of managed stands through time to ensure that rotated stands continue to provide landscapes associated with high woodcock productivity.

Importantly, the upper Great Lakes region BMPs call for the management of mixed-aged landscapes and suggest that woodcock management may benefit a suite of other associated species. This claim remains untested, a fact recognized by the Wildlife Management Institute (2009:3), which states that “each management practice will not benefit all species equally, and some practices may produce conflicting outcomes”, or more simply, management that benefits one species may harm another species. Further research is needed to determine the effects of woodcock management on associated species (e.g., Golden-winged Warblers; Peterson et al. 2016).

My models are informed by data collected over two years and thus additional data would likely be necessary to validate and improve my models. Data from additional years would likely help account for variation in woodcock survival and reproduction and improve the predictions of my models. However, even in the absence of nest and juvenile survival data from additional years, my models provide a useful tool that may help implement and guide management for woodcock in northern Minnesota and similar landscapes in the upper Great Lakes region. My models could also form the basis of productivity models for other portions of the woodcock breeding distribution with woodcock-cover type relations different than those I observed. Comparing models of full-season productivity of woodcock from other portions of their breeding distribution may also provide information on population-specific cover-type relationships and aid in

improving and implementing management strategies tailored for individual woodcock populations.

Table 1. Scale and polynomial function of landscape-scale variables used in predicting productivity for two survival periods in American Woodcock monitored at Tamarac NWR, Minnesota. Variables that were not included in both survival periods are indicated by “N/A”.

Landscape Variable	Nest Survival (<i>n</i> =48 nests; <i>n</i> =630 exposure days)		Juvenile Survival (Day 1-15) (<i>n</i> =90 individuals; <i>n</i> =1,014 exposure days)		Relationship with survival
	Scale (m)	Polynomial function	Scale (m)	Polynomial function	
Mature Forest	500	Linear	500	Linear	Mature forest is the most common cover type present on the landscape in northern Minnesota. Mature forest is purported to be used infrequently by American Woodcock (Kelly et al. 2008) and long-term succession of young forests without additional disturbance or management is thought to be a cause of declines in woodcock populations. I included mature forest as a model covariate in both nest survival rate and juvenile survival rate models because some birds nested within mature forest and the amount of mature forest on the landscape may influence the predator community and the survival of nests

					and juveniles.
Grassland	500	Linear	N/A	N/A	Grassland is reportedly important to woodcock for display and mating. I included grassland in models of nest survival rate because grassland is relatively uncommon on the landscape and may be associated with different predator communities resulting in tradeoffs between nesting near grassland and survival as observed in other young-forest species (Peterson et al. 2016).
Upland shrubland	500	Linear	1,000	Linear	I included upland shrubland in my models as American woodcock are believed to be a young-forest specialist species and most management plans call for the creation of more upland shrubland to increase productivity and abundance.
Wetland shrubland	N/A	N/A	250	Linear	Wetland shrubland is structurally similar to upland shrubland, but may have different predator populations and a differential effect on survival in juvenile woodcock. Although woodcock rarely nest in wetland shrublands, they often nest nearby and proximity may be important to the

survival of juvenile woodcock as wet
areas are often associated with diurnal
feeding areas in adult woodcock.

Table 2. AIC_c rankings of composite models used to predict survival rate of American Woodcock during the nesting and juvenile periods. I used specific models reflecting the landscape surrounding a given pixel (1 m²) at the impact radius of each important landscape factor to predict survival rate during each period. See Table 1 for detailed information on parameter selection and determination of impact radii. Null models contained only estimates of the intercept.

Nest Survival Rate Models		
Model	ΔAIC_c	K
Upland Shrubland 500 + Grassland 500 ^a	0.00	3
Mature Forest 500 + Upland Shrubland 500 + Grassland 500	0.70	4
Grassland 500	1.59	2
Mature Forest 500 + Grassland 500	3.37	3
Upland Shrubland 500	4.21	2
Mature Forest 500	4.89	2
Null	5.34	1
Mature Forest 500 + Upland Shrubland 500	5.86	3
Juvenile Survival Rate Models		
Model	ΔAIC_c	K
Upland Shrubland 1000 + Wetland Shrubland 250 ^b	0.00	3
Mature Forest 500 + Upland Shrubland 1000 + Wetland Shrubland 250	2.00	4

Wetland Shrubland 250	8.46	2
Mature Forest 500 + Wetland Shrubland 250	9.20	3
Mature Forest 500 + Upland Shrubland 1000	10.29	3
Upland Shrubland 1000	10.47	2
Mature Forest 500	10.66	2
Null	11.66	1

^a Top model AIC_c was 146.11.

^b Top model AIC_c was 176.81.

Figure 1. Example of digitized landscape (A) derived from satellite imagery (B). An American Woodcock nest is located near the center of all images and denoted by a black triangle. Panels C-H demonstrate the process of isolating and quantifying the amount of landscape variables at different impact radii surrounding nests. In this example, I investigated the amount of mature forest (C), forested wetland (D), wetland shrubland (E), grassland (F), shrubby edge (G), and upland shrubland (H) within 500 m of a nest. I extracted the area of each of these cover types at different radii and use generalized linear models to determine if one impact radius best explained juvenile and nest survival rate for each cover type.

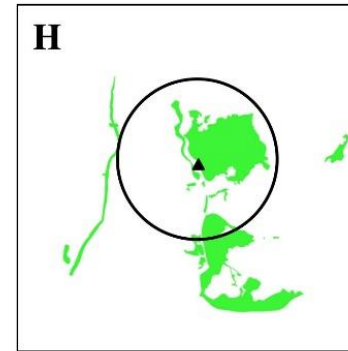
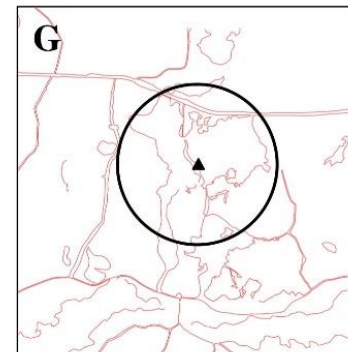
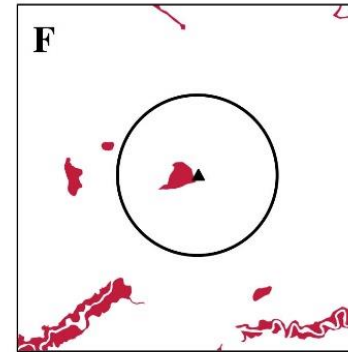
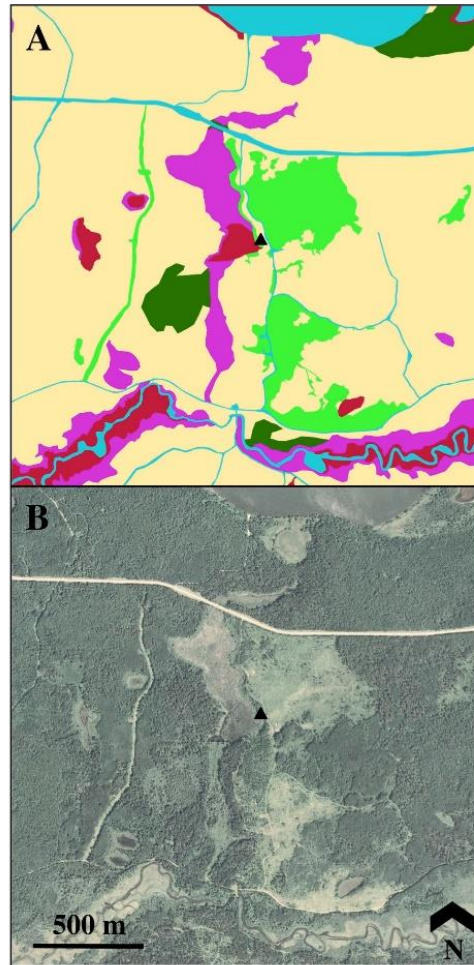
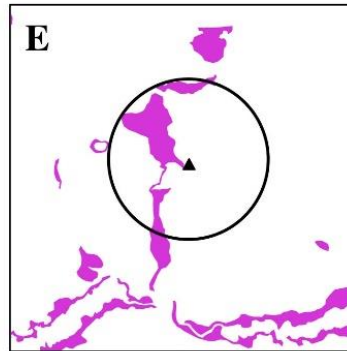
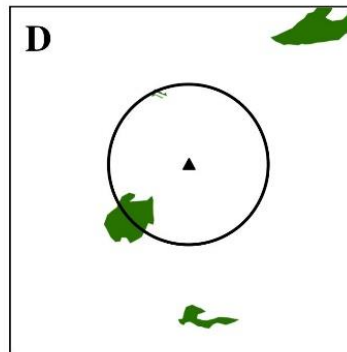
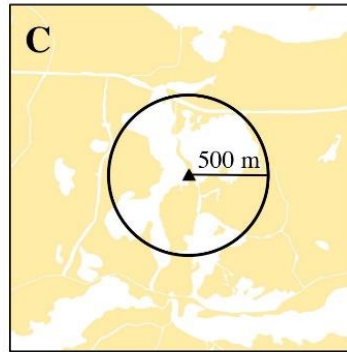


Figure 2. Predicted versus observed full-season productivity (i.e., number of juveniles surviving to day 15) of American Woodcock at Tamarac National Wildlife Refuge, Minnesota, USA. Slope of regression line is significantly different from zero ($\bar{x} = 0.96$, $t = 3.44$, $P = 0.001$).

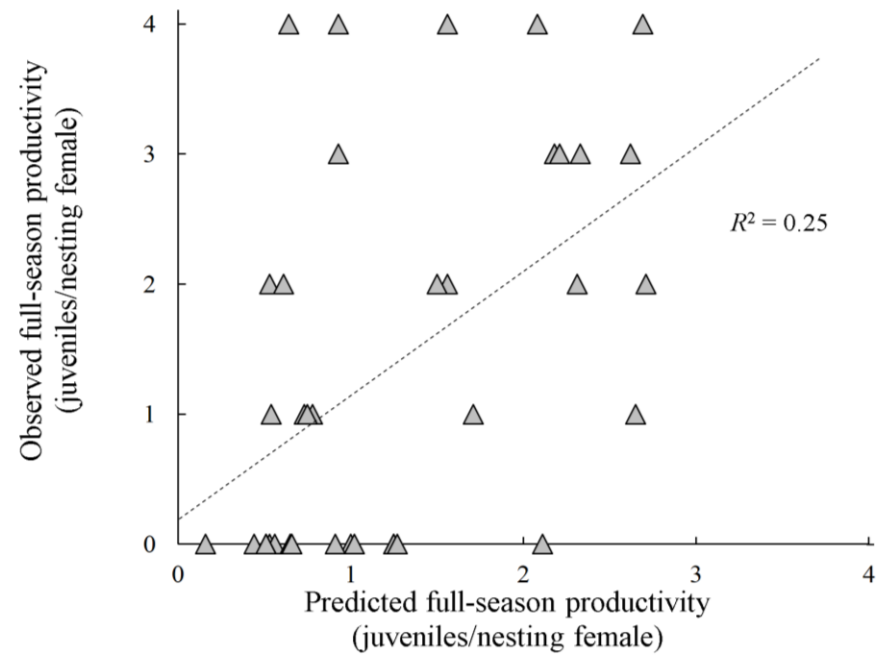


Figure 3. Aerial photograph (A) of a portion of Tamarac National Wildlife Refuge, Minnesota with a mix of cover types. Upland shrubland is delineated by hatched lines and grassland is marked with a thick gray border. Panel (B) shows the predicted full-season productivity (i.e., number of juveniles produced reaching 15-days of age) of the landscape in (A) with cooler colors representing lower productivity and warmer colors representing higher productivity. Panel (C) shows the full-season productivity of the landscape if the main grassland area at the center of the map is replaced with upland shrubland. Panel (D) shows the predicted full-season productivity of the same landscape if the grassland area at the center of the map is transformed into wetland shrubland. See main text for definition of land cover types.

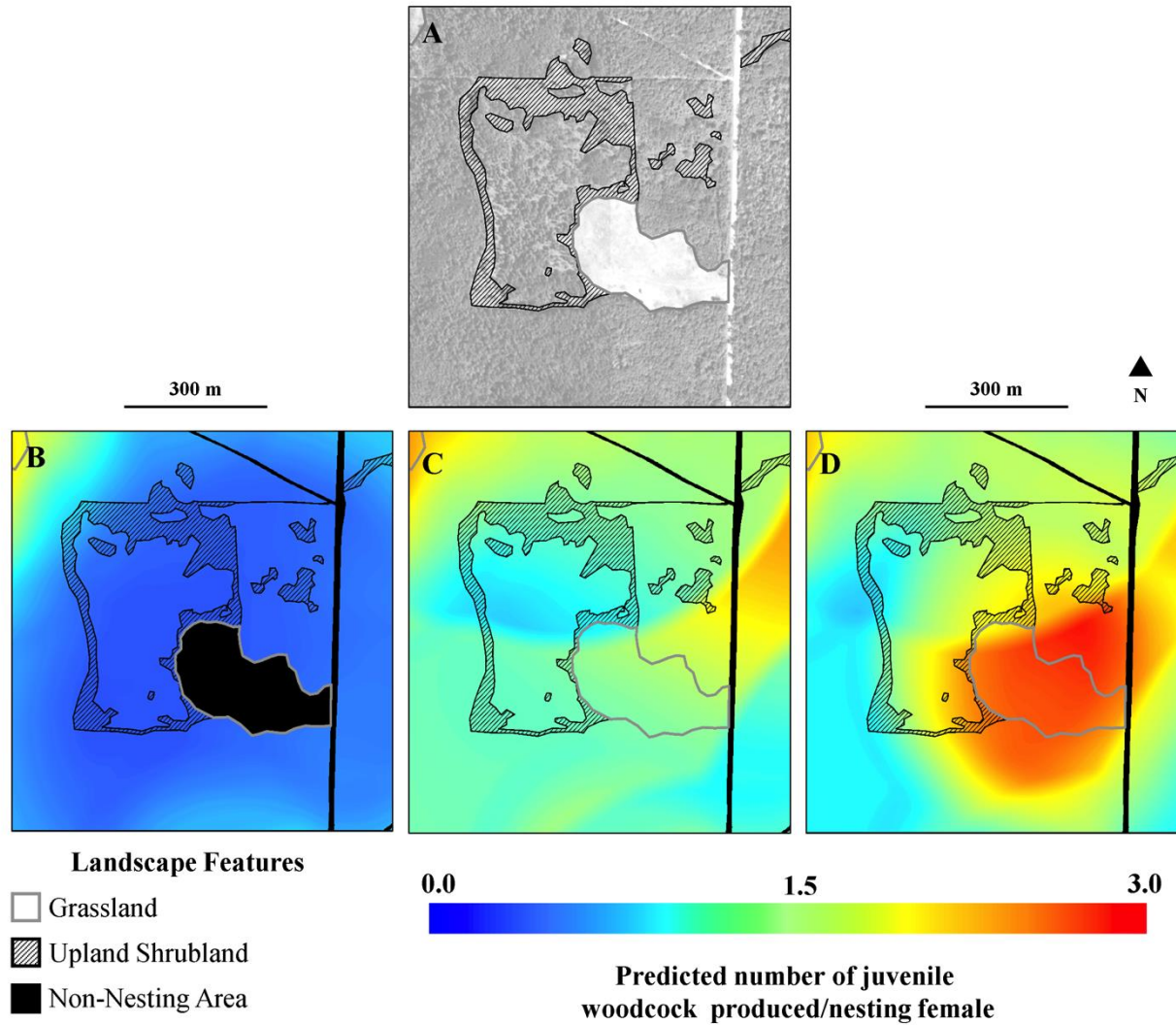


Figure 4. Aerial photograph (A) of a portion of Tamarac National Wildlife Refuge, Minnesota composed primarily of mature forest with several small patches of upland shrubland (hatched lines). Panel (B) shows the predicted full-season productivity (i.e., number of juveniles produced reaching 15-days of age) of the landscape in (A) with cooler colors representing lower productivity and warmer colors representing higher productivity. Panel (C) displays the predicted full-season productivity following the simulated clearcutting of a 16.2-ha (40 acre) patch of mature forest and upland shrubland resulting in only upland shrubland in the clearcut area. See main text for definition of land cover types.

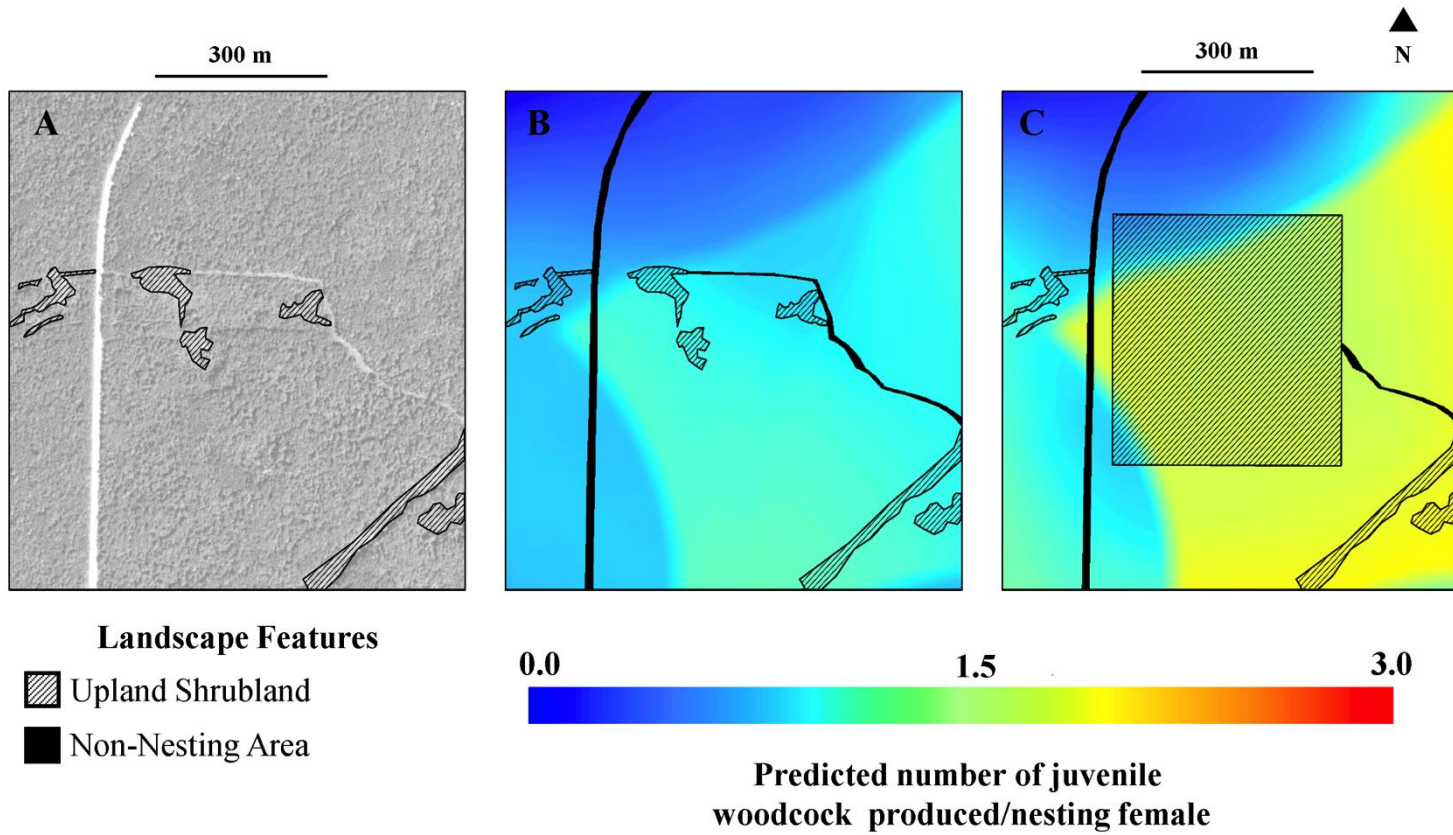
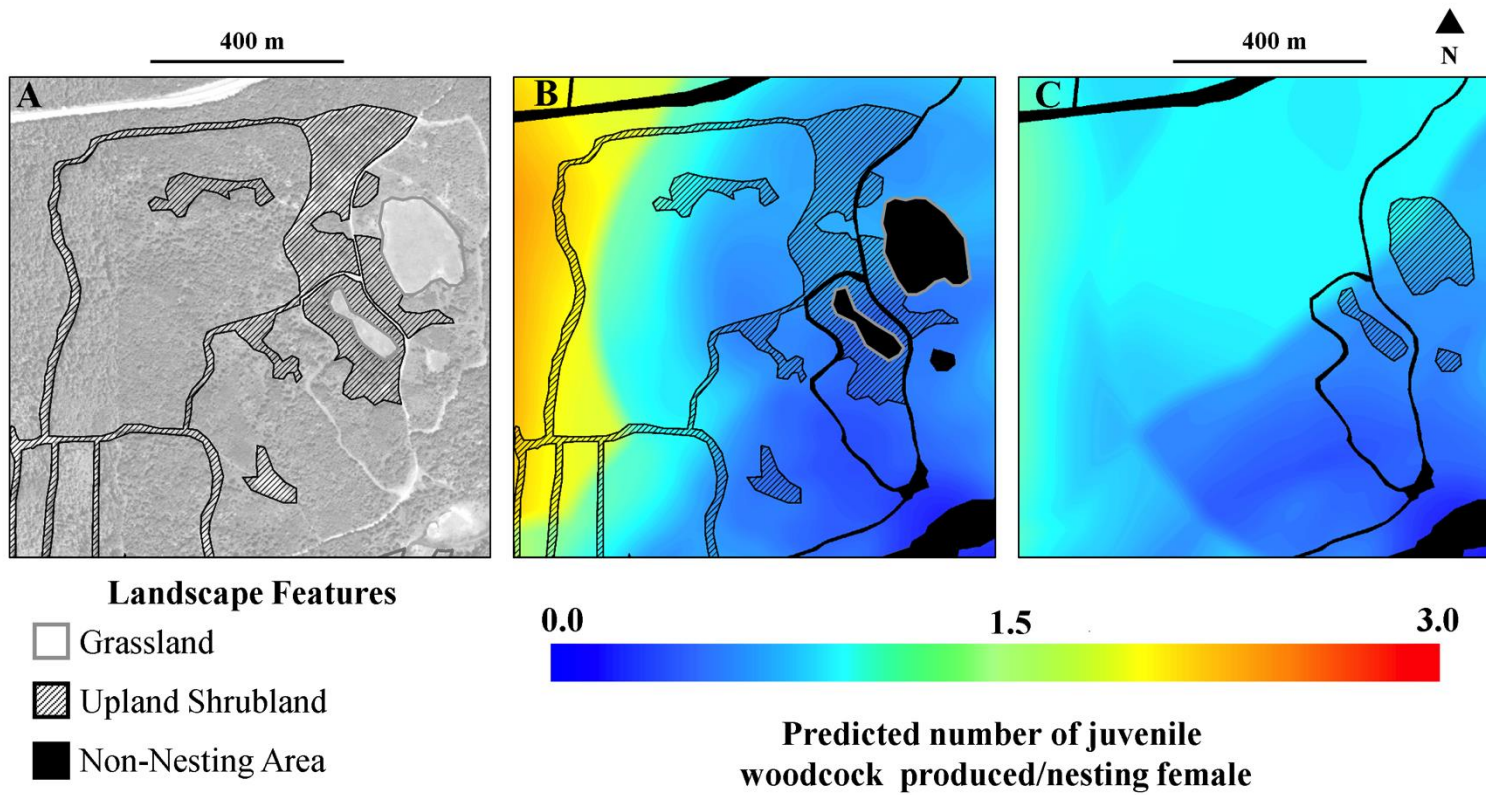


Figure 5. Aerial photograph (A) of a portion of Tamarac National Wildlife Refuge, Minnesota composed of a variety of land cover types with a complex and varied configuration. Upland shrubland (hatched lines) is present in large patches, and also small linear firebreaks. Grassland (solid gray lines) is also present on the landscape. Panel (B) shows the predicted full-season productivity (i.e., number of juveniles produced reaching 15-days of age) of the landscape in (A) with cooler colors representing lower productivity and warmer colors representing higher productivity. Panel (C) displays the predicted full-season productivity following the simulated succession of the landscape without any additional disturbance and/or management. In this scenario, I simulated upland shrubland succeeding to mature forest, and grassland succeeding to upland shrubland. See text for detailed description of land cover types.



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Appendix A. Summary of points used to calculate mean estimated location of male Golden-winged Warblers during the nonbreeding period (with SD in parentheses). Points are transition-derived estimates of location calculated by multiplying the likelihood of five subsequent transitions with a given twilight and exporting the coordinates of the cell with the maximum likelihood. RL denotes individuals marked at Rice Lake National Wildlife Refuge, Minnesota, USA; DF denotes individuals marked at Delaware State Forest, Pennsylvania, USA; CM denotes individuals marked at North Cumberland Wildlife Management Area, Tennessee, USA. I averaged the latitude and longitude of transition-derived points from 1 November – 28 February falling within 250 km of the delineated nonbreeding distribution of Golden-winged Warblers to calculate a single nonbreeding site for each warbler.

ID	Points	Longitude	Latitude	Year
RL03 ^a	10	85.70°W (2.01)	13.48°N (2.66)	2013
RL05	116	85.73°W (1.77)	15.76°N (5.20)	2013
RL06	29	87.38°W (1.39)	17.72°N (3.13)	2013
RL11	141	85.48°W (0.94)	12.65°N (1.91)	2013
RL12	31	89.25°W (1.65)	18.92°N (2.56)	2013
RL14	5	83.88°W (2.17)	13.72°N (3.40)	2013
RL15	11	89.96°W (1.99)	16.92°N (2.80)	2013
RL16	65	85.25°W (2.15)	15.01°N (5.55)	2013
RL20	115	85.62°W (1.20)	14.31°N (4.56)	2013
RL25	80	84.51°W (1.75)	12.74°N (2.65)	2014

RL29	104	84.93°W (1.81)	13.27°N (5.08)	2014
RL36	97	89.43°W (0.83)	17.38°N (3.25)	2014
DF05	23	68.56°W (1.88)	8.36°N (2.61)	2014
DF11	3	63.08°W (1.90)	9.05°N (4.85)	2014
CM05	199	72.41°W (0.93)	10.17°N (1.97)	2013
CM06	80	73.22°W (0.89)	10.56°N (0.92)	2013
CM09	3	71.93°W (1.73)	8.55°N (2.61)	2013
CM10	37	71.84°W (1.82)	9.94°N (2.41)	2013
CM13 ^b	20	71.02°W (2.72)	9.05°N (1.75)	2013
CM16	92	71.75°W (1.01)	11.05°N (1.41)	2013
CM21 ^b	73	71.48°W (1.26)	10.63°N (2.26)	2014

^a Light sensor on geolocator was covered in mud upon recovery, selected period was apparently before mud caused errors in light collection

^b Same individual marked in subsequent years

Appendix B. Number of nonbreeding transitions (i.e., sunrises and sunsets) derived from light-level geolocator data used to calculate nonbreeding-site joint likelihood estimates for individual Golden-winged Warblers at three breeding sites across their breeding distribution. RL denotes individuals marked at Rice Lake National Wildlife Refuge, Minnesota, USA; DF denotes individuals marked at Delaware State Forest, Pennsylvania, USA; CM denotes individuals marked at North Cumberland Wildlife Management Area, Tennessee, USA. Transitions refer to the number of transition periods (sunrises and sunsets) used to create an individual's nonbreeding period probability density function (the probability that an individual bird was located at each possible location).

ID	Transitions	Date range	Year
RL03 ^{a,b}	28	14 Sep to 28 Sep	2013
RL05	114	1 Jan to 28 Feb	2013
RL06	107	1 Jan to 28 Feb	2013
RL11	115	1 Jan to 28 Feb	2013
RL12	110	1 Jan to 28 Feb	2013
RL14 ^b	103	1 Jan to 26 Feb	2013
RL15 ^b	20	27 Dec to 6 Jan	2013
RL16	112	1 Jan to 28 Feb	2013
RL20	116	1 Jan to 28 Feb	2013
RL25	116	1 Jan to 28 Feb	2014
RL29	115	1 Jan to 28 Feb	2014

RL36	117	1 Jan to 28 Feb	2014
DF05	111	1 Jan to 28 Feb	2014
DF11	117	1 Jan to 28 Feb	2014
CM05	117	1 Jan to 28 Feb	2013
CM06	116	1 Jan to 28 Feb	2013
CM09	115	1 Jan to 28 Feb	2013
CM10	117	1 Jan to 28 Feb	2013
CM13 ^c	110	1 Jan to 28 Feb	2013
CM16	115	1 Jan to 28 Feb	2013
CM21 ^c	116	1 Jan to 28 Feb	2014

^a Light sensor on geolocator was covered in mud upon recovery, selected period was apparently before mud caused errors in light collection

^b Geolocator stopped recording data prematurely

^c Same individual marked in subsequent years

Appendix C. AICc rankings of landscape variables at different scales and polynomial functions used to aid identification of impact radii of cover types for two survival periods (nest success, juvenile survival from day 1-15) of American Woodcock. Terms in bold were included in final survival models.

Nest Landscape Variables					
Forested Wetland					
Model	N	K	AIC	AICc	Delta AICc
Forested Wetland 500 ^a	630	2	149.128	149.175	0
Forested Wetland 500 ^{^2}	630	3	150.883	150.977	1.802
Forested Wetland 250 ^{^3}	630	4	151.130	151.287	2.112
Null Model	630	1	151.492	151.507	2.332
Grassland					
Model	N	K	AIC	AICc	Delta AICc
Grassland 500	630	2	147.653	147.700	0
Grassland 500 ^{^2}	630	3	149.647	149.741	2.041
Grassland 100 ^{^3}	630	4	150.222	150.222	2.522
Null Model	630	1	151.492	151.507	3.807
Mature Forest					
Model	N	K	AIC	AICc	Delta AICc
Mature Forest 500 ^{^3}	630	4	149.900	150.057	0
Mature Forest 500 ^{^2}	630	3	150.224	150.318	0.26
Mature Forest 500	630	2	150.931	150.978	0.92
Null Model	630	1	151.492	151.507	1.45
Shrubby Edge					
Model	N	K	AIC	AICc	Delta AICc
Shrubby Edge 100 ^{^3}	630	4	150.836	150.993	0
Shrubby Edge 500 ^{^3}	630	4	151.096	151.253	0.260
Null Model	630	1	151.492	151.507	0.514
Upland Shrub					
Model	N	K	AIC	AICc	Delta AICc
Upland Shrub 500 ^{^2}	630	3	149.159	149.253	0
Upland Shrub 50 ^{^2}	630	3	149.561	149.655	0.402
Upland Shrub 25 ^{^2}	630	3	149.728	149.822	0.569
Upland Shrub 500	630	2	150.273	150.320	1.067
Upland Shrub 100 ^{^2}	630	3	150.406	150.500	1.247
Upland Shrub 250 ^{^2}	630	3	150.877	150.971	1.718
Upland Shrub 500 ^{^3}	630	4	151.136	151.293	2.040
Upland Shrub 25	630	2	151.432	151.479	2.226
Null Model	630	1	151.492	151.507	2.254
Shrubby Wetland					

Model	N	K	AIC	AICc	Delta AICc
Shrubby Wetland 25 ³	630	4	150.751	150.908	0
Null Model	630	1	151.492	151.507	0.600

Juvenile Survival Landscape Variables

Forested Wetland

Model	N	K	AIC	AICc	Delta AICc
Forested Wetland 1000 ^a	1,014	2	188.198	188.221	0
Forested Wetland 750	1,014	2	188.240	188.263	0.042
Forested Wetland 500	1,014	2	188.363	188.386	0.165
Null Model	1,014	1	188.455	188.473	0.252

Grassland

Model	N	K	AIC	AICc	Delta AICc
Null Model	1,014	1	188.455	188.473	0

Mature Forest

Model	N	K	AIC	AICc	Delta AICc
Mature Forest 500	1,014	2	187.445	187.468	0
Null Model	1,014	1	188.455	188.473	1.005

Shrubby Edge

Model	N	K	AIC	AICc	Delta AICc
Null Model	1,014	1	188.455	188.473	0

Upland Shrubland

Model	N	K	AIC	AICc	Delta AICc
Upland Shrubland 1000	1,014	2	187.255	187.277	0
Upland Shrubland 750	1,014	2	187.406	187.429	0.152
Null Model	1,014	1	188.455	188.473	1.194

Wetland Shrubland

Model	N	K	AIC	AICc	Delta AICc
Wetland Shrubland 250	1,014	2	185.247	185.270	0
Wetland Shrubland 500	1,014	2	185.925	185.948	0.678
Wetland Shrubland 1000	1,014	2	187.298	187.321	2.051
Wetland Shrubland 100	1,014	2	188.221	188.244	2.974
Null Model	1,014	1	188.455	188.473	3.203

^a We did not include forested wetland as a parameter in our final models despite it outperforming the null model because it was relatively uncommon on the landscape and many nest sites did not contain any forested wetland within the impact radius and we wanted to limit the number of parameters in our models.

Appendix D. Parameter values for landscape variables for logistic exposure survival equations of landscape variables (Chapter 2, Table 1) for nest survival rates and juvenile survival rates of American Woodcock breeding at Tamarac National Wildlife Refuge, Minnesota. I selected one of these models for each pixel (i.e., potential nesting site) in my study area based on the landscape variables surrounding that pixel at the identified impact radii of the specific cover types.

Nest Survival Rate Models						
Null Model						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	3.3354	0.2242	2.9272	3.8026	221.41	<0.001
Mature Forest						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	3.0601	0.2510	2.6024	3.5790	148.67	<0.001
Mature Forest 500	0.1800	0.1142	0.0081	0.4607	2.35	0.125
Upland Shrubland						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	3.8118	0.3747	3.1365	4.6157	103.51	<0.001
Upland Shrubland 500	-0.0456	0.0251	-0.0945	0.0043	3.31	0.069
Mature Forest, Upland Shrubland						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	2.9769	1.3455	0.3720	5.7151	4.89	0.027
Mature Forest 500	0.0177	0.0280	-0.0357	0.0750	0.40	0.528
Upland Shrubland 500	-0.0326	0.0316	-0.0969	0.0284	1.06	0.304

Grassland						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	3.8792	0.3316	3.2622	4.5740	136.84	<0.001
Grassland 500	-0.1050	0.0386	-0.1810	-0.0218	7.40	0.006

Mature Forest, Grassland						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	3.2989	1.1727	1.0393	5.6570	7.91	0.005
Mature Forest 500	0.0128	0.0254	-0.0350	0.0644	0.26	0.612
Grassland 500	-0.0914	0.0463	-0.1846	0.0038	3.90	0.048

Upland Shrubland, Grassland						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	4.3849	0.4506	3.5608	5.3187	94.71	<0.001
Upland Shrubland 500	-0.0475	0.0248	-0.0955	0.0013	3.68	0.055
Grassland 500	-0.1076	0.0382	-0.1811	-0.0257	7.96	0.005

Mature Forest, Upland Shrubland, Grassland						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	6.5793	1.9954	2.8253	10.5843	10.87	<0.001
Mature Forest 500	-0.0409	0.0351	-0.1086	0.0287	1.36	0.244
Upland Shrubland 500	-0.0786	0.0377	-0.1537	-0.0076	4.34	0.037
Grassland 500	-0.1537	0.0569	-0.2658	-0.0427	7.30	0.007

Juvenile Survival Rate Day 1-15 Models

Null Model						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value

Intercept	3.6494	0.2022	3.2756	4.0734	325.80	<0.001
Mature Forest						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	4.7855	0.7037	3.4496	6.2232	46.24	<0.001
Mature Forest 500	-0.0287	0.0162	-0.0601	0.0037	3.13	0.077
Upland Shrubland						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	3.1066	0.3020	2.5587	3.7404	105.80	<0.001
Upland Shrubland 1000	0.0278	0.0136	0.0021	0.0555	4.22	0.040
Mature Forest, Upland Shrubland						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	4.0471	0.7635	2.6372	5.6314	28.10	<0.001
Mature Forest 500	-0.0228	0.0161	-0.0543	0.0089	2.002	0.160
Upland Shrubland 1000	0.0260	0.0143	-0.0013	0.0549	3.32	0.068
Wetland Shrubland						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	3.2938	0.2379	2.8524	3.7947	191.68	<0.001
Wetland Shrubland 250	0.2230	0.1118	0.0284	0.4754	3.980	0.046
Mature Forest, Wetland Shrubland						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	4.0756	0.7483	2.6734	5.6367	29.67	<0.001
Mature Forest 500	-0.0184	0.0162	-0.0505	0.0135	1.29	0.256
Wetland Shrubland 250	0.3413	0.1135	0.1361	0.5879	9.04	0.003
Upland Shrubland, Wetland Shrubland						

Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	2.0656	0.4207	1.2545	2.9144	24.11	<0.001
Upland Shrubland 1000	0.0538	0.0183	0.0207	0.0935	8.67	0.003
Wetland Shrubland 250	0.3413	0.1135	0.1361	0.5779	9.04	0.003
Mature Forest, Upland Shrubland, Wetland Shrubland						
Parameter	Estimate	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit	Wald Chi-square	P-value
Intercept	2.2015	0.8288	0.7266	3.9687	7.05	0.008
Mature Forest 500	-0.0028	0.0147	-0.0327	0.0248	0.04	0.847
Upland Shrubland 1000	0.0532	0.0187	0.0189	0.0932	8.15	0.004
Wetland Shrubland 250	0.3334	0.1198	0.1165	0.5945	7.7395	0.005