Association between American Woodcock Seasonal Productivity and Landscape Composition and Configuration in Minnesota

GUNNAR R. KRAMER,[1,2] Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Biology, *University of Minnesota, St. Paul, Minnesota, USA*

KYLE O. DALY,[3] Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Biology, *University of Minnesota, St. Paul, Minnesota, USA*

HENRY M. STREBY, Department of Environmental Sciences, *University of Toledo, Toledo, Ohio, USA*

DAVID E. ANDERSEN, U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit, *University of Minnesota, St. Paul, Minnesota, USA*

ABSTRACT The effects of landscape composition and configuration on productivity of most bird species, including American woodcock (*Scolopax minor*), are largely unknown. Understanding landscape components and cover-type configurations associated with productivity can be useful in developing more effective management strategies that increase recruitment. We used data on nest and juvenile survival rates of American woodcock from northern Minnesota from 2011 and 2012 to inform logistic exposure models of survival and predict productivity through the period when juveniles are capable of sustained flight (~15 days post-hatch). We used those models to link landscape features with nest survival rate and juvenile survival rate, predict spatially explicit productivity across our study area, and identify areas of high productivity within our study landscape. Lastly, we used simulations to explore the consequences of potential management actions aimed at improving productivity and the effects of long-term succession of young-forest cover types. We found that associations between land-cover composition and different components of productivity (i.e., nest and juvenile survival rates) were scale-specific. Generally, our models suggested stand-level composition (i.e., the amount of each cover type within 250–500 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, our models predicted lower nest survival rates in landscapes with greater amounts of grassland and upland shrubland. The amounts of wetland shrubland and upland shrubland at stand- (i.e., 250–500 m) and landscape-level (i.e., 1,000 m) scales were positively associated with juvenile survival rate. Our findings demonstrate that the effects of management actions depend on the context and configuration of cover types within the surrounding landscape and that spatially explicit models of productivity may be useful for informing management strategies. Furthermore, our results suggest that relationships between survival and specific land-cover types may change throughout the reproductive cycle in American woodcock.

Proceedings of the American Woodcock Symposium 11: 107–121

KEY WORDS: juvenile survival, landscape composition, landscape structure, nest success, productivity surface, *Scolopax minor*

1 email: gunnarrkramer@gmail.com
2 current affiliation: Department of Environmental Sciences, University of Toledo, Toledo, Ohio, USA
3 current affiliation: U.S. Fish & Wildlife Service, Wildlife and Sport Fish Restoration Program, Bloomington, Minnesota, USA

https://doi.org/10.24926/AWS.0115
CC BY 4.0

Productivity (i.e., producing young that survive to reach a biological milestone) is a crucial component of population dynamics and a key element in models of population growth. Productivity differs from recruitment in that it is a measure of the within-season production of young, whereas recruitment usually refers to the addition of new individuals to subsequent breeding populations (i.e., necessarily incorporating survival during migration and the nonbreeding period in the case of migratory birds; Braun 2005). Estimating effects of landscape composition and configuration 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). Incorporating accurate estimates of vital rates (e.g., adult female survival rate, nest survival rate, juvenile survival rate) into population models is important for understanding the influences of different life stages on population trends (Van Horne 1983, Connelly et al. 1988, Derleth and Sepik 1990, Wisdom and Mills 1997). In birds, including both nest and juvenile survival rates in models of productivity is important because the relationships among survival and landscape components may be stage-specific and/or change over time (e.g., Connelly et al. 1988, Roberts et al. 1995, Streby et al. 2014b). Additionally, many bird species require or select different cover types for rearing juveniles than for nesting (Klebenow 1969, Holbrook et al. 1987, Rotella and Ratti 1992, Streby and Andersen 2011).

Previous studies outline species-specific relationships between edge (Horn et al. 2005), forest fragmentation (Robinson and Wilcove 1994, Faaborg et al. 1995, Bayne and Hobson 1997, Lloyd et al. 2005), urban development (Ausprey and Rodewald 2011), and population growth rates or individual aspects of productivity such as nest success rate or juvenile survival rate. Management strategies that do not include information on the relationships among landscape structure and demographic rates across multiple life stages may lead to the creation of low-production landscapes or ecological traps (Schlaepfer et al. 2002, Streby and Andersen 2011). Nest failure and juvenile mortality are primarily driven by predation in most avian systems (Martin 1993); thus, landscape factors that influence the composition of the predator community may affect population demographic rates (Hoover et al. 1995, Brawn and Robinson 1996, Chalfoun et al. 2002). Furthermore, predators may respond (i.e., behaviorally or numerically) to landscape variation at different spatial scales than breeding birds and, consequently, some aspects of the landscape may influence the survival rates of nests and juveniles more than others (Stephens et al. 2005). Therefore, consideration of landscape components at biologically meaningful scales is required to inform predictions of productivity across a spatial extent relevant for population-level management (Levin 1992).

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 population trends vary regionally, with eastern breeding populations generally exhibiting declining trends and populations breeding in the western Great Lakes region exhibiting numerically stable trends based on standardized breeding-grounds surveys of singing males conducted since the mid-1960s (Seamans and Rau 2016). Additionally, juvenile/adult female ratios measured from wing-collection surveys of hunters imply declines in recruitment of juveniles into the fall population (Seamans and Rau 2016). These declines in apparent abundance and recruitment of juveniles into the fall population 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 for creating and sustaining woodcock habitat (BMPs; Kelley et al. 2008, Wildlife Management Institute 2010).

The implementation of woodcock BMPs is intended to increase the amount and availability of high-quality woodcock habitat at a landscape scale (~200–800 ha), thus increasing woodcock vital rates. 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 increase following targeted vegetation management (Dwyer et al. 1988, McAuley et al. 1996), and previous research suggests microhabitat structure and composition have small or nonexistent effects on survival rates of woodcock nests and juveniles (Daly 2014); the influence of large-scale landscape components and their configuration on woodcock productivity, however, is largely unknown.

We used the methods outlined by Peterson et al. (2016) to assess relationships between landscape structure and composition and the productivity of woodcock breeding in northwestern Minnesota. We created spatially explicit models of productivity and used those models to predict

productivity over our study area. Our models combine estimates of nest survival rate and juvenile survival rate, each as a function of landscape structure and composition, to predict productivity from nest initiation through the period ending when juvenile woodcock are capable of sustained flight (~15 days post-hatch). Finally, we used our models to investigate whether common management strategies for woodcock are likely to be effective in increasing productivity at managed sites.

Methods

STUDY AREA

We 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 at the confluence of 3 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*). Over the past 30 years, portions of the refuge were harvested (i.e., logged), burned, and sheared to create and maintain early successional forest and provide breeding, nesting, and brood-rearing habitat for woodcock and associated species (Boyle et al. 2010).

DEMOGRAPHIC DATA COLLECTION

We used nest and survival data from adult female and juvenile woodcock captured and marked from April–June during 2011–2012 (Daly et al., this volume, Evaluating techniques for estimating post-breeding-season age ratios). Daly (2014) captured adult female woodcock using mist nets and attached radio-transmitters using a glue-on, backpack-style harness (≤3% of their total body mass; ~4.8 g, model A5410, Advanced Telemetry Systems, Isanti, MN; McAuley et al. 1993a, 1993b). As part of the study, 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 (Daly et al., this volume, breeding season survival of woodcock). 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). We 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 radio-marking and tracking a subset of juveniles within the broods of radio-marked females. Daly et al. (this volume, Evaluating techniques) also found recently hatched (≤5 d) broods of unmarked adult female woodcock using trained pointing dogs and captured and radio-marked juveniles in these broods. Juvenile woodcock are precocial but tend not to exhibit daily movements >100 m during the first week post-hatching, and they generally use a constrained area during this period, so we are confident that these juveniles were close to their nest site (Gregg 1984, Steketee and Robinson 1995). 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 they grew. All transmitter and harness packages were ≤3% of the marked individual's mass, and there was no indication of an effect of transmitters on the survival rate of juvenile woodcock (Daly et al. 2015). Additionally, Daly et al. (2015) found no evidence of dependence among juvenile woodcock in the same brood (reanalyzed in Breeding Season Survival of Woodcock, Appendix II, page 62), and we therefore treated the fate of all juveniles in our sample as statistically independent. Daly et al. (this volume, Evaluating techniques) attached radio-transmitters to 1–4 randomly selected juveniles per brood (Fig. 1) that were subsequently monitored ~3 times per week (based on 4–7 attempts per week to relocate individuals either by relocating radio-marked juveniles or females) to eval-

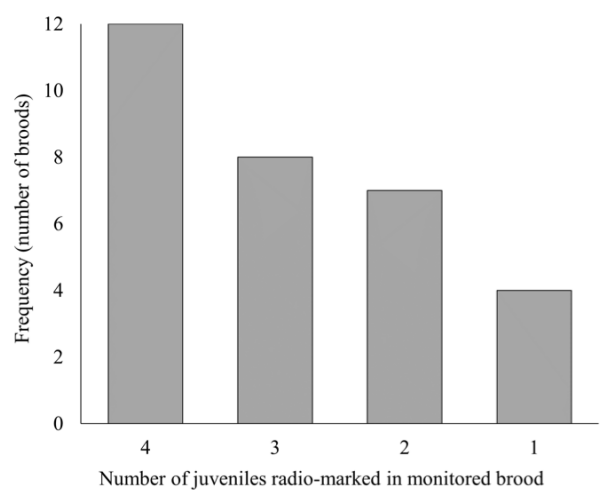

Figure 1. Frequency distribution of the number of radio-marked juvenile American woodcock in each monitored brood at Tamarac National Wildlife Refuge, Minnesota, USA from 2011–2012.

uate survival rate of both marked and unmarked juveniles within the same brood.

We considered juveniles within the same brood as independent experimental units in our study because there was no evidence of intra-brood dependence among juveniles based on Winterstein's (1992) third Chi-squared goodness-of-fit test (average $P = 0.32$; Breeding Season Survival of Woodcock, Appendix II, page 62). Thus, the survival of a juvenile woodcock was not statistically linked to the survival of broodmates, making it appropriate to treat each juvenile within a brood as an individual sample. Determining the appropriate experimental unit (e.g., colony, nest, brood, individual) for wildlife species that exist within groups is important because violating the independence assumption may lead to a biased survival rate estimate and to improperly drawn inferences regarding habitat-survival relationships (Winterstein 1992). On the other hand, if there is no evidence of dependence among juveniles from the same brood, treating juveniles as individual samples can increase effective sample sizes for estimating survival rates and improve resolution of habitat-survival relationships. Our treatment of woodcock juveniles as independent samples differs from other studies that found evidence of intra-brood dependence (e.g., Winterstein 1992, DeMaso et al. 1997), highlighting the importance of testing for independence among broodmates in different species.

LANDSCAPE ATTRIBUTES

We followed the methods and definitions used by Peterson (2014) and Peterson et al. (2016) to model the effects of landscape composition and configuration on the productivity of golden-winged warblers (*Vermivora chrysoptera*) at Tamarac NWR during the same study period. Woodcock and golden-winged warblers co-occur broadly across their breeding distributions and are associated with similar dynamic forest systems with diversity in vegetation age and structure. These 2 species are often described as having similar habitat requirements and are regularly touted as surrogate species for one another, or as umbrella species for young- and early-successional forest communities (Bakermans et al. 2015, Masse et al. 2015). We categorized 6 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 software (Environmental Systems Research Institute, Redlands, CA). We confirmed the cover types classified from aerial photographs using >2,500 locations visited at our study site. We classified cover types into 5 broad categories (deciduous forest, upland shrubland, forested wetland, grassland, and wetland shrubland) based primarily on vegetation structure that we believed influenced the predator community most likely to depredate woodcock nests and juveniles (e.g., mesopredator mammals and raptors; Storm et al. 1976, Boal et al. 2005). We defined mature forest as stands with canopies >20 m and average canopy closure >60% (Brohman and Bryant 2005). Most mature stands in our 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.

We classified areas dominated by vegetation from 1–3 m tall as shrublands. In our 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. We differentiated between wetland and upland shrublands in our study because previous research in the same system identified differences in golden-winged warbler productivity between wetland and upland shrublands (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. We classified less common cover types including forested wetlands of tamarack (*Larix laricina*) or black ash (*Faxinus 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 we did not consider as an important cover type for breeding woodcock in our study.

We investigated the importance of 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). We included edge density in addition to the 5 other cover types because edge is known to be important to woodcock in habitat selection (Hudgins et al. 1985) and generally influences avian nest survival (Rudnicky et al.1993, Manolis et al. 2002, Meunier et al. 2006) and juvenile survival (Peterson et al. 2016) rates. We characterized the relationship between each landscape component and nest survival rate and juvenile survival rate using >600 exposure days for each period (Table 1).

We used a two-step approach in modeling the effects of landscape components on nest and juvenile survival rates in woodcock. First, we used linear models to identify the radius at which different cover types were most associated with period-specific survival rates. To do this, we explored the relationship between cover type and survival rate at different spatial scales by modeling the impact radius for each of the 6 model covariates described above following the methods described in Peterson (2014) and Peterson et al. (2016). The impact radius represented the scale at which each landscape variable was most strongly supported in univariate models of nest and juvenile survival rate. We determined the impact radius for each landscape variable by buffering each nest location with circles with different radii (Fig. 2). We used the landscape composition and configuration surrounding nests to inform models of both nest

survival and juvenile survival rates because adaptive nest-site selection (i.e., selection of nest sites that maximizes productivity) needs to account for survival rates during both the nesting stage and the juvenile stage (Refsnider and Janzen 2010, Streby et al. 2014a). We explored the relationships between cover types and nest survival rate at radii of 25, 50, 100, 250, and 500 m. We tested some of the same, and larger radii (100, 250, 500, 750, and 1,000 m) in our exploration of factors influencing juvenile survival rate to account for the mobility of juveniles (Daly 2014). The

Table 1. Scale and polynomial function of landscape-scale variables used in predicting productivity for 2 survival-rate periods in American woodcock monitored at Tamarac National Wildlife Refuge, Minnesota, USA, during 2011–2012. Variables that were not included in both survival-rate periods are indicated by "N/A".

	Nest Survival Rate (*n* = 48 nests; *n* = 630 exposure days)		**Juvenile Survival Rate (Day 1–15) (*n* = 90 individuals; *n* = 1,014 exposure days)**		
Landscape Variable	**Scale (m)**	**Polynomial function**	**Scale (m)**	**Polynomial function**	**Relationship with survival rate**
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. We included mature forest as a covariate in both nest survival rate and juvenile survival rate models because some woodcock nested within mature forest and the amount of mature forest on the landscape may influence the predator community and the survival rate of nests and juveniles.
Grassland	500	Linear	N/A	N/A	Grassland is reportedly important to woodcock for display and mating. We 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 rate as observed in other young-forest species (Peterson et al. 2016).
Upland shrubland	500	Linear	1,000	Linear	We included upland shrubland in our 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 rate in juvenile woodcock. Although woodcock rarely nest in wetland shrublands, they often nest nearby, and proximity may be important to the survival rate of juvenile woodcock as wet areas are often associated with diurnal feeding areas in adult woodcock.

smallest and largest radii do not necessarily represent the minimum or maximum distances that juveniles could or did travel from the nest site during the first 15 d post-hatching. Instead, these radii represent the scale at which cover types might generally be available to juvenile woodcock during the first 15 d post-hatching as the quantity, composition, and configuration of cover types surrounding the nest site may affect the survival rate of juveniles by influencing the ability of juveniles to escape detection by predators (e.g., Spears et al. 2007), and/or by influencing the local predator community (e.g., Sovada et al. 2000).

We 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 rate at each scale (i.e., impact radii). We constructed linear models (including those with quadratic and cubic parameters) relating landscape components and survival rate using a logistic exposure function (Shaffer 2004) and the glm function in R (R Core Team 2016). We ranked models of nest survival rate and juvenile survival rate using Akaike's Information Criterion adjusted for sample size

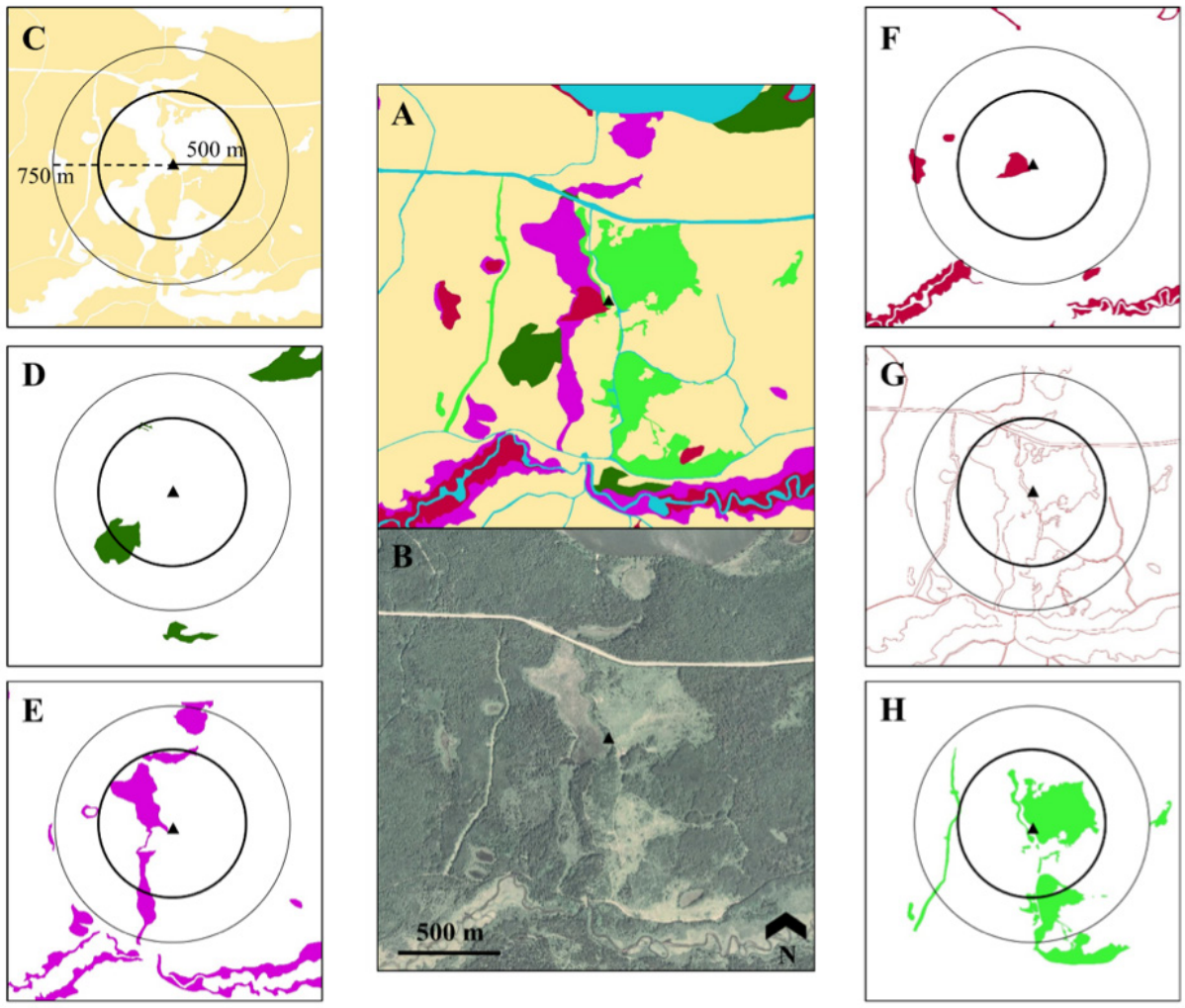

Figure 2. Example of digitized landscape (A) derived from satellite imagery (B). An American woodcock nest is located near the center of all images and denoted by a black triangle. Panels C–H demonstrate the process of isolating and quantifying the amount of landscape variables at different impact radii surrounding nests. In this example, we investigated the amount of mature forest (C), forested wetland (D), wetland shrubland (E), grassland (F), shrubby edge (G), and upland shrubland (H) within 500 and 750 m of a nest. We extracted the area of each of these cover types at different radii and used generalized linear models to determine if 1 impact radius best explained juvenile and nest survival rates for each cover type.

(AIC_c; Burnham and Anderson 2002). We 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 [<250 m] and vice versa), and biologically informed predictions to select cover types and impact radii to include as covariates in productivity models (Peterson 2014, Peterson et al. 2016; presented in Kramer 2017).

The second step of our modeling approach involved using the covariates (i.e., cover types and associated impact radii) identified in the first step to build logistic-exposure survival-rate models (Shaffer 2004) for each potential combination of important landscape components at their determined impact radius. We applied these models to each pixel (1 m^2) on the digitized landscape such that the survival rate estimate at any pixel was informed by the specific landscape composition and configuration within the previously determined impact radius specific to each landscape component. Following the methods of Peterson (2014) and Peterson et al. (2016), we estimated daily survival rate (S) within each period for each observed combination of landscape structure and composition ($_l$) and survival-rate period ($_p$) as:

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

where α is the estimated intercept and β_1 is the estimated coefficient for the landscape variable x_1.

To estimate survival rate over the entire period (i.e., nest and juvenile survival rates) we raised the estimate of daily survival rate 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). We applied this logistic-exposure survival-rate equation to the landscape for each survival-rate period (i.e., nest, juvenile; [$_p$]) based on the surrounding landscape composition and structure ($_l$). At each pixel on the landscape, we 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 rate from laying to hatching) and juvenile survival rate (i.e., from hatch day to day 15) of woodcock.

We predicted nest productivity (i.e., number of juveniles hatching; NP) given the assumed ability for 1 renesting attempt (i.e., 1 additional nesting attempt following previous nest failure; McAuley et al. 1990), using a mean hatched brood of 4 juveniles,

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

where NS is nest success rate. We calculated productivity to day 15 post-hatch (i.e., the number of young raised to day 15; P15) as,

$$P15 = NP * JS$$

where JS is juvenile survival rate (from hatch day to day 15). We applied these equations to the digitized landscape and produced surfaces containing values for NP, JS, and P15 of theoretical woodcock nests placed within each pixel (1 m^2) of our study area. We used these models to identify areas of high and low productivity on the landscape and predict the effects of management actions on the productivity of woodcock breeding at Tamarac NWR.

APPLICATION OF SPATIALLY-EXPLICIT MODELS OF PRODUCTIVITY

We predicted the effects of 3 realistic land-cover management scenarios on the productivity of woodcock at Tamarac NWR to investigate the relationships among cover types and period-specific survival rates and resulting productivity. In ArcGIS, we applied hypothetical management on landscapes within our study area to illustrate (1) the effect of grassland succession into upland and wetland shrubland, (2) the effects of creating a ~16 ha (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. We constrained our models to areas we expected woodcock might use for nesting based on field observations of woodcock nest locations. Thus, we 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 our analysis. We averaged each pixel in our productivity surface with all pixels within a 25-m radius to smooth visualizations of landscape productivity.

We selected 3 distinct areas of our study site to test the effects of potential management on the productivity of woodcock by altering the input values of landscape parameters into our spatially explicit models. First, we predicted the change in productivity following the conversion of non-nesting habitat (grassland) into upland shrubland and wetland shrubland. These scenarios (Scenario 1a and Scenario 1b; Table 2) investigated the relative productivity of woodcock in upland and wetland shrubland cover types while controlling for the surrounding landscape structure and composition. 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 (Wildlife Management Institute 2010). Our second scenario (Scenario 2; Table 2) predicted 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. Lastly, we 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 (Scenario 3; Table 2). We chose an area with a patchy and irregular distribution of diverse cover types that reasonably represented a non-managed landscape. We investigated the difference between productivity in each scenario by averaging productivity across all potential nesting sites in the study area. We 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 resulting landscape.

Federal and State permits for capture, banding, and radio-marking woodcock as part of the study by Daly (2014) were granted by the U.S. Geological Survey Bird Banding Laboratory (Permit # 06258, Wayne Brininger, USFWS), and the Minnesota Department of Natural Resources (Permit #s 17377 and 17973, W. Brininger, USFWS). Animal welfare and handling protocols in Daly's (2014) study were approved by the University of Minnesota Institutional Animal Care and Use Committee under Protocol #1103A97333.

Results

Daly (2014) and Daly et al. (this volume, Evaluating techniques) 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. We created 14 logistic exposure models (Table 3) predicting survival rate across 2 periods (nesting and juvenile survival from hatching to day 15). Our spatially explicit models of nest and juvenile survival rates explained more variation than the null (intercept-only) models (nest survival, ΔAIC_c from null = -4.69; juvenile survival, ΔAIC_c from null = -9.66; Fig. 3). We did not detect a correlation between nest survival rate and juvenile survival rate (r = -0.09, P = 0.50). However, nest survival rate explained more variation in productivity than juvenile survival rate (AIC_c = 82.63 and AIC_c = 137.50, respectively).

EFFECTS OF ALTERING INPUT COVER TYPE VALUES ON PREDICTED PRODUCTIVITY

Altering the input values for underlying landscape parameters of our study area resulted in biologically significant changes in predicted productivity of woodcock. Altering the input landscape parameters to reflect conversion of a large grassland to upland and wetland shrubland (Scenario 1a; Table 2) increased the area available for nesting by 8% (4.5 ha). Converting grassland to upland shrubland increased the predicted mean productivity (i.e., the mean number of juveniles surviving 15 days post-hatching from breeding attempts at a random pixel [1 m^2]) by 128% from 0.59 juveniles/breeding female (SD = 0.23) to 1.35 juveniles/breeding female (SD = 0.28; Fig. 4C). After accounting for the increase of available nesting cover, the estimated productivity of the upland-shrubland landscape increased by 147%. When we altered the input landscape parameters to indicate conversion of the grassland to wetland shrubland (Scenario 1b; Table 2), the predicted mean productivity increased by 190% from 0.59 juveniles/breeding female (SD = 0.23) to 1.71 juveniles/breeding female (SD = 0.54; Fig. 4D). After accounting for the increase of appropriate nesting cover, converting grassland to wetland shrubland increased the productivity of woodcock on this landscape by 213%.

Changing the underlying landscape parameters to reflect clear-cutting and subsequent succession of a 16-ha mature deciduous forest stand to upland shrubland (Scenario 2; Table 2) increased predicted mean productivity 52% from 0.88 juveniles/breeding female (SD = 0.26) to 1.34 juveniles/breeding female (SD = 0.51; Fig. 5). We assumed that woodcock would nest throughout the intact patch of mature forest prior to management in this scenario, and therefore our estimate of productivity is not

Table 2. Cover type input values (ha) used in models to predict the number of juvenile American woodcock surviving to 15 d post-hatching produced under different management scenarios at Tamarac National Wildlife Refuge, Minnesota, USA. See text for descriptions of scenarios.

	Amount (ha) of cover type pre-management				Amount (ha) of cover type post-management			
	Mature forest	Upland shrubland	Wetland shrubland	Grassland	Mature forest	Upland shrubland	Wetland shrubland	Grassland
Scenario 1a	45.0	14.0	0	4.7	45.0	18.5	0	0.2
Scenario 1b	45.0	14.0	0	4.7	45.0	14.0	4.5	0.2
Scenario 2	60.2	2.2	0	0	45.2	0	18.7	0
Scenario 3	76.6	14.8	0	3.5	92.0	3.5	0	0

dependent on the available amount of nesting cover types. Only ~10% of female woodcock Daly (2014) monitored nested in expansive stands of mature forest >200 m from other cover types. Therefore, if we assume only 10% of the mature forest in this landscape (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, altering the input landscape parameters to represent forest succession of a diverse and patchy forest matrix of upland shrubland, mature forest, and grassland (Scenario 3; Table 2) resulted in an estimated 19% decline in woodcock productivity from 1.01 juveniles/breeding female (SD = 0.56) to 0.82 juveniles/breeding female (SD = 0.23; Fig. 6). When we accounted for the change in available nesting habitat following succession of grasslands to shrublands, and shrublands to mature forest, we found the area available for nesting on the landscape increased by 3.8% (3.5 ha) following management, which slightly mitigated declines in productivity of the entire landscape that we estimated to be -16%.

Discussion

We constructed spatially explicit models and predicted the nest survival rate and 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). Our models related structural and composition characteristics of cover types across a varied and complex landscape to survival rates of woodcock nests and juveniles. These models allow for identification of areas of high- and low-productivity (based on the location of the nest site) and 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-productivity 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. Like all statistical models of complex biological processes, our models should be interpreted considering their limitations and may not provide reliable predictions in other portions of the woodcock breeding distribution. The relatively small sample sizes and relatively data-driven method of arriving at final models prevented us from reasonably subsetting our data as required for 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 our study, these models provide a means of evaluating relative productivity across our study area.

Overall, our models generally corroborated the findings of other studies reporting no relationship between woodcock nest success and the cover type or vegetation structure immediately surrounding the nest (e.g., McAuley et al. 1996). Daly et al. (this volume, Breeding season survival of woodcock) reported similar stem density at woodcock nests over their 2-year study period, suggesting female woodcock selected nest sites with similar micro-scale features regardless of the composition of the greater landscape. We found that composition and configuration of cover types influenced woodcock nest survival rate at the landscape-scale (i.e., within 500-m radius of the nest). Based on the observed nesting behaviors of woodcock in our study 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 m^2/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 et al. (this volume, Breeding Season Survival of Woodcock). If female woodcock choose nest sites with similar micro-scale characteristics, it is logical that the greater surrounding landscape may be more likely to influence the survival rates of nests and juveniles and that females may select nest

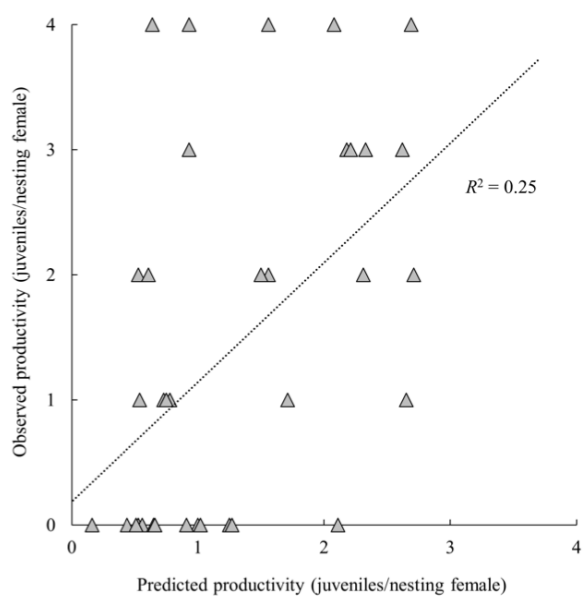

Figure 3. Predicted versus observed productivity (i.e., number of juveniles surviving to day 15) of American woodcock at Tamarac National Wildlife Refuge, Minnesota, USA. Slope of regression line is significantly different from zero ($\bar{x}$= 0.96, t = 3.44, P =0.001).

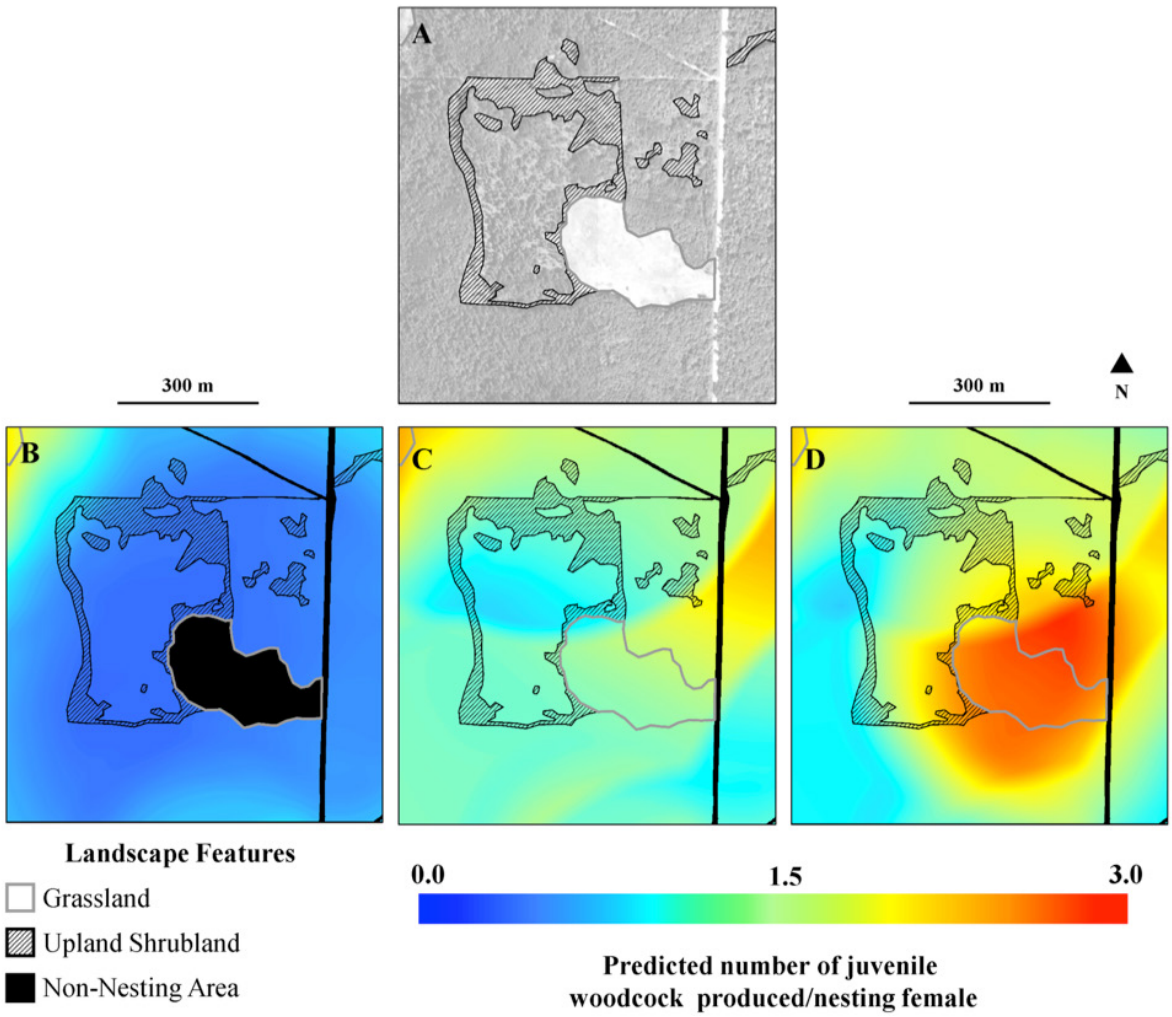

Figure 4. Aerial photograph (A) of a portion of Tamarac National Wildlife Refuge, Minnesota, USA, with a mix of cover types. Upland shrubland is delineated by hatched lines and grassland is marked with a thick gray border. Panel (B) shows the predicted productivity (i.e., number of juveniles produced 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 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 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.

sites that are nearer to cover types and landscape components that confer greater juvenile survival rates (Streby et al. 2014a). As such, management intended to increase the amount or quality of breeding habitat for woodcock may be most effective when managers fully account for the context of the surrounding landscape. Managing an area (e.g., a refuge or property) to contain all the landscape components that are required for highly productive woodcock populations may not be necessary, nor may it always be the best course of action. The inverse relationships between influential cover types (e.g., grassland and wetland shrubland) and the abundance of these cover types on the surrounding landscape may influence whether a manager creates more grassland, or allows a shrubland to mature depending on the context of the surrounding landscape. Our models can be used to help aid in these predictions.

We did not account for weather variables in our 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 rates of juvenile woodcock (Sheldon 1971, Owen 1977, Daly et al. 2015), weather-related stress

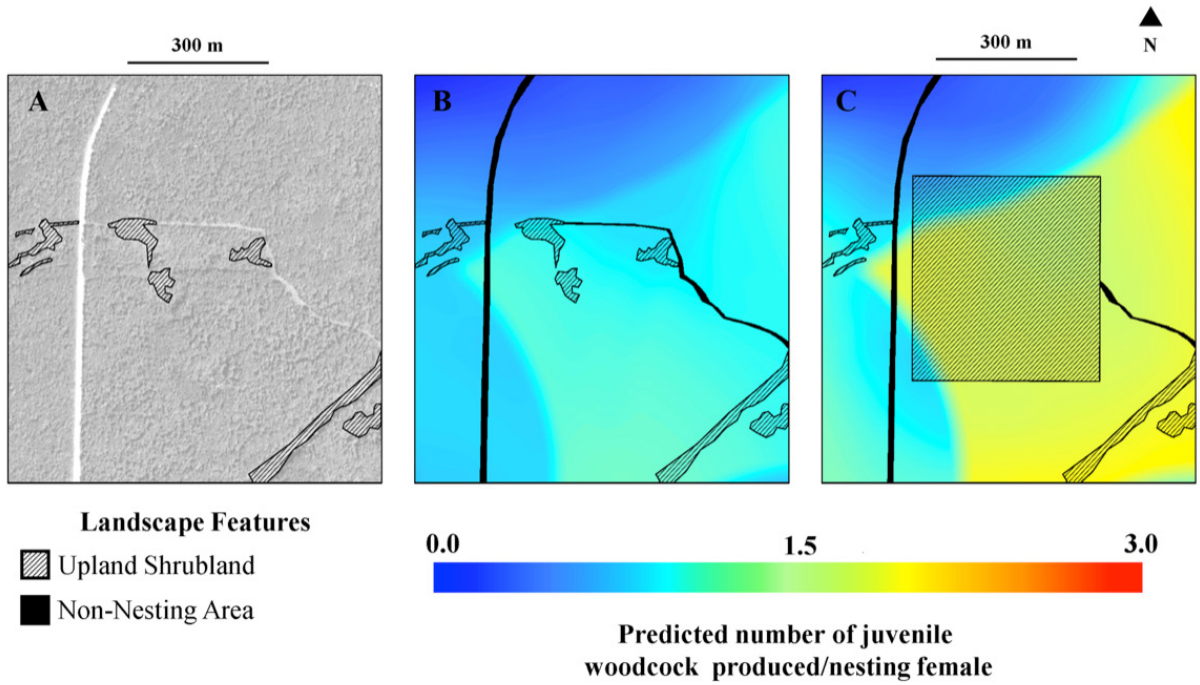

Figure 5. Aerial photograph (A) of a portion of Tamarac National Wildlife Refuge, Minnesota, USA, composed primarily of mature forest with several small patches of upland shrubland (hatched lines). Panel (B) shows the predicted productivity (i.e., number of juveniles produced reaching 15 days of age) of the landscape in (A), with cooler colors representing lower productivity and warmer colors representing higher productivity. Panel (C) displays the predicted productivity following alteration of input landscape parameters to represent clearcutting 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.

and juvenile woodcock growth rates (Rabe et al. 1983), 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 our primary goal was to determine the effects of different landscape compositions and configurations on the productivity of woodcock at our 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 mortality events. Additionally, some land-cover types may be more or less suitable to woodcock during inclement weather events and our models may include some effect of the interaction between weather and cover type. Future research may continue investigating 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, our models and predictions of 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 our 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 for 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). Our models generally suggest these wetlands may confer greater 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 or other open areas) that amount to ≤20% of the overall landscape. Our models demonstrated a negative relationship between grassland and survival rate of woodcock nests and, therefore, an upper limit closer to 5% of

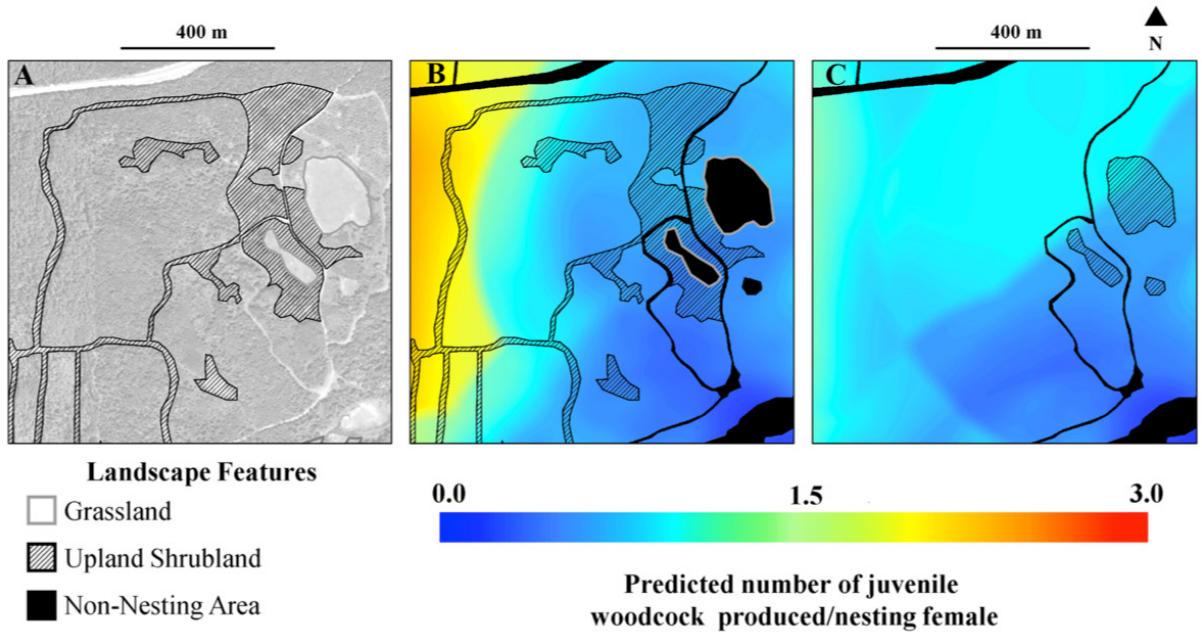

Figure 6. Aerial photograph (A) of a portion of Tamarac National Wildlife Refuge, Minnesota, USA, composed of a variety of land cover types with a complex and varied configuration. Upland shrubland (hatched lines) is present in large patches, and also small linear firebreaks. Grassland (solid gray lines) is also present on the landscape. Panel (B) shows the predicted 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 productivity following the alteration of input landscape parameters to represent succession of the landscape without any additional disturbance and/or management. In this scenario, our models allowed upland shrubland to succeed to mature forest, and grassland to succeed to upland shrubland. See text for detailed description of land cover types.

the landscape (e.g., 2 ha for every 40 ha managed) might lead to greater nest productivity in the region we studied. Woodcock are known to be territorial during the breeding period, with a single male often dominating a display area (i.e., peenting site; Weeks 1969). Woodcock are also known to use small clearings for displays, so limiting the amount of grassland on the landscape is unlikely to inhibit the ability for woodcock to display and attract mates (Gutzwiller and Wakeley 1980). However, in addition to serving as areas to display, open fields and grassland areas are known to be used by woodcock for foraging and roosting during the breeding and nonbreeding periods (Krohn 1971, Berdeen and Krementz 1998). Therefore, it may be informative to experimentally investigate the effects of the abundance of grassland cover on the occupancy and density of singing males, productivity of nesting females, and space use of nonbreeding, post-breeding, or migratory woodcock throughout the annual cycle to determine the relative importance of grassland cover for woodcock.

To maintain a diverse landscape suitable for woodcock, 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 4 age classes: 0–10, 11–20, 21–30, and 31–40 years post-harvest. As such, our models may be used to assess the geometry and configuration of managed stands through time to ensure that stand rotation continues to provide landscapes associated with high woodcock productivity. It is also critical to account for how the implementation of management may create landscapes that, at first, do not contain the desired or appropriate vegetation structure or land-cover type or contain cover types that are associated with low predicted productivity (e.g., clear-cutting does not immediately result in a dynamic shrubland; see Streby et al. 2018). This may result in infrequent use of these sites by woodcock and/or lower predicted productivity until the desired cover type or vegetation structure is achieved. Similarly, the value of particular landscapes for woodcock may peak and then decline as vegetation succeeds, which influences how managers might implement management to maximize the value of the management as the rates at which vegetation grows and matures is likely to be dependent on the region, climate, vegetation types, and soil types at a given site.

Our models are informed by data collected over 2 years; additional data would thus likely be necessary to validate and improve our models. Data from additional years would likely help account for variation in woodcock survival rate and reproduction and improve the predictive power of our models. However, even in the absence of nest and juvenile survival rate data from additional years, our 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. These types of models might be useful for investigations of woodcock productivity in other portions of the breeding distribution with woodcock-cover type relations different than those we observed. Comparing models of 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.

Acknowledgments

W. Brininger and T. Cooper were integral in developing this project and providing logistical support. We thank J. Nelson, M. Johnson, D. Page, and J. Lehman for their efforts capturing, radio-marking, and tracking woodcock, and we are especially grateful to D. Dustin and E. Johnson for volunteering many hours of their and their dogs' time to find woodcock nests and broods at Tamarac National Wildlife Refuge. We thank J. Fieberg, and S. Peterson for providing valuable assistance that aided in the development of our productivity models and for reviewing previous drafts of this manuscript. We thank Tamarac National Wildlife Refuge staff for logistical support. Comments by B. Collier, D. Diefenbach, and one anonymous reviewer greatly improved the quality of the manuscript. Use of trade names does not imply endorsement by the U.S. Government or the University of Minnesota. This project was funded by the U.S. Fish and Wildlife Service Webless Migratory Game Program through Research Work Order No. 91 at the U.S. Geological Survey Minnesota Cooperative Fish and Wildlife Research Unit, with additional funding provided by Woodcock Minnesota.

Literature Cited

Ausprey, I.J., and A.D. Rodewald. 2011. Postfledging survivorship and habitat selection across a rural-to-urban landscape gradient. Auk 128:293–302.

Bakermans, M.H., C.L. Ziegler, and J.L. Larkin. 2015. American woodcock and golden-winged warbler abundance and associated vegetation in managed habitats. Northeastern Naturalist 22:690–703.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18:1482–1491.

Bayne, E.M., and K.A. Hobson. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. Conservation Biology 11:1418–1429.

Berdeen, J.B., and D.G. Krementz. 1998. The use of fields at night by wintering American woodcock. Journal of Wildlife Management 62:939–947.

Boal, C.W., D.E. Andersen, and P.L. Kennedy. 2005. Foraging and nesting habitat of breeding male northern goshawks in the Laurentian mixed forest province, Minnesota. Journal of Wildlife Management 69:1516–1527.

Boyce, M.S., P.R. Vernier, S.E. Nielsen, and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modeling 157:281–816.

Boyle, B., T. Luke, K. Blackledge, W. Brininger, L. Deede, G. Muehlenhardt, G. DeAlessio, and J. Hodgins. 2010. Tamarac National Wildlife Refuge and Wetland Management District Comprehensive Conservation Plan. U.S. Fish and Wildlife Service, Tamarac National Wildlife Refuge, Rochert, MN, USA.

Braun, C.E., editor. 2005. Techniques for wildlife invstigations and management. Sixth edition. The Wildlife Society, Bethesda, Maryland, USA.

Brawn, J.D. and S.K. Robinson. 1996. Source-sink population dynamics may complicate the interpretation of long-term census data. Ecology 77:3–12.

Brohman, R.J., and L.D. Bryant, editors. 2005. Existing vegetation classification and mapping technical guide version 1.0. U.S.D.A. Forest Service General Technical Report WO-67. Washington, D.C., USA.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Second Edition. Springer-Verlag, New York, New York, USA.

Chalfoun, A.D., F.R. Thompson III, and M.J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. Conservation Biology 16:306–318.

Connelly, J.W., H.W. Browers, and R.J. Gates. 1988. Seasonal movements of sage grouse in southeastern Idaho. Journal of Wildlife Management 52:116–122.

Daly, K.O. 2014. Assessment of techniques to evaluate American woodcock population response to Best Management Practices applied at the demonstration-area scale. Thesis, University of Minnesota, St. Paul, Minnesota, USA.

Daly, K.O., D.E. Andersen, W.L. Brininger, T.R. Cooper. 2019. Evaluating techniques for estimating post-breeding-season age ratios for American woodcock. Pages 35–44 *in* D.G. Krementz, D.E. Andersen, and T.R. Cooper, Editors. Proceedings of the Eleventh American Woodcock Symposium. University of Minnesota Libraries Publishing, Minneapolis, Minnesota, USA.

Daly, K.O., D.E. Andersen, W.L. Brininger, T.R. Cooper. 2019. Breeding season survival of American woodcock at a habitat demonstration area in Minnesota. Pages 45–63 *in* D.G. Krementz, D.E. Andersen, and T.R. Cooper, Editors. Proceedings of the Eleventh American Woodcock Symposium. University of Minnesota Libraries Publishing, Minneapolis, Minnesota, USA.

Daly, K.O., D.E. Andersen, W.L. Brininger, and T.R. Cooper. 2015. Radio-transmitters have no impact on survival of pre-fledged American woodcocks. Journal of Field Ornithology 86:345–351.

DeMaso, S.J., A.D. Peoples, S.A. Cox, and E.S. Parry. 1997. Survival of northern bobwhite chicks in western Oklahoma. Journal of Wildlife Management 61:846–853.

Derleth, E.L., and G.F. Sepik. 1990. Summer-fall survival of American woodcock in Maine. Journal of Wildlife Management 54:97–106.

Dwyer, T.J., G.F. Sepik, E.L. Derleth, and D.G. McAuley. 1988. Demographic characteristics of a Maine woodcock population and effects of habitat management. U.S. Fish and Wildlife Service, Fish Wildlife Resource Report 4, Washington, D.C., USA.

ESRI 2016. ArcGIS Desktop: Release 10.1. Environmental Systems Research Institute. Redlands, California, USA.

Faaborg, J., M.C. Brittingham, T.M. Donovan, and J. Blake. 1995. Habitat fragmentation in the temperate zone. Pages 357–380 *in*

T.E. Martin and D.M. Finch, Eds. Ecology and management of Neotropical migratory birds. Oxford University Press, Oxford, UK.

Gregg, L. 1984. Population ecology of woodcock in Wisconsin. Wisconsin Department of Natural Resources, Technical Bulletin 144. Madison, Wisconsin, USA.

Gutzwiller, K.J., and J.S. Wakeley. 1980. Differential use of woodcock singing grounds in relation to habitat characteristics. Pages 51–54 *in* T.J. Dwyer and G.L. Storm, Eds. 7th American Woodcock Symposium. U.S. Fish and Wildlife Service, Wildlife Resource Report 14, Washington, D.C., USA.

Holbrook, H.T., M.R. Vaughan, and P.T. Bromley. 1987. Wild turkey habitat preferences and recruitment in intensively managed Piedmont forests. Journal of Wildlife Management 51:182–187.

Hoover, J.P., M.C. Brittingham, and L.J. Goodrich. 1995. Effects of forest patch size on nesting success of wood thrushes. Auk 112:146–155.

Horn, D.J., M.L. Phillips, R.R. Koford, W.R. Clark, M.A. Sovada, and R.J. Greenwood. 2005. Landscape composition, patch size, and distance to edges: interactions affecting duck reproductive success. Ecological Applications 15:1367–1376.

Hudgins, J.E., G.L. Storm, and J.S. Wakely. 1985. Local movements and diurnal-habitat selection by male American woodcock in Pennsylvania. Journal of Wildlife Management 49:614–619.

International Panel on Climate Change (IPCC). 2014. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Cambridge University Press, Cambridge, UK.

Kelley, J.R., S.J. Williamson, and T.R. Cooper, Eds. 2008. American Woodcock Conservation Plan: a summary of and recommendations for woodcock conservation in North America. Wildlife Management Institute, Washington, D.C., USA.

Klebenow, D.A. 1969. Sage grouse nesting and brood habitat in Idaho. Journal of Wildlife Management 33:649–662.

Kramer, G.R. 2017. Nonbreeding and migratory ecology of golden-winged warblers and effects of landscape composition and configuration on American woodcock productivity. Thesis, University of Minnesota, St. Paul, USA.

Krohn, W.B. 1971. Some patterns of woodcock activities on Maine summer fields. Wilson Bulletin 83:396–407.

Leopold, A. 1933. Game Management. Charles Scribner's Sons, New York.

Levin, S.A. 1992. The problem of pattern and scale in ecology: The Robert MacArthur Award Lecture. Ecology 73:1943–1967.

Lloyd, P., T.E. Martin, R.L. Redmond, U. Langner, and M.M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. Ecological Applications 15:1504–1514.

Manolis, J.C., D.E. Andersen, and F.J. Cuthbert. 2002. Edge effect on nesting success of ground nesting birds near regenerating clearcuts in a forest dominated landscape. Auk 119:955–970.

Martin, T.E. 1993. Nest predation and nest sites. Bioscience 43:523–532.

Masse, R.J., B.C. Tefft, and S.R. McWilliams. 2015. Higher bird abundance and diversity where American woodcock sing: fringe benefits of managing forests for woodcock. Journal of Wildlife Management 79:1378–1384.

McAuley, D.G., J.R. Longcore, D.A. Clugston, W. Haltman, and G.F. Sepik. 2010. Survival of American woodcock broods and chicks in Maine. Pages 175–184 *in* C.A. Stewart and V.R. Frawley, Eds. Proceedings of the Tenth American Woodcock Symposium, Michigan Department of Natural Resources and Environment, Lansing, Michigan, USA.

McAuley, D.G., J.R. Longcore, and G.F. Sepik. 1990. Renesting by American woodcocks (*Scolopax minor*) in Maine. Auk 107:407–410.

McAuley, D.G., J.R. Longcore, and G.F. Sepik. 1993a. Methods of woodcock research: experiences and recommendations. Pages 5–11 *in* J.R. Longcore and G.F. Sepik, Eds. Eighth American Woodcock Symposium. U.S. Fish and Wildlife Service, Wildlife Resource Report 16, Washington, D.C., USA.

McAuley, D.G., J.R. Longcore, and G.F. Sepik. 1993b. Behavior of radio-marked breeding American woodcocks. Pages 116–125 *in* J.R. Longcore and G.F. Sepik, Eds. Eighth American Woodcock Symposium. U.S. Fish and Wildlife Service, Wildlife Resource Report 16, Washington, D.C., USA.

McAuley, D.G., J.R. Longcore, G.F. Sepik, and G.W. Pendleton. 1996. Habitat characteristics of American woodcock nest sites on a managed area in Maine. Journal of Wildlife Management 60:138–148.

Meunier, J., R.S. Lutz, K.E. Doherty, D.E. Andersen, E. Oppelt, and J.G. Bruggink. 2006. Fall diurnal habitat use by adult female American woodcock in the western Great Lakes region. Pages 83–94 *in* C.A. Sterward and V.R. Frawley, Eds. Proceedings of the Tenth American Woodcock Symposium, Michigan Department of Natural Resources and Environment, Lansing, Michigan, USA.

Owen, Jr., R.B. 1977. American woodcock (*Philohela minor* = *Scolopax minor* of Edwards of 1974). Pages 149–186 *in* G.C. Sanderson, Ed. Management of migratory shore and upland game birds in North America. International Association of Fish and Wildlife Agencies, Washington, D.C., USA.

Peterson, S.M. 2014. Landscape productivity and the ecology of brood division in golden-winged warblers in the western Great Lakes region. Thesis, University of Minnesota, St. Paul, USA.

Peterson, S.M., H.M. Streby, and D.E. Andersen. 2016. Spatially explicit models of full-season productivity and implications for landscape management of golden-winged warblers in the western Great Lakes region. Pages 141–160 *in* H.M. Streby, D.E. Andersen, and D.A. Buehler, Eds. Golden-winged warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, Florida, USA.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rabe, D.L., H.H. Prince, and E.D. Goodman. 1983. The effect of weather on bioenergetics of American woodcock. Journal of Wildlife Management 47:762–771.

Refsnider, J.M., and F.J. Janzen. 2010. Putting eggs in one basket: ecological and evolutionary hypotheses for variation in oviposition-site choice. Annual Review of Ecology, Evolution, and Systematics 41:39–57.

Roberts, S.D., J.M. Coffey, and W.F. Porter. 1995. Survival and reproduction of female wild turkeys in New York. Journal of Wildlife Management 59:437–447.

Robinson, S.K., and D.S. Wilcove. 1994. Forest fragmentation in the temperate zone and its effects on migratory songbirds. Bird Conservation International 4:223–249.

Roboski, J.C., and M.K. Causey. 1981. Incidence, habitat use, and chronology of woodcock nesting in Alabama. Journal of Wildlife Management 47:762–771.

Rotella, J.J., and J.T. Ratti. 1992. Mallard brood survival and wetland habitat conditions in southwestern Manitoba. Journal of Wildlife Management 56:499–507.

Rudnicky, T.C., and M.L. Hunter, Jr. 1993. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. Journal of Wildlife Management 57:358–364.

Sauer, J.R., and J.B. Bortner. 1991. Population trends from the American woodcock Singing-ground Survey, 1970–88. Journal of Wildlife Management 55:300–312.

Seamans, M.E., and R.D. Rau. 2016. American woodcock population status, 2016. U.S. Fish and Wildlife Service, Laurel, Maryland, USA.

Sepik, G.F., W.H. Goudy, and D.R. Dessecker. 2000. Factors influencing recruitment and condition of American woodcock in

Minnesota. Pages 65–76 *in* D.G. McAuley, J.G. Bruggink, and G.F. Sepik, Eds. Proceedings of the Ninth American Woodcock Symposium, U.S. Geological Survey, Information and Technology Report 2000-0009, Laurel, Maryland, USA.

Shaffer, T.L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.

Sheldon, W.G. 1971. The book of American woodcock. University of Massachusetts Press, Amherst, Massachusetts, USA.

Shlaepfer, M.A., M.C. Runge, and P.W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 17:474–480.

Sovada, M.A., M.C. Zicus, R.J. Greenwood, D.P. Rave, W.E. Newton, R.O. Woodward, and J.A. Beiser. 2000. Relationships of habitat patch size to predator community and survival of duck nests. Journal of Wildlife Management 64:820–831.

Spears, B.L., M.C. Wallace, W.B. Ballard, R.S. Phillips, D.P. Holdstock, J.H. Brunjes, R. Applegate, M.S. Miller, and P.S. Gipson. 2007. Habitat use and survival of preflight wild turkey broods. Journal of Wildlife Management 71:69–81.

Steketee, A.K., and W.L. Robinson. 1995. Use of fluorescent powder for tracking American woodcock broods. Auk 112:1043–1045.

Stephens, S.E., J.J. Rotella, M.S. Lindberg, M.L. Taper, and J.K. Ringelman. 2005. Duck nest survival in the Missouri Coteau of North Dakota: landscape effects at multiple spatial scales. Ecological Applications 15:2137–2149.

Storm, G.L., R.D. Andrews, R.L. Phillips, R.A. Bishop, D.B. Siniff, and J.R. Tester. 1976. Morphology, reproduction, dispersal, and mortality of Midwestern red fox populations. Wildlife Monographs No. 49.

Streby, H.M., and D.E. Andersen. 2011. Seasonal productivity in a population of migratory songbirds: why nest data are not enough. Ecosphere 2(78):1–15.

Streby, H.M., G.R. Kramer, S.M. Peterson, and D.E. Andersen. 2018. Evaluating outcomes of management targeting the recovery of a migratory songbird of conservation concern. PeerJ 6:e4319 https://doi.org/10.7717/peerj.4319

Streby, H.M., J.M. Refsnider, and D.E. Andersen. 2014a. Redefining reproductive success in songbirds: moving beyond the nest success paradigm. Auk 131:718–726.

Streby, H.M., J.M. Refsnider, S.M. Peterson, and D.E. Andersen. 2014b. Retirement investment theory explains patterns in songbird nest-site choice. Proceedings of the Royal Society of London B: Biological Sciences 1117:20131834.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Weeks, H.P., Jr. 1969. Courtship and territorial behavior of some Indiana woodcocks. Proceedings of the Indiana Academy of Science 79:162–171.

Whiting, Jr., R.M. 2006. American woodcock singing-ground surveys: should they be expanded? Pages 153–159 *in* C.A. Steward and V.R. Frawley, Eds. Proceedings of the Tenth American Woodcock Symposium, Michigan Department of Natural Resources and Environment, Lansing, Michigan, USA.

Wildlife Management Institute. 2009. Best Management Practices for woodcock and associated bird species: Upper Great Lakes Woodcock and Young Forest Initiative. Wildlife Management Institute. <http://www.wildlifemanagementinstitute.org>

Wildlife Management Institute. 2010. Implementing the American Woodcock Conservation Plan: progress to date. Wildlife Management Institute, Washington D.C., USA.

Winterstein, S.R. 1992. Chi-square tests for intrabrood independence when using the Mayfield method. Journal of Wildlife Management 56:398–402.

Wisdom, M.J., and L.S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. Journal of Wildlife Management 61:302–312.