

# Spatially Explicit Models of Full-Season Productivity and Implications for Landscape Management of Golden-winged Warblers in the Western Great Lakes Region\*

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**Abstract.** The relationship between landscape structure and composition and full-season productivity (FSP) is poorly understood for most birds. For species of high conservation concern, insight into how productivity is related to landscape structure and composition can be used to develop more effective conservation strategies that increase recruitment. We monitored nest productivity and fledgling survival of Golden-winged Warblers (*Vermivora chrysoptera*), a species of high conservation concern, in managed forest landscapes at two sites in northern Minnesota, and one site in southeastern Manitoba, Canada from 2010 to 2012. We used logistic exposure models to identify the influence of landscape structure and composition on nest productivity and fledgling survival. We used the models to predict spatially explicit, FSP across our study sites to identify areas of low relative productivity that could be targeted for management. We then used our models of spatially explicit, FSP to simulate the impact of potential management actions on our study sites with the goal of increasing total population productivity. Unlike previous studies that suggested wetland cover types provide higher quality breeding habitat for Golden-winged Warblers, our models predicted 14% greater productivity in upland

cover types. Simulated succession of a 9-ha grassland patch to a shrubby upland suitable for nesting increased the total number of fledglings produced by that patch and adjacent upland shrublands by 30%, despite decreasing individual productivity by 13%. Further simulated succession of the same patch described above into deciduous forest reduced the total number of fledglings produced to independence on a landscape by 18% because of a decrease in the area available for nesting. Simulated reduction in the cumulative length of shrubby edge within a 50-m radius of any location in our landscapes from 0.6 to 0.3 km increased FSP by 5%. Our models demonstrated that the effects of any single management action depended on the context of the surrounding landscape. We conclude that spatially explicit, FSP models that incorporate data from both the nesting and postfledging periods are useful for informing breeding habitat management plans for Golden-winged Warblers and that similar models can benefit management planning for many other species of conservation concern.

**Key Words:** fledgling survival, landscape composition, landscape structure, nest success, productivity surface, songbird.

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Estimates of productivity are important for modeling population growth and identifying habitat features that affect productivity is important for informing management plans. For example, management directed at identification and elimination of habitat features that comprise ecological traps could increase population growth rate (Battin 2004). Most models of songbird population dynamics include estimates of nest success, but lack consideration of fledgling 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). It is important to include survival of both nests and fledglings in estimates of full-season productivity (FSP) because habitat characteristics can have different effects on different life stages (Streby et al. 2014), and many songbirds appear to have different habitat requirements for nesting than for rearing fledglings (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2007, Streby and Andersen 2011).

Previous studies have described the 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, Rush and Stutchbury 2008), deforestation (Askins et al. 1987), and urban encroachment (Ausprey and Rodewald 2011) and individual aspects of songbird productivity such as nest success, fledgling survival, or observed population growth. Comparatively few efforts have assessed the influence of landscape structure and composition to model productivity across multiple life stages, or simultaneously assessed both multiple landscape components and multiple life stages (Streby and Andersen 2011). In many landscapes, predation is a primary source of both nest failure (Martin 1993) and fledgling mortality (Chapter 8, this volume). Landscape composition can have substantial impact on the composition of the predator community and thus songbird productivity (Robinson 1992, Porneluzi et al. 1993, Hoover et al. 1995, Brawn and Robinson 1996, Chalfoun et al. 2002). Furthermore, predators may be using a landscape at a different spatial scale than breeding songbirds. As a consequence, some aspects of the landscape may influence productivity more than others (Stephens et al. 2005), and it is only when the entire landscape is considered that productivity can be assessed across a spatial extent relevant for management at the population level.

Golden-winged Warblers (*Vermivora chrysoptera*) are a species of conservation concern that nest in patches of upland shrubland or wetland shrubland within a

matrix of mature forest with a dense understory in the Appalachian Mountains, northeastern and north-central United States, and adjacent southern Canada (Confer et al. 2011). Relationships between Golden-winged Warbler breeding and landscape configuration are largely unknown, although Confer et al. (2010) observed significantly higher nest success in swamp forests in a Golden-winged Warbler population in New York, and suggested that populations using those cover types may act as sources for populations using upland cover types. Across much of the breeding distribution, however, declines in populations of Golden-winged Warblers have been attributed to loss of early successional upland forest stands and hybridization with the closely related Blue-winged Warbler (*Vermivora cyanoptera*; Buehler et al. 2007, Confer et al. 2011). Efforts to mitigate or reverse population declines have concentrated on forest management and the creation or maintenance of early successional upland forest stands (Huffman 1997, Roth and Lutz 2004, Kubel and Yahner 2008, Percy 2012) or wetland shrublands (Rossell et al. 2003, Rush and Post 2008, Confer et al. 2010). However, management strategies to date have been developed without a clear understanding of how landscape structure and composition influences FSP and how to best incorporate landscape effects into management plans.

To assess the relationship between landscape structure and composition and productivity, we studied three populations of Golden-winged Warblers in the western Great Lakes region of central North America and derived estimates of FSP at a landscape scale. We constructed spatially explicit models of FSP as a function of landscape structure and composition, and used our models to estimate FSP across our study areas. The resulting estimates of FSP combined estimates of nest success and fledgling survival, each as a function of landscape structure and composition to derive estimates of productivity across our study sites. We used spatially explicit estimates of FSP to evaluate the efficacy of potential management actions.

## METHODS

### Study Areas

We studied Golden-winged Warblers at Tamarac National Wildlife Refuge (NWR) in Becker County, Minnesota (47.049°N, 95.583°W) from 2010 to 2012, and at Rice Lake NWR in Aitkin

County, Minnesota (46.529°N, 93.338°W) and Sandilands Provincial Forest (PF) in southeastern Manitoba, Canada (49.637°N, 96.247°W) from 2011 to 2012. All three sites were located in the northern hardwood transition zone between boreal forest and tallgrass prairie in the western Great Lakes region of central North America. Each site contained a mix of forest of various seral stages and vegetation structures. The three most abundant cover types at each site were upland forests generally dominated by quaking aspen (*Populus tremuloides*), shrublands dominated by hazel (*Corylus* spp.), and wetland shrublands dominated by alder (*Alnus* spp.). For a detailed description of the study sites, see Chapter 8 (this volume).

### Data Collection

We searched for nests of Golden-winged Warblers at all three sites using radiotelemetry to monitor adult females and using standard nest-searching methods (Martin and Geupel 1993). We attached VHF radio transmitters (Blackburn Transmitters, Nacogdoches, TX) to passively mist-netted adult female Golden-winged Warblers using a figure-eight harness design (~4.1% of mean adult mass; Rappole and Tipton 1991, Streby et al. 2015). We used homing on radio signals to locate marked females and find their nests during nest building, egg laying, or early incubation. Radio transmitters had no measurable effect on any aspect of productivity during our study (Streby et al. 2013).

We recorded nest locations using handheld Global Positioning System units (GPSMAP 76 or eTrex Venture HC Global Positioning System, Garmin Ltd., Schaffhausen, Switzerland), averaging 100 points to ensure <5 m accuracy. We monitored nests at 4-day intervals until nestlings fledged (rarely 3-, 5-, or 6-day intervals due to inclement weather or logistical constraints). When possible, we assessed the condition of nests from a distance using binoculars and approached nests from various directions on different visits to minimize nest-site disturbance. We considered nests to be successful if at least one nestling fledged and, to reduce inaccurately assigned nest fates, we considered nests to have failed if we found them empty before a possible fledge date at nestling day 7, if they had cold eggs and were unattended for >2 observation intervals during the incubation stage, or if radio-tagged fledglings were depredated and

no broodmates were detected in the vicinity of the nest (Streby and Andersen 2013).

At 6–9 days after hatching (counting hatch day as day 1), we banded all nestlings with a standard U.S. Geological Survey leg band and attached a radio transmitter to 1–5 randomly selected individuals at each nest (commonly two individuals) using a figure-eight harness (~4.6% of mean nestling mass). Additionally, we attached transmitters to 10 fledglings from known nests captured 1–8 days after fledging. We tracked fledglings daily to assess survival and right-censored 19 individuals (10% of fledglings we monitored) with unknown fates because transmitters were dropped. We focused on the impact of predation in this analysis, so we also censored individuals that died due to exposure ( $n = 11$ ). We focused analysis on the early postfledging period, days 1–8 after fledging, because the early period included most of the fledgling mortality we observed (86%; Chapter 8, this volume). We divided the early postfledging period into two stages for modeling: days 1–3, characterized by low mobility and high and variable daily mortality; days 4–8, characterized by greater mobility and relatively low mortality (Chapter 8, this volume; Peterson 2014).

### Landscape Attributes

To model the impact of cover types on nest success and fledgling survival, we categorized 11 cover types using aerial photographs in Arc 10.1 Geographic Information System (GIS) software (Environmental Systems Research Institute, Redlands, CA). For Tamarac NWR and Rice Lake NWR, we used 1-m resolution digital orthophoto quadrangles (2009; Minnesota Department of Natural Resources). For Sandilands PF, we used georeferenced 1-m resolution satellite images obtained from Google Earth™ 6.2 (2010; Google Inc., Mountain View, CA). We confirmed the cover types derived from aerial photographs and satellite images using >2,500 locations visited at our study sites. Each additional cover type doubled the number of possible unique combinations of cover types present on a landscape, so we collapsed the 11 cover types into six broad categories (deciduous forest, upland shrubland, forested wetland, grassland, wetland shrubland, and coniferous forest), included an additional covariate related to edge density, and used seven categories as potential variables in our FSP model (Table 9.1).

TABLE 9.1

*Categorization, definition, and total exposure days used for three logistic exposure models (N = nest success, E = fledgling survival days 1–3, L = fledgling survival days 4–8) of similar cover types present on landscapes used by three Golden-winged Warbler populations studied in the western Great Lakes region of North America, 2010–2012.*

Landscape structure and composition cover-type category	Definition	Total exposure days	Cover type <sup>a</sup>
Coniferous forest	Forest dominated by coniferous trees	N = 18 E = 15 L = 33	Coniferous forest
Deciduous forest	Forest with >60% canopy closure and dominated by deciduous trees >5 m in height	N = 817 E = 364 L = 463	Mature forest Sapling-dominated clear-cut
Shrubby edge	Edge between shrubland and coniferous forest, forested wetland, or deciduous forest	N = 760 E = 442 L = 534	N/A
Forested wetland	Perennially wet forest dominated by trees >5 m in height	N = 106 E = 57 L = 211	Forested wetland
Grassland	Landscape dominated by grass or sedge	N = 573 E = 270 L = 279	Grassy wetland Upland grassland
Wetland shrubland	Perennially wet shrubland with a canopy <5 m in height	N = 501 E = 211 L = 288	Wetland shrubland
Upland shrubland	Perennially dry shrubland or sapling-dominated clear-cut with a canopy <5 m in height	N = 716 E = 359 L = 386	Firebreak/power-line right-of-way Shrub-dominated clear-cut

<sup>a</sup> For detailed description of cover types see Chapter 8 (this volume).

With the exception of coniferous forest, which was adjacent to only one site, and forested wetland, which was an uncommon cover type at each site, we modeled the relationship between each cover-type category and nest success and fledgling survival using  $\geq 200$  exposure days for each period (Table 9.1).

In addition to cover-type variables, we included a covariate for edge density (i.e., length of edge within a specified area) in our models to assess how productivity was related to the density of forest–shrubland edge present. We used Arc GIS 10.1 to identify edges between deciduous forest, coniferous forest, or forested wetland with a canopy height >5 m and two shrubland cover

types: upland shrubland and wetland shrubland. We limited our measure of edge density to edges between forest and shrubland cover types because those are the cover type edges with which Golden-winged Warblers are most commonly associated (Confer et al. 2011). We excluded less ecologically significant edges such as edges between grassland and shrubland.

For each of the seven model covariates (six cover types and edge density; hereafter, “landscape variables”), we calculated an “impact radius.” The impact radius defined the scale at which each landscape variable was most strongly related to survival of nests and fledglings. To calculate the radius, we buffered each nest location

with circles with radii in 25-m increments from 25 to 200 m and at 100-m increments from 200 to 500 m. For nest survival and fledgling survival from day 1 to 3, we used a range of 25–200 m for potential impact radii and for fledgling survival from day 4 to 8, we used a range of 25–500 m for potential impact radii, corresponding with the distance that adults moved fledglings (Chapter 10, this volume). We summed the total area (ha) for each cover type and total linear distance of edge (km) for each buffer distance around each nest location. The impact radius of each landscape variable could be at a scale unique to that landscape variable: deciduous forest might be related to nest success at a 50-m radius, whereas wetland shrubland might be related to nest success at a 200-m radius. Thus, we independently estimated survival using each combination of scale and polynomial function (linear, quadratic, or cubic relationships) for each variable by fitting logistic exposure models to survival data from all three sites and years for three different periods (nest survival, fledgling survival day 1–3, and fledgling survival day 4–8) using PROC NLMIXED (SAS Institute, Chicago, IL; Shaffer 2004). For example, to determine the impact radius and polynomial function of deciduous forest in relation to nest success, we compared 24 different deciduous forest models ranging from a linear relationship with a 25-m impact radius to a cubic relationship with a 200-m impact radius.

We treated our models as exploratory and did not attempt to predict what relationships might occur between landscape structure or composition and survival. We used multiple potential polynomial functions to account for the possibility of curvilinear relationships among modeled variables to account for the potential of diminishing returns or exponential increases in the impact of any landscape variable on survival. We included nest or fledgling age as a covariate in models for nest survival and fledgling survival from day 1 to 3. Survival was relatively constant after the first three days (Chapter 8, this volume), and we did not include age as a variable when modeling fledgling survival from day 4 to 8. For models of fledgling survival in both the early and late fledgling periods, we used brood as a random effect. Previous modeling of this study population determined that there were no site or year effects on nest or fledgling depredation (Streby et al. 2014), so we

did not include those variables in our models. We centered all impact radii on the nest because fledgling survival during the first eight days outside the nest was directly related to nest location (Streby et al. 2014; Chapter 8, this volume). Fledglings moved farther from the nest after the first three days (Peterson 2014), so we increased the range of potential impact radii to 25–500 m to model fledgling survival from day 4 to 8, but we still centered radii around the nest because nest location was the strongest predictor of survival during this period in previous models (Chapter 8, this volume). We did not include survival data from day 9 to independence because survival was consistently high and largely unrelated to habitat use or nest location during this period (Chapter 8, this volume). For each landscape variable, we ranked models of nest or fledgling survival using Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ; Burnham and Anderson 2002) and selected the best supported combination of polynomial function and impact radius for use in modeling productivity on a landscape (for complete  $AIC_c$  rankings, see Peterson 2014:appendix B). We defined null models with age for nest survival and fledgling survival from day 1 to 3 or constant survival for fledgling survival from day 4 to 8 as null models. If all combinations of polynomial function and impact radius for a variable were less supported than the null model for that survival period, we considered that variable to be noninformative and excluded it from survival models.

### Modeling Survival for a Landscape

For each survival period, we used methods similar to techniques used for resource selection functions (Manly et al. 2002) to estimate survival related to landscape structure and composition around any given location at our study sites. We combined the best supported impact radius and polynomial function for each landscape variable into composite survival models that incorporated all landscape variables present at every location (1-m<sup>2</sup> pixel) across our study sites. We used survival models and estimates of renesting rates and brood size to create spatially explicit estimates of the number of fledglings that could be produced to fledgling day 8 at any given location. In contrast to resource selection functions, which estimate the probability of presence or use on a landscape,

our models of FSP estimated productivity for a hypothetical breeding pair that may choose to nest at any 1-m<sup>2</sup> pixel on our study sites.

For each landscape variable, we built a “landscape variable map” that delineated the area over which that variable was related to each component of survival (nest, fledgling days 1–3, fledgling days 4–8). We used the vector cover-type layer delineated using aerial or satellite imagery and isolated each cover type. We individually converted all landscape variable maps to 1 m × 1 m resolution raster layers and then used a neighborhood function in Arc GIS 10.1 to calculate a value at every 1 m × 1 m pixel on the map equal to the quantity (i.e., area or length, “variable quantity map”) of each landscape variable within its impact radius for each survival period. For example, the explanatory variable deciduous forest was related to the response variable fledgling survival from day 1 to 3 at a 25-m scale; we therefore created a variable quantity map that for each pixel contained a value equal to the number of ha of deciduous forest within 25 m of that pixel.

We estimated survival separately for each period because Golden-winged Warbler nest and fledgling survival are associated differently with landscape composition around a nest (Streby et al. 2014). For each survival period, we used all variable quantity maps to create a map comprising landscape structure and composition values representing each unique combination of variable quantity values present at every pixel. To do this, we used raster algebra to identify the

landscape variables present within their respective impact radii around each pixel (i.e., those with variable quantities >0, including edge density). Our approach created 32 unique combinations of five informative landscape variable compositions (groups; Table 9.2; see Peterson 2014:appendix B for full model results), ranging from simple landscapes with a pixel with only one cover type within its impact radius to more complex landscape areas with a pixel with several cover types and edge density within their respective impact radii. Coniferous forest and forested wetland were not included in the groups used for the results presented here because they were not present at the specific stands analyzed in this manuscript.

For each survival period (nest, fledgling days 1–3, fledgling days 4–8), we used PROC GENMOD in SAS and built logistic exposure survival models corresponding to the landscape variable composition group associated with each pixel (SAS Institute, Chicago, IL; Shaffer 2004). We assigned each of these equations to each pixel based on the landscape structure and composition surface described above. Our approach allowed the effect of each landscape variable to differ depending on landscape structure and composition around each pixel. For example, quantity of deciduous forest might be related to nest survival differently depending upon whether deciduous forest is adjacent to wetland shrubland or grassland. We estimated daily survival (*S*) within each period for each observed combination of landscape

TABLE 9.2  
*Scale and polynomial function of top-ranked survival models for each landscape variable and survival period for three populations of Golden-winged Warblers in the western Great Lakes region.*

Landscape variable	Nest survival		Day 1–3 fledgling survival		Day 4–8 fledgling survival	
	Scale (m)	Polynomial function	Scale (m)	Polynomial function	Scale (m)	Polynomial function
Coniferous forest	50	Linear	50	Quadratic	N/A	N/A
Deciduous forest	N/A	N/A	25	Linear	25	Linear
Edge	50	Cubic	200	Cubic	400	Cubic
Forested wetland	175	Linear	125	Cubic	400	Cubic
Grassland	200	Quadratic	200	Linear	175	Quadratic
Wetland shrubland	200	Linear	N/A	N/A	300	Cubic
Upland shrubland	N/A	N/A	N/A	N/A	N/A	N/A

Noninformative landscape variables are indicated by “N/A”.



structure and composition (l) and survival period (p) on the logit scale as follows:

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

where

$\alpha$  is the estimated intercept

$\beta_i$  is the estimated coefficient for landscape variable  $x_i$ .

To apply the equation defined above to a landscape, we created coefficient maps for each  $\beta$  value derived from each logistic exposure survival equation. We assigned the calculated  $\beta$  values for each survival period (p) to each pixel based on its corresponding landscape structure and composition value (l). For example, if  $x_i$  for an equation represented the amount of wetland shrubland within 200 m (i.e., the impact radius of wetland shrubland associated with nest success), the value at any given pixel on the coefficient map for  $x_i$  was equal to the  $\beta_i$  value calculated by the logistic exposure survival equation for the landscape structure and composition value at that pixel.

At each pixel on a landscape, we used the previously assigned values of (1) the amount of each landscape variable surrounding that pixel and (2) the  $\beta$  coefficients for the logistic exposure survival equation for the appropriate landscape variable to estimate nest success, fledgling survival from day 1 to 3, and fledgling survival from day 4 to 8. For example, to calculate fledgling survival from day 4 to 8 for a pixel at the center of a circle with 3/4 of the landscape made up of deciduous forest and 1/4 of the landscape made up of shrubby wetland, with a straight shrubby edge separating the cover types at a right angle, the survival equation would be as follows:

$$\text{Daily survival} = \frac{\exp(4.2177 + (0.4524 * \text{deciduous forest}) - (0.0010 * \text{edge}) + (2.7450 * 10^{-7} * \text{edge}^2) + (1.6789 * \text{shrubby wetland}) - (0.5959 * \text{shrubby wetland}^2) + (0.0454 * \text{shrubby wetland}^3))}{1 + \exp(4.2177 + (0.4524 * \text{deciduous forest}) - (0.0010 * \text{edge}) + (2.7450 * 10^{-7} * \text{edge}^2) + (1.6789 * \text{shrubby wetland}) - (0.5959 * \text{shrubby wetland}^2) + (0.0454 * \text{shrubby wetland}^3))}$$

where each numerical value was the assigned  $\beta$  coefficient for that landscape variable. Each pixel that fell within the deciduous forest and edge landscape would be assigned those  $\beta$  coefficients and the value for the number of ha of deciduous forest within 25 m, the number of ha of shrubby wetland within 300 m, and km of edge within 400 m of that pixel. The hypothetical fledgling's nest described above would exist on a landscape with 0.147 ha of deciduous forest within 25 m, 7.068 ha of shrubby wetland within 300 m, and 0.8 km of edge within 400 m; the fledgling would have a 0.6508 probability of surviving during days 4–8 (daily survival = 0.9177).

We calculated nest productivity as the number of juveniles fledged by a breeding pair (NP), assuming up to two nesting attempts if the first nest failed and a mean fledged brood of four fledglings (H. M. Streby, unpubl. data) as follows:

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

where NS is nest success. We calculated fledgling survival (FS) as follows:

$$FS = ES * LS,$$

where

ES is fledgling survival in the early period (days 1–3)

LS is fledgling survival in the late period (days 4–8).

Assuming negligible mortality until independence (Chapter 10, this volume), we calculated FSP or the number of young raised eight days postfledging as follows:

$$FSP = NP * FS.$$

After applying these equations, each pixel on the map had a value for NP, FS, and FSP, the product of NP and FS that represented the expected productivity for a pair nesting within that pixel. We then used these values to identify areas of high and low productivity on a landscape. A more detailed description of the process we used to estimate spatially explicit productivity is presented in Peterson (2014:appendix A).

No standard method is available for assessment of the robustness of our spatially explicit models of FSP, so we assessed whether our models predicted

survival better than null models using k-fold cross-validation (Boyce et al. 2002, Koper and Manseau 2009). We evenly divided the sample for each survival period by randomly assigning nests or broods to eight equal folds. For each fold, we used the remaining seven folds to train a set of spatially explicit models of survival and a null model with either age as a variable (for nests and for fledglings from days 1 to 3) or constant survival (for fledglings from days 4 to 8). We then calculated a Spearman's rank correlation between observed survival and survival predicted by both the null model and the spatially explicit model of survival.

### Application of Spatially Explicit Models of Full-Season Productivity

To assess the effects of potential management actions designed to increase FSP of Golden-winged Warblers, we used Arc GIS 10.1 to simulate altered landscapes at our study sites. At each of our study sites, we applied spatially explicit models of FSP to existing and hypothetical landscapes and present estimates of productivity that used all landscape categories in various combinations, except forested wetland and coniferous forest. The scenarios we selected were chosen to illustrate (1) differences between wetland and upland cover types, (2) the effects of grassland succession to upland shrubland and then to mature forest, and (3) the effect of management of shrubby edge density on a landscape. We considered all roads, open water, grassland, or any cover types >100 m from upland shrubland or wetland shrubland to be areas unused for nesting by Golden-winged Warblers and did not include those values in our analyses. We smoothed all graphical representations of spatially explicit productivity estimates using a 25-m mean of productivity in Arc GIS 10.1 to reduce minor, abrupt transitions between landscape structure and composition categories.

In our first assessment, we evaluated the relative FSP of upland and wetland cover types while controlling for the effect of surrounding landscape structure and composition on productivity. Although Golden-winged Warblers use both upland and wetland cover types as nesting habitat, Confer et al. (2010) suggested that productivity in wetland cover types may be greater than productivity in upland cover types. For our study site at Rice Lake NWR (Figure 9.1a) we evaluated the

difference in FSP between landscapes dominated by wetland cover types and those dominated by upland cover types. For a wetland-dominated portion of that study site, we used Arc GIS 10.1 to simulate the conversion of the same landscape with all wetland cover types to structurally similar upland cover types. We performed this assessment not to encourage converting wetland to upland cover types on managed landscapes, but to measure the difference in estimated FSP in structurally similar patches. We quantified the difference between wetland and upland cover types by calculating the mean productivity within 100 m of known nest sites for this scenario. We also used logistic exposure to model productivity in the absence of landscape data by dividing nests located in wetland versus upland cover types, as a separate assessment of the difference between cover-type productivity.

In our second assessment, we simulated management to increase productivity at Tamarac NWR, where grassland cover comprised 9 ha of our study area and could be managed for Golden-winged Warblers. We simulated modifying an open grassland (Figure 9.1b) within a forested landscape to evaluate how succession of an open area would affect FSP of Golden-winged Warblers. We simulated converting grassland to upland shrubland and adding shrubby edges where the altered grassland patch abutted deciduous forest to simulate early successional cover. We then simulated upland shrubland continuing to succeed into deciduous forest and merged it with the adjoining deciduous forest patch. The landscape simulation at Tamarac NWR not only altered productivity but also the area available for nesting. We quantified the difference between management scenarios at Tamarac NWR by multiplying the area available for nesting in each scenario by the mean productivity for that area, therefore accounting for both productivity and changes in area available for nesting.

In our final assessment, we identified two areas with low productivity (estimates of <1 fledgling produced per  $1 \text{ m} \times 1 \text{ m}$  pixel) associated with >0.6 km of edge within 50 m of a pixel at our Sandilands PF site (Figure 9.1c). In these areas, we simulated forest management that would result in lesser edge density, either by allowing upland shrubland to succeed into deciduous forest or by harvesting forest to create a lesser edge density (i.e., <0.3 km of edge length within 50 m of a pixel). We quantified the difference between



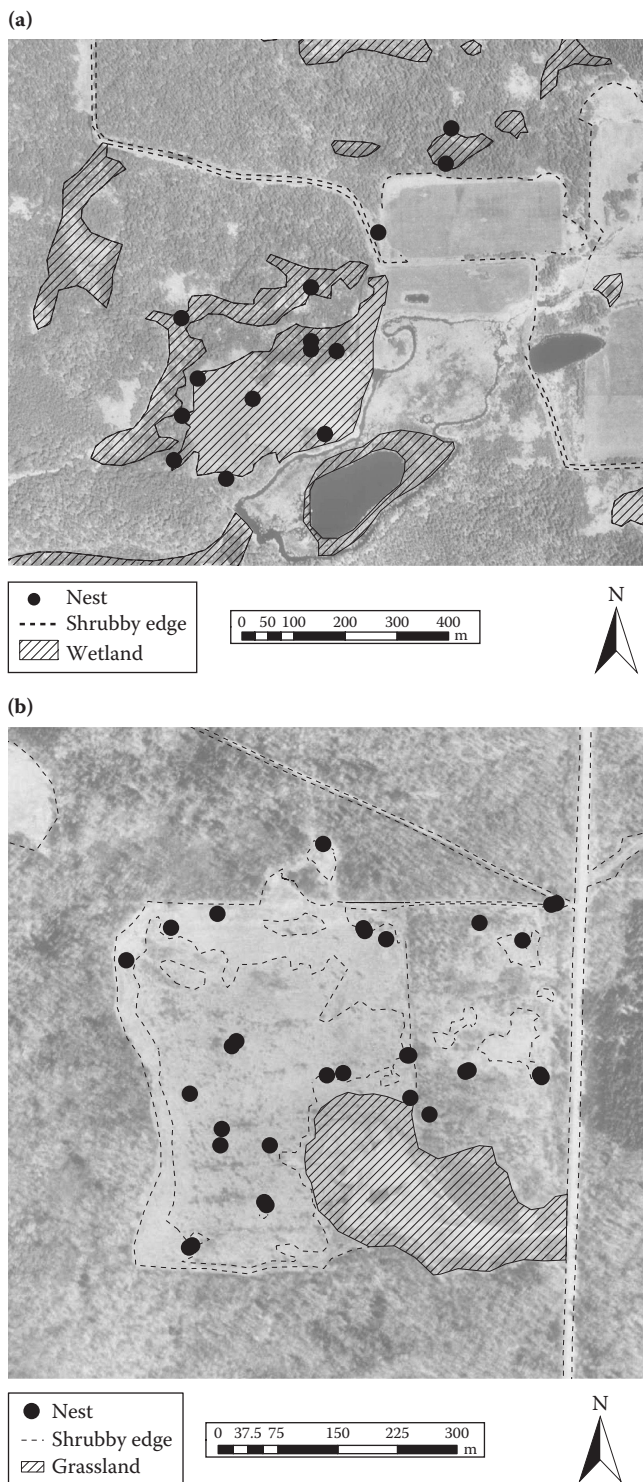


Figure 9.1. Aerial photographs of three Golden-winged Warbler study sites in the western Great Lakes region of North America from 2010 to 2012 with nest locations marked with a circle, soft shrubby edges marked by a dashed line and (a) wetland cover types delineated by thick gray boundary at Rice Lake NWR, (b) grassland delineated by red hatched lines at Tamarac NWR. (Continued)

(c)

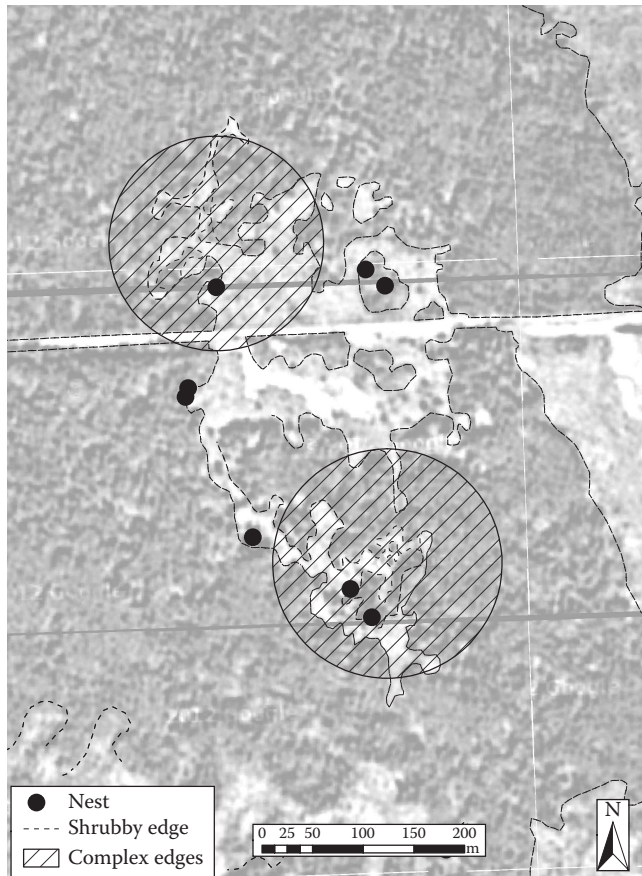


Figure 9.1. (*Continued*) Aerial photographs of three Golden-winged Warbler study sites in the western Great Lakes region of North America from 2010 to 2012 with nest locations marked with a circle, soft shrubby edges marked by a dashed line and (c) areas with complex edges indicated by red hatched lines at Sandilands PF.

these edge densities by calculating the mean productivity within the impact radius of altered cover types.

## RESULTS

We monitored 29 nests and 49 fledglings in Sandilands PF and 56 nests and 47 fledglings at Rice Lake NWR from 2011 to 2012, and 131 nests and 94 fledglings at Tamarac NWR from 2010 to 2012. Of 216 nests and 190 fledglings we monitored, 127 nests (59%) and 70 fledglings were depredated (37%). We constructed a total of 96 logistic exposure models (for full model results see Peterson 2014: appendix C). For all three survival periods, the spatially explicit models we developed (Nest  $r_s = 0.30$ , Fledgling days 1 – 3  $r_s = 0.19$ , Fledgling days 4 – 8  $r_s = 0.11$ ) explained more variation in survival than

the null model (Nest  $r_s = 0.14$ , Fledgling days 1 – 3  $r_s = 0.00$ , Fledgling days 4 – 8  $r_s = -0.14$ ), indicating that our spatially explicit models were more informative than the null models.

## Simulation of Management Options

All three of our simulations of altering landscapes at our study areas led to biologically significant changes in FSP. When we simulated converting wetland cover types to upland cover types at Rice Lake NWR, estimated mean FSP from breeding attempts at a random pixel increased 14% from 1.62 fledglings per pixel (SD = 0.74) to 1.84 fledglings per pixel (SD = 0.65; [Figure 9.2a,b](#)). When we modeled productivity in wetland and upland cover types without including landscape variables, we estimated that wetland

cover types would produce a mean of 1.05 fledglings per pixel and upland cover types would produce a mean of 1.59 fledglings per pixel, a 51% increase. At Tamarac NWR, when we simulated succession from grassland to upland shrubland, the area available for nesting (i.e., upland shrubland and deciduous forest <100 m from upland shrubland) increased from 18.3 to 27.3 ha (Figure 9.3a,b). However, estimated FSP decreased in this simulation from 1.97 fledglings per pixel (SD = 0.51) to 1.73 fledglings per pixel (SD = 0.40), largely because of decreased fledgling and nest survival in areas that had previously been positively impacted by the presence of nearby grassland cover. Despite estimated mean

productivity decreasing by 13%, the increase in available nesting area caused total landscape productivity to increase by 30%. Simulated further succession from upland shrubland to deciduous forest reduced available nesting area by 22% to 21.2 ha and resulted in estimated landscape productivity 18% lower than what we estimated in the upland shrubland simulation, despite increasing estimated mean FSP from 1.73 fledglings per pixel to 1.86 fledglings per pixel (SD = 0.39; Figure 9.3c). Finally, when we simulated reduced edge density in two small areas with high edge density (i.e., >0.6 km of edge within 50 m of a given pixel; <1 ha of altered area) that had lower estimated FSP than the surrounding landscape at

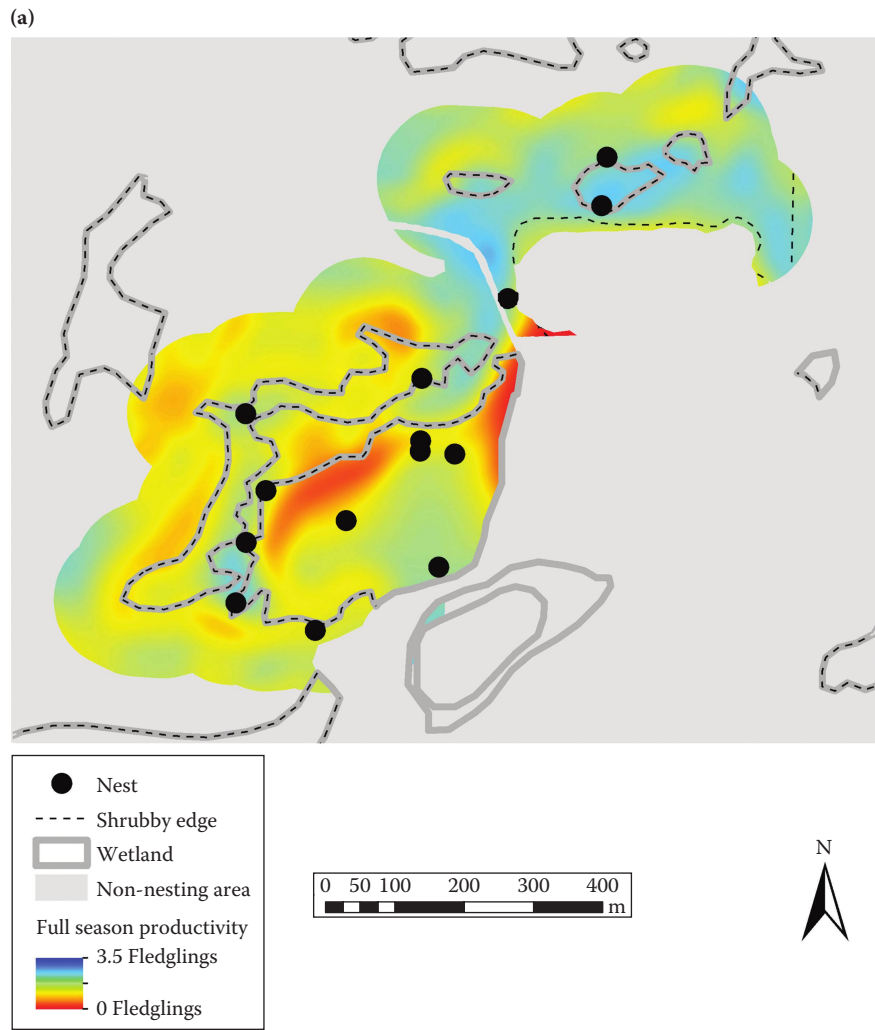


Figure 9.2. Estimated FSP (fledglings per 1-m<sup>2</sup> pixel) modeled from Golden-winged Warbler populations studied from 2010 to 2012 in the western Great Lakes region of North America of (a) a wetland at Rice Lake NWR. (Continued)

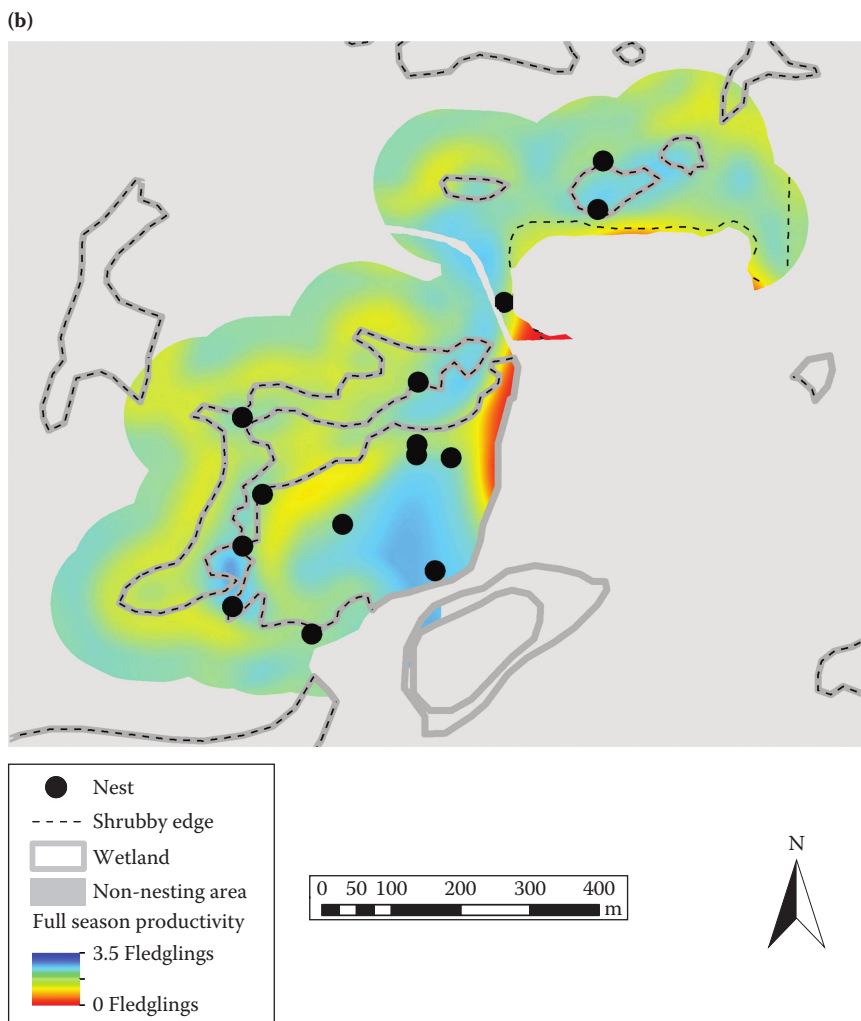


Figure 9.2. (Continued) Estimated FSP (fledglings per 1-m<sup>2</sup> pixel) modeled from Golden-winged Warbler populations studied from 2010 to 2012 in the western Great Lakes region of North America of (b) a hypothetical upland with identical landscape structure. Soft shrubby edges are marked by a dashed line, nests are marked with a circle, wetland cover types are delineated by red hatched lines, and areas unused for nesting (grassland, roads, open water, and deciduous forest >100 m from shrubby cover types) are marked by solid black.

Sandilands PF, estimated mean productivity in 22.5 ha of breeding habitat increased 5% from 1.93 fledglings per pixel (SD = 0.52) to 2.03 fledglings per pixel (SD = 0.43; Figure 9.4a,b).

## DISCUSSION

We developed spatially explicit models of FSP across landscapes at three study areas in the western Great Lakes region, where relatively little information about breeding habitat relations exists, but where a significant portion of

the global population of Golden-winged Warblers breeds. With spatially explicit models of FSP, we estimated productivity at any given location based on landscape characteristics around that location. Models of FSP allowed us to address questions about low-productivity areas, assess productivity across a landscape, and evaluate management effects on productivity prior to implementation. Perhaps the most important finding from our simulations of potential management options was that any management action can have considerably different effects on Golden-winged Warbler

FSP depending on the context of the surrounding landscape. Therefore, we cannot use the results of the simulations presented here to provide broad, generalizable recommendations with regard to any one-size-fits-all management option. Instead, we provide a tool that can be used to assess the influence of specific management actions on individual landscapes, each with their own intrinsic complexities. Within the western Great Lakes

region and, potentially, other regions with similar predator communities and cover types, the models provided here may be used to predict productivity and the impact of management actions.

In contrast to Confer et al. (2010), our results suggested that management of upland cover types on our study sites would increase FSP more than management of wetland cover types, which were generally associated with lesser FSP

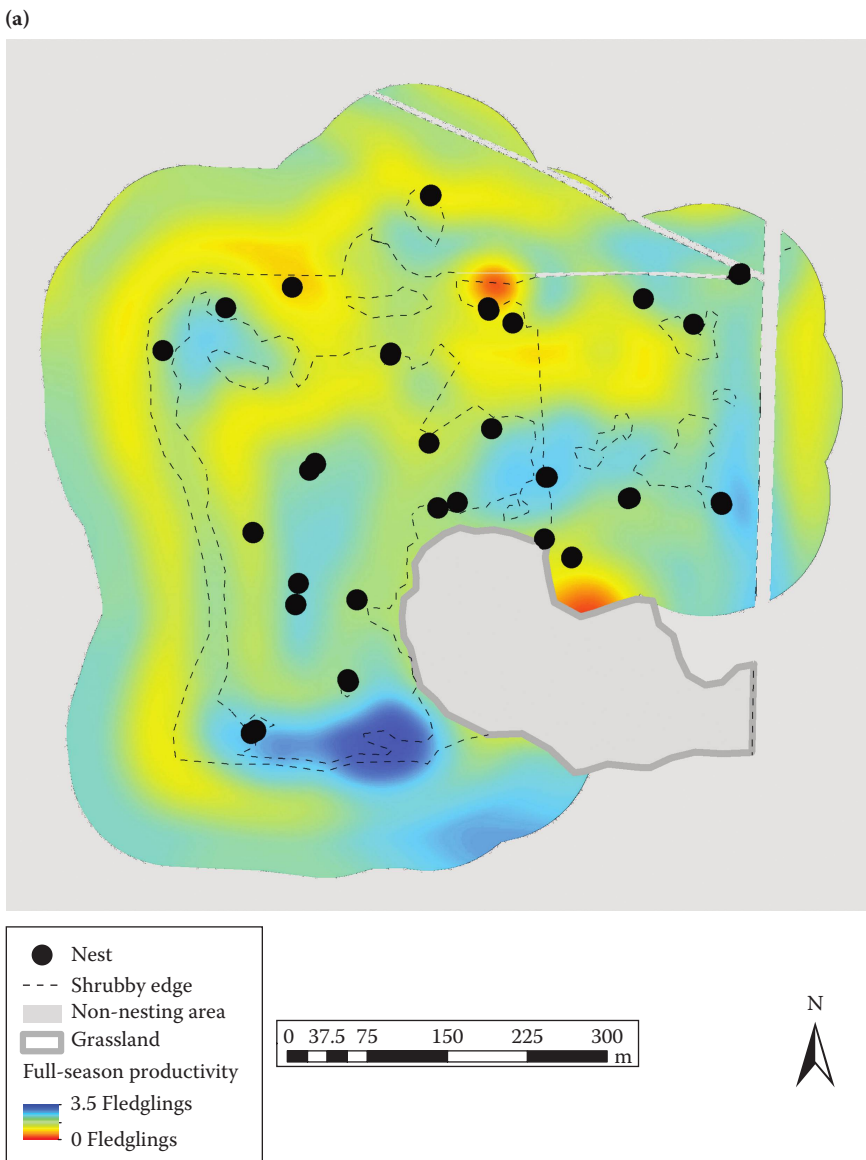


Figure 9.3. Estimated FSP (fledglings per 1-m<sup>2</sup> pixel) modeled from Golden-winged Warbler populations studied from 2010 to 2012 in the western Great Lakes region of North America of (a) upland shrubland and deciduous forest landscape at Tamarac NWR with an open grassland southeast of the site. (Continued)



in our study area when compared with similar upland cover types. Lesser FSP predicted by our models was supported by similar estimates calculated from nests found in wetland versus upland cover types at our sites. The difference between our findings and those of Confer et al. (2010) with regard to the value of wetlands to Golden-winged Warbler productivity may result from differences in structure and composition between wetland shrub communities in our

study areas and swamp forests studied in New York. The difference may also be due in part to our assessment of FSP. We included fledgling survival, a critical component of productivity that is affected by the wetland cover type differently than nest success, whereas Confer et al.'s (2010) study was based on nest success.

At Tamarac NWR, we evaluated how succession of grassland to upland shrubland cover types influenced Golden-winged Warbler productivity in a

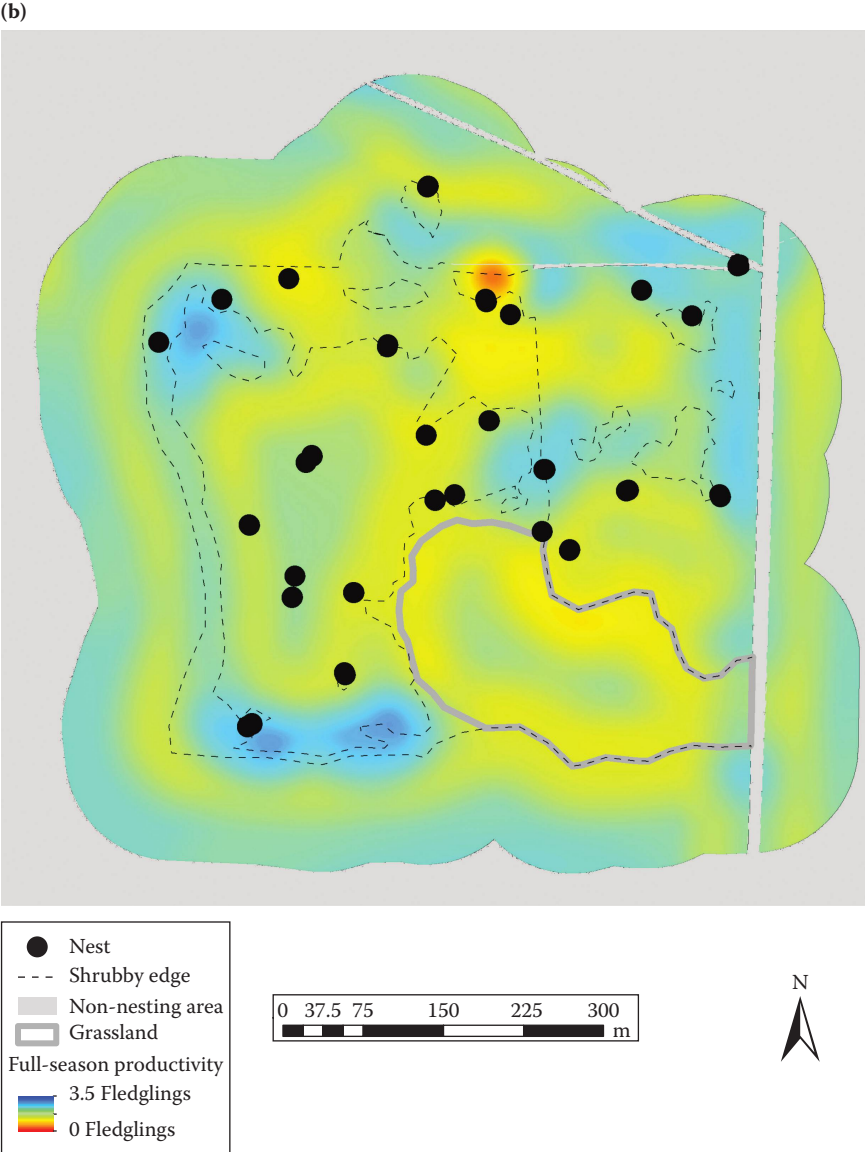


Figure 9.3. (Continued) Estimated FSP (fledglings per 1-m<sup>2</sup> pixel) modeled from Golden-winged Warbler populations studied from 2010 to 2012 in the western Great Lakes region of North America of (b) early stages of succession, with open grassland replaced by upland shrubland. (Continued)



(c)

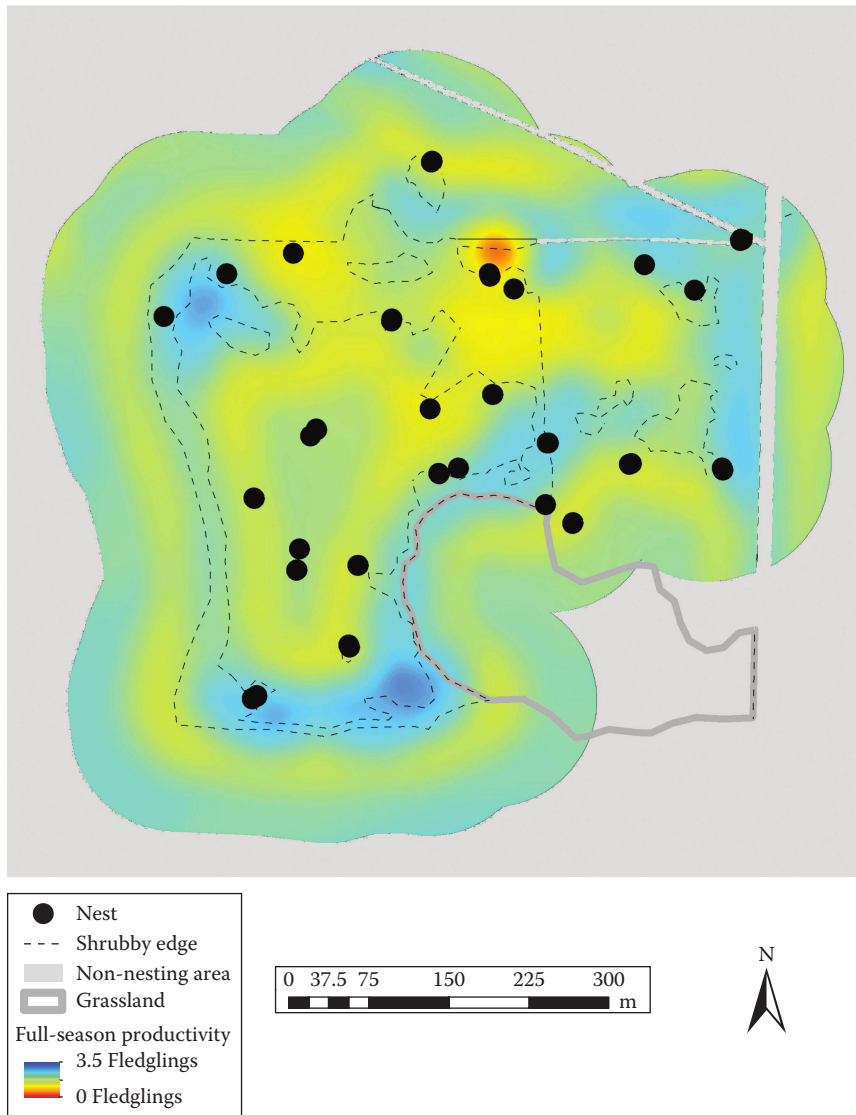


Figure 9.3. (Continued) Estimated FSP (fledglings per 1-m<sup>2</sup> pixel) modeled from Golden-winged Warbler populations studied from 2010 to 2012 in the western Great Lakes region of North America of (c) later stages of succession, with open grassland replaced with deciduous forest. Soft shrubby edges are marked by a dashed line, nests are marked with a circle, grassland is delineated by thick gray boundary, and areas unused for nesting (grassland, roads, open water, and deciduous forest >100 m from shrubby cover types) are marked by solid gray.

landscape that already hosted high productivity. Succession of a grassland patch to an upland shrubland patch increased the area available for nesting by 9 ha (49%) and increased the total estimated productivity of the landscape by 30%, in spite of mean estimated FSP decreasing by 0.24 fledglings per 1-m<sup>2</sup> pixel (12%). Our results demonstrate that there may be scenarios in which increasing the area available for nesting can result in increasing

overall productivity within a landscape, even while decreasing overall nest-site quality. However, our result appears to be management-scale and landscape-context dependent. For example, given the mean estimated FSP presented here for the grassland (1.97 fledglings per pixel) and upland shrubland (1.73 fledglings per pixel) cover types, if we only increased the area available for nesting by 2 ha, total estimated productivity of the landscape

would decrease by 3%. If we extended this scenario to include succession of this 2-ha patch to deciduous forest (1.86 fledglings produced per pixel), the deciduous forest scenario would produce 5% more fledglings than the grassland cover type and 8% more fledglings than the upland shrubland cover type. Our results demonstrate how sensitive the models are to the size and landscape context of the proposed management.

Last, our assessment of landscape characteristics related to Golden-winged Warbler nest and fledgling survival indicated that highly complex shrubland-forest edges (e.g., Figure 9.4) were associated with lower rates of FSP of

Golden-winged Warblers in the western Great Lakes region. Similar to observations of nest success in Indigo Buntings (*Passerina cyanea*; Weldon and Haddad 2005), we predicted lower FSP near complex forest edges. However, we note that the relationship between edge and productivity can vary substantially depending on the surrounding landscape structure and composition and the amount of edge within the impact radius at any location. For many of the models we developed, the amount of edge was positively related to FSP until an apparent threshold (~0.5 km of shrubby edge within 50 m of any given point), after which increasing the amount of edge led

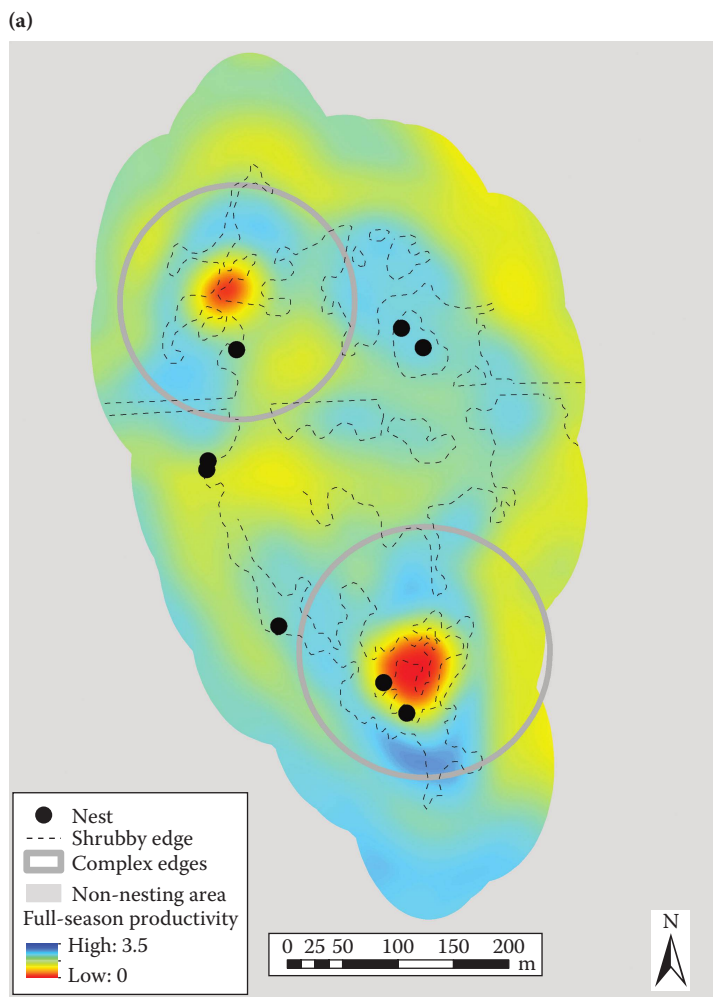


Figure 9.4. Estimated FSP (fledglings per 1-m<sup>2</sup> pixel) modeled from Golden-winged Warbler populations studied from 2010 to 2012 in the western Great Lakes region of North America of (a) an upland shrubland at Sandilands PF with complex edges in the northwest and south portions of the clear-cut. (Continued)

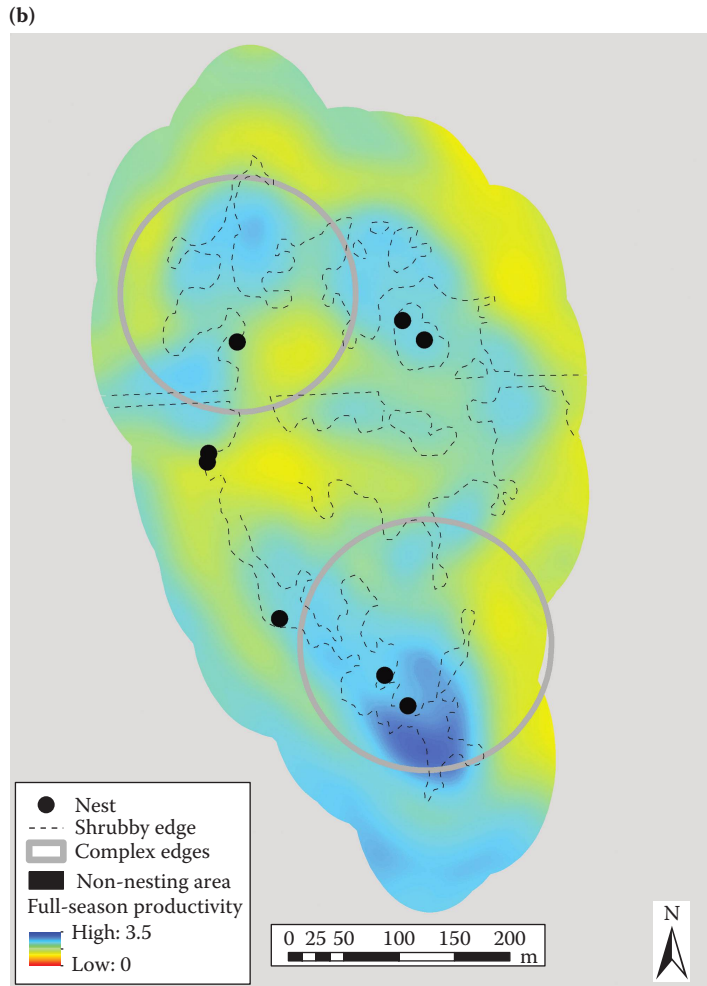


Figure 9.4. (Continued) Estimated FSP (fledglings per 1-m<sup>2</sup> pixel) modeled from Golden-winged Warbler populations studied from 2010 to 2012 in the western Great Lakes region of North America of (b) the same upland with complex edges removed or reduced. Soft shrubby edges are marked by a dashed line, nests are marked with a circle, complex edges are circled with a red hatched lines, and areas unused for nesting (grassland, roads, open water, and deciduous forest >100 m from shrubby cover types) are marked by solid black.

to reduced FSP (Peterson 2014:appendix C). Importantly, the edges we assessed were those between shrubland and forest cover types, and not the smaller scale, micro-edges within shrublands discussed in Chapter 7 (this volume), which may have a different relationship with productivity from the one we observed at a larger spatial scale.

Unlike resource selection functions (Manly et al. 2002), which have been used extensively to assess factors related to species presence (Beerens et al. 2011, Refsnider et al. 2013, Slaght et al. 2013), our spatially explicit models of FSP predict both

the amount and quality of breeding habitat, and how the spatial distribution of cover types across a landscape influences productivity. We assessed our models by comparing predicted and estimated values of FSP in a cross-validation framework. The results of that cross-validation indicated that our models of the relationship(s) between FSP and landscape structure and composition explained more variation in both nest success and fledgling survival than models that did not incorporate landscape structure and composition. We suggest, however, that a more thorough validation of our approach is warranted, given the low Spearman's

rank correlation from k-fold cross-validation and the general difficulties of validating models of binary and highly stochastic phenomena such as nest success or fledgling survival.

We also note that there are limitations to our analytical approach. As currently presented, our FSP models do not predict the likelihood any location will be selected as a home range or nest site (i.e., second to third order selection, Johnson 1980). Incorporating these probabilities into a composite model may make it possible to identify the most used and the most productive areas on a landscape. Additionally, the renesting rate and brood sizes we used in our models may not apply to populations other than those in the western Great Lakes region. Applying our models to other regions would also likely require region-specific information for demographic parameters.

Our models of FSP predict the potential productivity of a specific location, regardless of whether a breeding pair uses that location. For each pixel across our study sites, our nesting model produced a value that represented the probability that a successful nest could occur in that pixel during the season; that value includes the probability of a first nest succeeding, the probability that a second nest is possible at that location (i.e., did the first nest fail?), and the probability of a second nest succeeding. Our model produces the same estimates of productivity regardless of movements between nesting attempts because the estimates are for any first nest and any second nest at each location, and does not require that those attempts be from the same female or breeding pair. For simplicity, the FSP estimate for each location can be viewed as a modeled estimate of the number of young raised to independence by a breeding pair that nested, and potentially renested, at that specific location. Generally Golden-winged Warblers do not renest at the same location (Streby et al. 2014), although violation of this simplifying assumption would not change our results or conclusions.

For the landscapes we studied, our models provided several insights into Golden-winged Warbler ecology and conservation. First, modeling FSP across landscapes allowed us to identify specific areas where management could be directed to have the largest, positive influence on productivity. Second, simulation of the effects of proposed management can inform decisions about how best to use resources to affect population dynamics. Third, spatially explicit models of

FSP can identify areas of high productivity, which may be areas to avoid manipulating or to emulate in other landscapes. Fourth, this modeling process may alter previous management recommendations that wetlands provide better habitat for Golden-winged Warblers than shrubby uplands. Last, assuming comparable demographic data are collected, our approach can be used to simultaneously assess likely impacts on FSP of other species in the same associated with the same landscape successional forests, such as American Woodcock (*Scolopax minor*), to better understand how management for a single species can benefit the avian community.

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