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Left out in the rain: Comparing productivity of two associated species exposes a leak in the umbrella species concept

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ABSTRACT

Multi-species approaches to wildlife management have become commonplace and purport to benefit entire biological communities. These strategies aim to manage different, often taxonomically distant species under a single regime based on shared habitat associations and/or co-occurrence in the landscape. We tested the efficacy of multi-species management in the context of creating and maintaining early-successional forest cover types using two species of migratory birds that breed in eastern North America and are each the focus of intensive, concurrent, and overlapping management. American woodcock (*Scolopax minor*) and golden-winged warblers (*Vermivora chrysoptera*) breed in similar diverse-forest landscapes. Each species purportedly benefits from management for the other species and both are often used as flagship species for the creation of young forest and the conservation of associated avian communities. However, the landscape-species relationships that drive reproductive success and population stability in these species have not been explicitly compared. Here, we use previously published spatially-explicit models of productivity (the number of juveniles raised to a biologically significant milestone) to identify the relationship(s) between productivity of American woodcock and golden-winged warblers across a shared landscape. We found productivity to be negatively associated between these species on the same landscape at all spatial scales we modelled (1 m^2–100 ha). Our results suggest that, with regards to productivity, American woodcock and golden-winged warblers have opposing relationships with the composition of the landscapes in which they coexist and therefore should not be assumed to benefit similarly from any individual management action at any relevant spatial scale.

1. Introduction

Multi-species management (i.e., efforts intended to benefit an ecosystem or suite of organisms that co-occur) is becoming more common in the face of limited conservation resources and increasing threats to local and global biodiversity (Gaston, 2000; Brooks et al., 2006). The goal of creating and managing landscapes that are suitable to entire ecological communities is rooted in the desire to provide efficient solutions to specific conservation crises while simultaneously benefitting other non-focal species within the community (e.g., Suter et al., 2002). However, due to the complexity of ecological communities, managers often lack necessary information regarding species-habitat relationships, factors driving vital rates, and the effects of complex interactions (e.g., predator-prey dynamics) that are required to predict and understand management outcomes for both focal and non-focal species (Simberloff, 1998; Andelman and Fagan, 2000). Therefore, multi-species management often relies on the assumption that co-occurring species will similarly benefit from landscape management intended to create or improve habitat for an associated focal species (Leopold, 1933; Cardosa da Silva et al., 1996; Simberloff, 1998; Morrison et al., 2006; Carlisle et al., 2018b).

Many species' associations with specific environments and numeric responses to different types of landscape manipulation are well documented (e.g., Dwyer et al., 1988; Rempel et al., 1997). However, the more important measure of a landscape's functionality is arguably a community's sustainability and productivity (Callicott and Mumford, 1997), parameters that are often overlooked in perspectives on umbrella species conservation. Using estimates of occupancy, abundance, or density of a species to infer the “quality” or appropriateness of a specific landscape can be misleading as these measures can be poor

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indicators of productive populations (Van Horne, 1983; Vickery et al., 1992; but see Bock and Jones, 2004). This is concerning as many species are known to choose areas conferring low productivity (i.e., ecological traps or population sinks; Pulliam, 1988; Trine, 1998; Schlaepfer et al., 2002; Battin, 2004), emphasizing the importance of understanding the effects of landscape management on all species of concern within a targeted ecological community to avoid creating positive outcomes for some species only to negatively affect others.

The effectiveness of multi-species management practices varies by system, defined goals, and method of outcome assessment (Branton and Richardson, 2011). Rarely are managers aware of the effects of their actions on demographic rates (e.g., survival rates, reproduction rates) of associated species in a targeted biotic community (Van Horne, 1983). Therefore, the assumption that any numerical response of associated species to landscape modification is associated with their underlying demographic parameters often goes untested (Van Horne, 1983; Johnson, 2007; Grant et al., 2017). Ignoring, or lacking the capacity to measure, the potential effects of management on the productivity of associated species may (1) create population sinks, (2) create ecological traps, and/or (3) otherwise reduce the productivity of associated species (Van Horne, 1983). Similarly, the inability to quantify the effects of management on the productivity of the co-occurring species within a targeted biological community could also impede the recognition and dissemination of successful and effective management practices.

In eastern North America, multi-species management focused on young forest cover types provided an opportunity to assess whether two focal species benefit from management targeted at a co-occurring species. American woodcock (*Scolopax minor*; hereafter woodcock) are short-distance migrant, forest-nesting shorebirds (Charadriiformes) managed as a game species in the eastern United States and adjacent southern Canada. Golden-winged warblers (*Vermivora chrysoptera*; hereafter warblers) are Nearctic-Neotropical migrant songbirds (Passeriformes) that breed throughout the Laurentian Great Lakes states and provinces with vestiges of breeding populations along the Appalachian Mountains. Both species co-occur in many areas across their breeding distributions and are associated with similar dynamic forest systems with high patch-level diversity in vegetation age and structure. Both species are experiencing regionally variable population trajectories and are the focus of intensive breeding-habitat conservation efforts (Sauer and Bortner, 1991; Wildlife Management Institute, 2010; Roth et al., 2012; Sauer et al., 2017). These two species are often described as having similar habitat requirements and are regularly touted as surrogate species for one another, or umbrella species for young- and early-successional forest communities (e.g., Bakermans et al., 2015). A common assumption is therefore that management to benefit one of these species similarly benefits the other (Roth et al., 2012; Bakermans et al., 2015; Masse et al., 2015), although woodcock and warblers have different life-histories and likely do not compete for resources or niche-space (i.e., physical space, food). Predation of nests and juveniles is the primary factor limiting productivity in both woodcock and warblers (Derleth and Sepik, 1990; Peterson et al., 2016a; Streby et al., 2016) though weather also can affect woodcock productivity (Sepik et al., 2000). Additionally, predation pressure associated with certain cover types is known to influence patterns in space use during the breeding season in both woodcock (Masse et al., 2013) and warblers (Streby et al., 2014b). As such, it is possible that these species may have evolved similar relationships with landscape and habitat components in response to the selective pressure of predation and may respond similarly to management strategies if those strategies affect the distribution or abundance of predators (Wildlife Management Institute, 2010; Roth et al., 2012; Bakermans et al., 2015; Masse et al., 2015).

We tested the hypothesis that woodcock and warblers serve as surrogate or umbrella species for one another by comparing the productivity of each species using published data collected over the same period in the same landscape (Peterson et al., 2016a; Kramer et al., in press). Peterson et al. (2016a) and Kramer et al. (in press) used demographic data (i.e., nest and juvenile survival rates) to inform and build spatially-explicit models of productivity for both species. We used these spatially-explicit models to compare the productivity of both species at multiple spatial scales. We predicted that productivity of both species would respond similarly to cover-type factors and thus, both species could be managed together at relevant spatial scales under a single management regime.

2. Methods

2.1. Study area

We used published data from field studies of woodcock (Daly, 2014; Kramer et al., in press) and warbler (Peterson, 2014; Peterson et al., 2016a) productivity at Tamarac National Wildlife Refuge (NWR), in Becker County, Minnesota, USA (47.049°N, 95.583°W) from 2011–2012. Tamarac NWR encompassed > 17 000 ha of primarily forested cover types interspersed with lakes, rivers, and wetlands (Appendix). Data from the Breeding Bird Survey (Sauer et al., 2017) and the American Woodcock Singing-Ground Survey (Seamans and Rau, 2017) suggest that populations of warblers and woodcock in this region of Minnesota are numerically stable or slightly increasing. Additionally, reports of productivity of both warblers and woodcock breeding within Tamarac NWR suggest these populations are a source for both species (Daly, 2014; S. Peterson and H. Streby, unpubl. data).

2.2. Demographic data collection

Similar methods were used to monitor woodcock and warblers to estimate nest and juvenile survival rates (see Daly, 2014 and Peterson, 2014 for detailed descriptions of methods). Briefly, adult females were radio-marked and tracked to nests (Peterson et al., 2015). Nests were monitored at 2–3-day intervals until the nest failed (i.e., due to depredation or abandonment), or succeeded (i.e., evidence that ≥1 egg hatched for woodcock, or ≥1 offspring left the nest for warblers). Newly hatched juvenile woodcock are semiprecocial and leave the nest site soon after hatching. In contrast, warblers are altricial and remain in the nest ~9 days. Juveniles of both species remain reliant on adult care for multiple weeks after leaving the nest. Hereafter, we refer to young birds of each species that have left the nest as juveniles. A random subset of juveniles (usually 2, but up to 4 woodcock and 5 warblers) were marked from woodcock and warbler broods (i.e., groups of recently hatched juveniles from the same nest). Additional juvenile warblers were captured and marked during mist-netting operations, and juvenile woodcock were captured and marked using trained pointing dogs (Daly, 2014). Juveniles were tracked using ground-based radio telemetry 4–7 days per week to monitor survival. Juvenile mortalities that were attributed to exposure (i.e., inclement weather) were censored, as we were interested in the relationship between predation and cover-type factors (Appendix). Transmitters had no discernable effect on the survival rate of juvenile woodcock (Daly et al., 2015) or any measured aspect of warbler productivity (Streby et al., 2013; Appendix). All juvenile woodcock were treated as independent experimental units (based on tests of independence from Daly et al. [in press], Appendix) in models of survival rate whereas warblers were randomly sampled from independent sub-broods (Appendix).

2.3. Landscape attributes and model development

Nest-site selection in birds (and other animals) has fitness ramifications that extend beyond the survival of the nest contents because the location of a nest influences the conditions that will be experienced by recently hatched young (Refsnider and Janzen, 2010; Streby et al., 2014a). Therefore, Peterson et al. (2016a) and Kramer et al. (in press) investigated the effects of the landscape surrounding the nest sites of woodcock and warblers on nest survival rates and juvenile survival

Table 1
Demographic rates, survival-period length, and estimates of mean productivity of American woodcock (2011–2012) and golden-winged warblers (2010–2012) at Tamarac National Wildlife Refuge (NWR), Minnesota, USA.

	American woodcock	Golden-winged warbler
Apparent nest survival rate	27/48 (56%)	89/216 (41%)
Nest survival period length (d)	25	25
Apparent juvenile survival rate	65/90 (72%)	120/190 (63%)
Juvenile survival period length (d)	15	8[a]
Total nesting area (ha)	753	517
Mean productivity (juveniles/female)[b]	1.6	1.7
SD of productivity (juveniles/female)	0.8	0.7

[a] Juvenile survival period in warblers was split into "early" (i.e., days 1–3) and "late" (i.e., days 4–8) survival periods.
[b] Mean productivity of all possible nesting sites in a 900-ha portion of Tamarac NWR.

rates for periods when individuals were still linked spatially to the nest site and the surrounding landscape (Table 1, Appendix). Kramer et al. (in press) and Peterson et al. (2016a) investigated the relationship among period-specific survival rates and six land cover types: deciduous forest (hereafter mature forest), upland shrubland, forested wetland, grassland, wetland shrubland, and a linear measure of shrubland edge, which is purported to be important to both species (Wildlife Management Institute, 2010; Roth et al., 2012; Peterson, 2014; Kramer, 2017; see Appendix for definition of cover types). Relationship between cover type and period-specific survival rates of each species were explored at different spatial scales by modeling the impact radius for each of the six spatial covariates described above following the methods described in Peterson (2014), Peterson et al. (2016a), Kramer (2017), and Kramer et al. (in press). Simply, the impact radius identified the scale at which each landscape variable was most strongly associated with survival rates of nests and juveniles. The impact radius for each landscape variable was determined by buffering each nest location with circles of different radii. The 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 relevant survival period. Instead, these radii represent the scale at which cover types might generally be available to juvenile warblers and woodcock during unique survival periods 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). Relationships between the amount of each cover type and nest survival rates of woodcock and warblers were explored at radii of 25–500 m. The same set of radii (i.e., 25–500 m) were tested in the exploration of factors influencing juvenile warbler survival rates and larger radii were tested for juvenile woodcock (100–1 000 m) to account for the greater species-specific mobility of juveniles during this period (Daly, 2014; Peterson, 2014; Peterson et al., 2016b). Juvenile warblers are flightless 1–3 days post-fledging and therefore, smaller impact radii (i.e., 25–200 m) were tested that reflected a biologically relevant scale at which predators could potentially influence survival rates during this period (i.e., early juvenile survival).

The sum of the total area (ha) for each cover type and the total linear distance of edge (km) contained within each buffer around each nest location were used to model the relationships between landscape variables and survival rates at each scale (i.e., impact radii). Peterson et al. (2016a) constructed linear models and explored potential quadratic and cubic relationships between landscape components and survival rates of warblers using PROC GENMOD in SAS (SAS Institute, Chicago, IL). Kramer et al. (in press) followed identical methods to model relationships between landscape components and survival rates of woodcock but performed them in R (R Core Team, 2017). Both Peterson et al. (2016a) and Kramer et al. (in press) ranked models of nest and juvenile survival rate using Akaike's Information Criterion adjusted for sample size (AIC_c; Burnham and Anderson, 2002). Both Peterson et al. (2016a) and Kramer et al. (in press) selected cover types and impact radii as covariates in productivity models using a combination of AIC_c rankings and biologically informed predictions (full details and model output provided in Peterson, 2014, Peterson et al., 2016a, Kramer, 2017, and Kramer et al. in press).

Following the selection of model covariates, logistic exposure survival-rate models (Shaffer, 2004) were built for each potential combination of important landscape components at their determined impact radius (Table A.1, Table A.2, Table A.3) to estimate daily survival rate for each pixel (i.e., 1 m^2) on the digitized landscape (see Appendix for details of classification process) informed by the landscape composition and configuration surrounding that pixel. Daily survival rate (S) was estimated for each observed combination of landscape structure and composition ($_l$) and survival period ($_p$; e.g., nest period) as:

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

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

To predict survival rate over each entire period (i.e., nest and juvenile) the daily survival rate estimate was raised to a power equal to the number of days in the period (e.g., for woodcock this was 25 [days for the nesting period] and 15 [days for the juvenile period]). Peterson et al. (2016a) and Kramer et al. (in press) applied these species-specific logistic exposure survival rate equations to the landscape using the amount of each landscape variable surrounding a given pixel at the predetermined impact radius and the β-coefficients from the logistic exposure survival rate equations for each appropriate landscape variable to estimate survival rates of nests and juveniles of woodcock and warblers. Nest productivity (i.e., the number of juvenile woodcock hatching, the number of juvenile warblers leaving the nest; NP) was calculated given the assumed ability for one renesting attempt (i.e., one additional nesting attempt following previous nest failure), using a mean brood of four juveniles (Zammuto, 1986; Peterson et al., 2016a; Appendix) as,

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

where NS is nest survival rate. Both woodcock and warblers routinely initiate a new nest after experiencing nest failure but it is rare for females to renest more than once in a single breeding season (McAuley et al., 1990; Bulluck et al., 2013). Productivity (i.e., the number of juveniles raised to 8 days post-fledging [warblers], or 15 days post-hatching [woodcock]; P) was calculated as

$$P = NP * JS$$

where JS is juvenile survival rate from hatch day to day 15 in woodcock, and the product of the early (days 1–3 post-fledging) and late (days 4–8 post-fledging) juvenile period survival rates in warblers. These equations were applied to the digitized landscape to produce raster surfaces containing values for productivity of hypothetical woodcock and warbler nests placed within each pixel (1 m^2) of the study area. As for all statistical models of complex biological processes, Peterson et al. (2016a) and Kramer et al. (in press) caution these models should be interpreted with their limitations in mind. Here, we use the output of these models (namely, spatially-explicit productivity surfaces) to evaluate whether woodcock and warbler productivity was associated with landscape composition similarly. Detailed discussions of model assumptions and demonstration of validation (k-fold cross validation; Boyce et al., 2002) are provided in Peterson (2014), Peterson et al. (2016a), Kramer (2017), and Kramer et al. (in press).

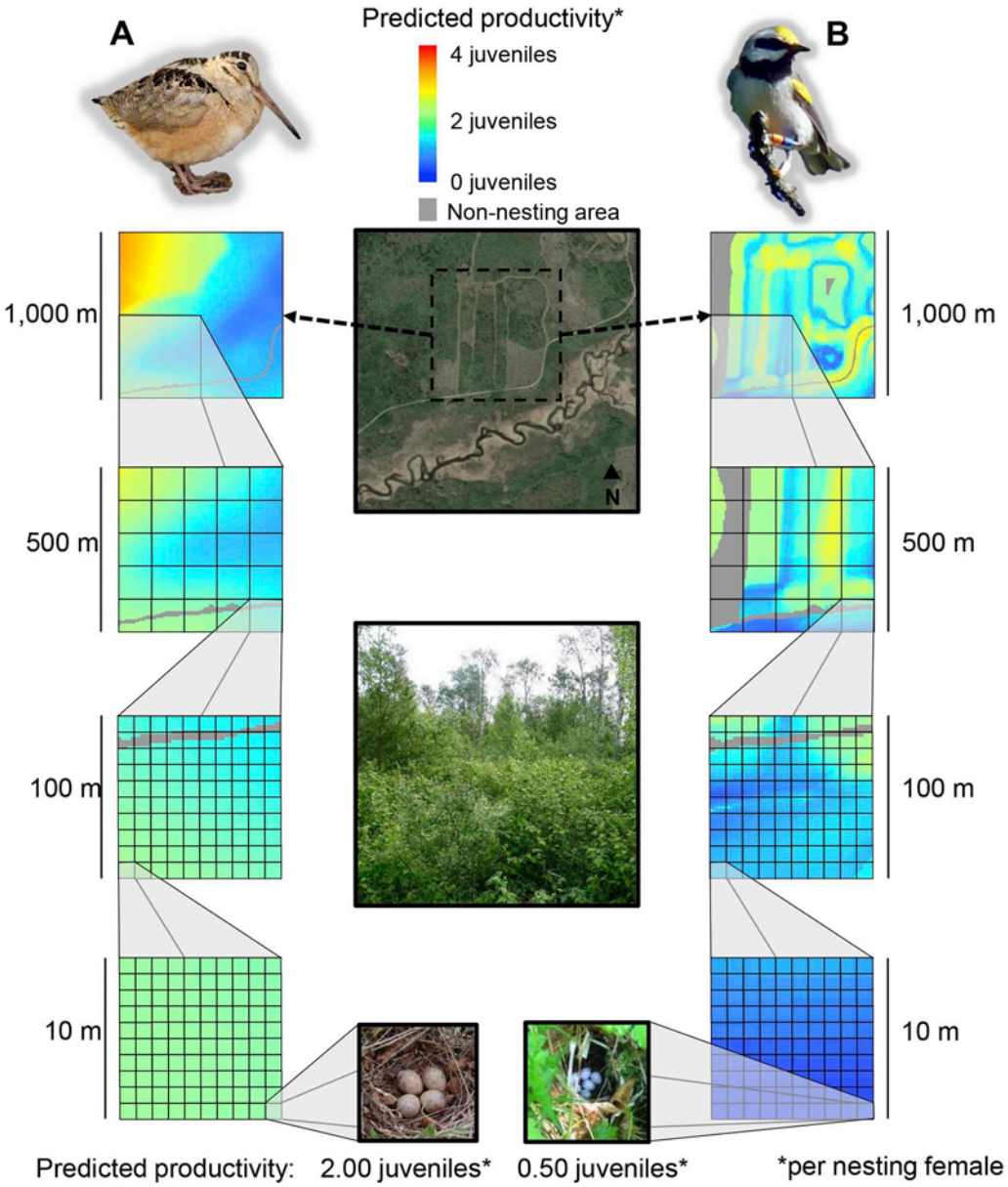

Fig. 1. Conceptual model for correlating and comparing productivity of American woodcock (A) and golden-winged warblers (B). We used spatially explicit models to predict the productivity (i.e., number of juveniles raised to a biologically relevant milestone per nesting female) across suitable nesting areas at Tamarac National Wildlife Refuge, Minnesota, USA from 2011-2012 (woodcock) and 2010-2012 (warblers). We estimated the average predicted productivity of the landscape for each species at different spatial scales from the nest-site level (1 m^2) to a broader landscape level (100 ha). We then compared predicted productivity (1 m^2) and average predicted productivity (0.1 ha–100 ha) of woodcock and warblers across the landscape at different spatial scales relevant to management to investigate whether landscapes that are productive for one of the species are similarly productive for the other.

2.4. Assessing productivity of two species on the same landscape

Using the spatially-explicit productivity surfaces produced by Peterson et al. (2016a) and Kramer et al. (in press), we compared productivity in a 900-ha portion of Tamarac NWR containing a range of land-cover types that were representative of the study area. We masked areas that were unsuitable or unused for nesting for both species based on observed nest locations determined through standard nest-searching protocols and radio telemetry (Daly, 2014; Peterson et al., 2016a). Thus, we masked roads, open water, grassland, and mature forest that was > 300 m from shrubland for woodcock and > 100 m from shrubland for warblers from our analysis. Areas beyond these limits were still used to inform models because of their proximity to nesting areas, but they were given no value for productivity as breeding locations because they were not used for nesting. We were not interested in comparing productivity of areas in which only one species would be expected to nest or where neither species would be expected to nest; therefore, we compared productivity of both species where their expected nesting areas overlapped; essentially the entire warbler nesting area. We compared the productivity of woodcock and warblers at each potential nesting site (1 m^2) and compared the average productivity of suitable nesting areas within 10, 100, 500, and 1 000 m of equally-spaced points throughout our focal area (Fig. 1) via correlation and simple linear regression (Kramer et al., 2019) in R (R Core Team, 2017).

3. Results

Peterson et al. (2016a) monitored 216 warbler nests and 190 warbler juveniles from 2010–2012 that informed our spatially-explicit model of warbler productivity at Tamarac NWR. Daly (2014) monitored 48 woodcock nests and 90 woodcock juveniles at Tamarac NWR from 2011–2012 that informed our spatially-explicit models of woodcock productivity reported in Kramer et al. (in press). Sixty-one percent of the warbler nests (n = 131) and 49% of the juveniles (n = 94) used to inform these models were monitored at Tamarac NWR (Appendix). One hundred percent of woodcock nests and juveniles used in this study were monitored at Tamarac NWR. Apparent nest survival rate was 56% (27/48) for woodcock and 41% (89/216) for warblers (Table 1). Apparent juvenile survival rate was 72% (65/90) for woodcock and 63% (120/190) for warblers. The area available to woodcock for nesting was

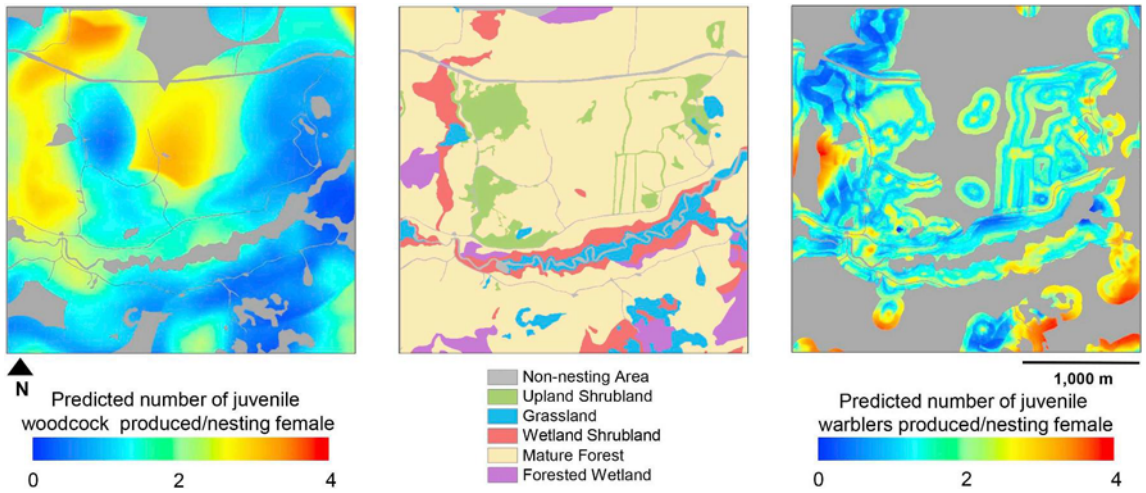

Fig. 2. Predicted productivity (i.e., number of juveniles raised to a biologically relevant milestone per nesting female) of American woodcock (left; 2011-2012) and golden-winged warblers (right; 2010-2012) over a 900-ha portion of Tamarac National Wildlife Refuge, Minnesota, USA. Warmer areas in the heat maps represent portions of the Refuge in which predicted productivity is high and cooler areas represent portions where predicted productivity is low. Areas denoted with hashed lines represent non-nesting areas (see text for definition of cover types and non-nesting area). The center map shows cover types used in spatially-explicit models of productivity. Woodcock predicted productivity surface is adapted from Kramer et al. (in press). Warbler predicted productivity surface is adapted from Peterson et al. (2016a).

27% greater than the area available to warblers. Therefore, our comparisons of productivity included ~75% of possible nesting sites of woodcock and all possible nesting sites of warblers (Table 1; Fig. 2).

Productivity of both species varied across the landscape (Fig. 2). Generally, woodcock experienced higher predicted productivity in areas with more wetland shrubland and fewer large patches of contiguous upland shrubland (Fig. 2). Warblers experienced higher predicted productivity in areas with a combination of forested wetland, upland shrubland, and mature forest (Fig. 2). The scale at which cover-type factors influenced productivity differed between woodcock and warblers. Across all survival periods, woodcock survival rates tended to be related to cover-type factors over a larger surrounding area (i.e., impact radii ≥250 m) than warbler survival rates. The nest survival rate of woodcock was related to cover-type factors within 500 m of the nest, whereas warbler nest survival rate was associated with cover-type factors within 200 m of the nest (Table A.1). Juvenile survival rates of woodcock were related to cover-type factors within 250–1 000 m (varied by cover type) whereas juvenile survival rates of warblers were associated with factors within 25–400 m. As a result, the variation in predicted productivity for woodcock and warblers differed in spatial distribution. In other words, areas across which we predicted woodcock to experience high or low productivity were larger and less variable than areas where we predicted that warblers would experience high or low productivity.

The productivity of woodcock and warblers was negatively associated at every spatial scale we compared (Fig. 3). At the nest-site scale (1 m^2), the overall relationship between predicted woodcock and warbler productivity at hypothetical nest sites (i.e., all pixels in appropriate nesting cover types; $\bar{x} = -0.32$, $F_{1,\ 4\ 523\ 387} = 589\ 714$, $P < 0.001$; Fig. 3) was similar to the relationships of predicted productivity at observed nests of both woodcock ($\bar{x}_{woodcock} = -0.23$, $F_{1,\ 43} = 3.9$, $P = 0.06$) and warblers ($\bar{x}_{warblers} = -0.33$, $F_{1,\ 143} = 27.6$, $P < 0.001$; Fig. 4), indicating that woodcock and warblers at Tamarac NWR chose nest sites in areas representing a broad range of predicted productivities and did not exhibit a tendency for selecting nest sites in areas with high predicted productivity for both species. Average productivity for both species over the entire study area (900 ha) was similar (Fig. 3), as was the variance in productivity (Table 1; Fig. A.1). Productivity was negatively correlated for woodcock and warblers at all scales we considered (Fig. 3; Fig. A.1), except that we were unable to assess whether there was a relationship between woodcock and warbler productivity at the 900-ha scale because our sample size at that scale was one.

4. Discussion

We found strong evidence that the composition and configuration of land-cover types was associated with productivity of both American woodcock and golden-winged warblers in our study area. However, we found no evidence to support our hypothesis that cover-type factors were related to productivity similarly between species. Our results indicated that areas associated with high woodcock productivity were associated with low warbler productivity across all spatial scales up to 900 ha. Woodcock productivity was related to factors at larger spatial scales than warbler productivity.

Recently, Grant et al. (2017) reported negative relationships between nest survival rates of songbirds and ducks (Anseriformes) co-occurring on the same managed landscape. Our findings suggest a similar issue: current management purported to benefit both woodcock and warblers may be falling short of its stated goal. At a broader scale (i.e., 900 ha), mean productivity of these two species was similar (Table 1), suggesting that in the same region or broader landscape context these two species might maintain productive populations when there is a high diversity and heterogeneity in land-cover types and configuration. However, we were unable to assess the relationship between woodcock and warbler productivity at this scale, and it is therefore not clear whether the negative associations we observed at smaller spatial scales exists at larger landscape scales. Importantly, we found that woodcock and warbler productivity were negatively correlated across multiple spatial scales including those that are the primary focus of management activities targeting these species (i.e., stand-level scales [1–100 ha]; Wildlife Management Institute, 2010; Roth et al., 2012). Although abundances of both species were high in our study area, there was significant variation in productivity across the landscape and we observed both species nesting in areas that appeared to confer low productivity. Animals are known to select breeding cover that is maladaptive and results in lower reproductive success (e.g., Schlaepfer et al., 2002; Chalfoun and Schmidt, 2012). Our observations demonstrate that the presence or abundance of nesting woodcock and warblers does not necessarily indicate highly productive habitat and therefore, the success of management intended to benefit either species should not be measured solely by apparent occupancy, abundance, or density (Van Horne, 1983; Crosby et al., 2015).

The disparity between woodcock and warbler productivity within the same landscape may result from differences in the predator

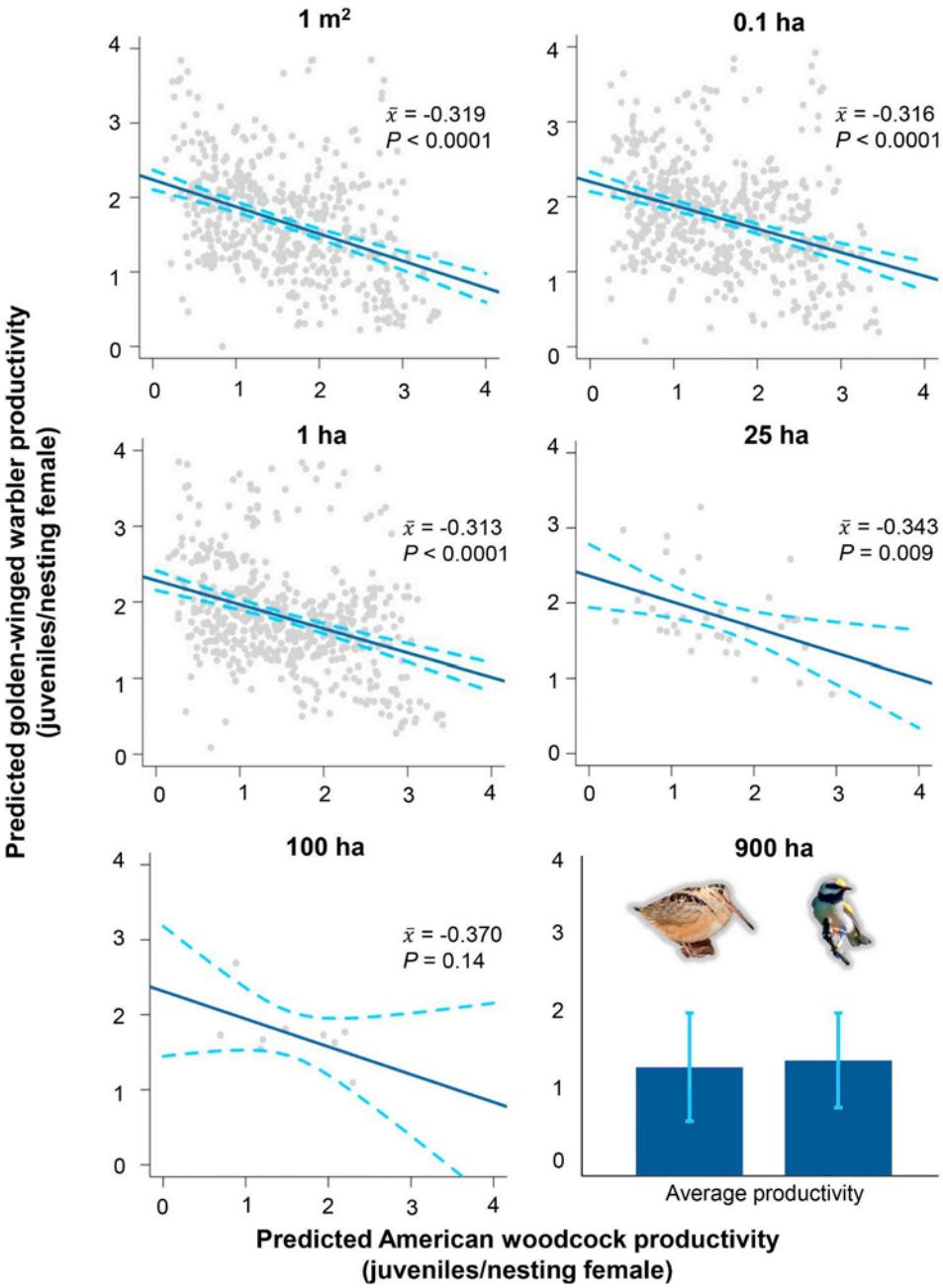

Fig. 3. Scatterplots depict relationships between predicted productivity (i.e., number of juveniles raised to a biologically relevant milestone per nesting female) of American woodcock (2011-2012) and golden-winged warblers (2010-2012) at different spatial scales (1 m^2–100 ha) at Tamarac National Wildlife Refuge, Minnesota, USA. Solid lines represent linear models and dotted lines represent 95% confidence intervals. Points (n = 500) displayed in the first three graphs (1 m^2, 0.1 ha, 1 ha) were randomly sampled (without replacement) from the full sample for display purposes. Similarly, confidence intervals for the first three graphs were created using the randomly sampled points because the large number of pixels (n = 4 531 848, n = 48 462, and n = 651, respectively) resulted in extremely small error estimates. Bar-chart (bottom-right) illustrates the average productivity (± SD) of both species across the entire 900-ha study area.

communities affecting these species. Predation is known to drive differences in observed space use (Breed et al., 2017), and is the primary factor limiting the survival rate of songbird nests (Martin, 1993) and juveniles (Anders et al., 1997). Predation is the primary factor limiting the reproductive success (i.e., nest survival rate and juvenile survival rate) of both woodcock and warblers (Derleth and Sepik, 1990; Peterson et al., 2016a). Woodcock nests tend to be depredated by mink (*Mustela vision*), striped skunks (*Mephitis mephitis*), red foxes (*Vulpes vulpes*), and other meso-predators whereas warbler nests are more susceptible to predation from small mammals including least chipmunks (*Tamias minimus*) and eastern chipmunks (*T. sciurus*), *Peromyscus* mice, and garter snakes (*Thamnophis* spp.) in addition to meso-predators (Daly, 2014; Peterson et al., 2016a). Juveniles of both woodcock and warblers are suitable prey for many of the same predators, but woodcock are larger than warblers and therefore may be less likely to be depredated by smaller predators (e.g., garter snakes, small mammals, etc.). Smaller predators generally have smaller home ranges and their dispersion and abundances are likely driven by smaller-scale variations in land cover (Harestad and Bunnell, 1979). Therefore, the scales at which different cover types were related to survival rates during different survival periods may be linked to the primary predator communities that are most likely to depredate nests and juveniles of each species (Streby et al., 2014b). Woodcock and warblers also have different migration strategies (Myatt and Krementz, 2007; Kramer et al., 2017) and although their breeding periods overlap substantially, woodcock can begin breeding earlier in the spring, potentially exposing nests and juveniles to a different suite of predators (e.g., fewer migratory raptors, prepartum mammalian predators). Furthermore, many predators of warbler nests and juveniles are preyed upon by predators of woodcock nests and juveniles, which suggests that predator dynamics and their influence on productivity of both woodcock and warblers in this system are complex and likely warrant further study (Dunn, 1977; Schmidt and Ostfeld, 2008). It is also possible that the abundance of predators and the composition of predator communities

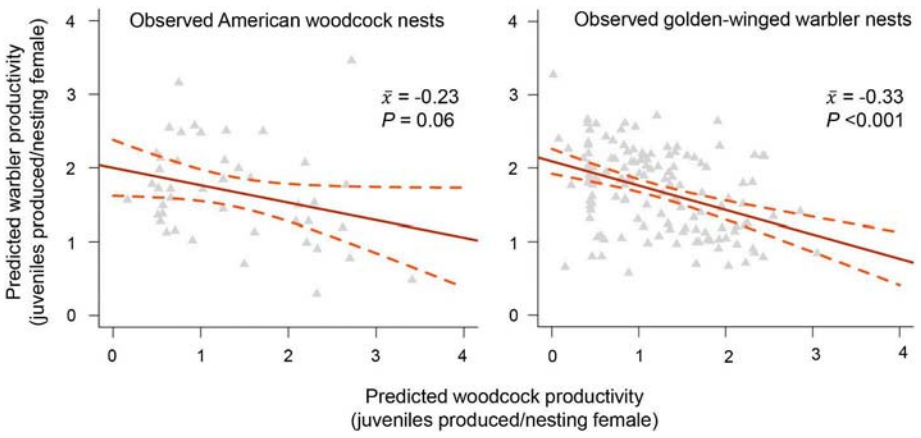

Fig. 4. Scatterplots showing the relationship between predicted productivity (i.e., number of juveniles raised to a biologically relevant milestone per nesting female) of American woodcock (2011-2012) and golden-winged warblers (2010-2012) at monitored nests. Observed nests within Tamarac National Wildlife Refuge, Minnesota, USA are represented by triangles. Slopes of linear regressions (solid lines) are presented with 95% confidence intervals (dashed lines).

may vary on timescales that exceed the duration of our study. As such, our observations of woodcock and warblers selecting nest-sites that are in areas that are associated with low productivity (i.e., potentially maladaptive) may represent an adaptive response to unpredictably variable trends in predation pressure (Rotenberry and Wiens, 1989). Similarly, the effects of seasonality and climatic variation on the productivity of these two species remain unknown and may be helpful in elucidating differences between productivity in these species. Lastly, the fitness of individuals is ultimately constrained by life-history traits (e.g., clutch size) and other factors that reflect adaptive tradeoffs between resource availability, parental investment, and fitness (Martin, 1987). Our measure of productivity accounts for variation in predator-caused mortality, which limits nest- and juvenile-survival rates of woodcock and warblers. Future studies in systems that exhibit greater variation in resource availability and focus on species with more variable life-history traits may benefit from including these factors into models of productivity.

We caution that every landscape is unique and the size of proposed management actions, surrounding landscape composition, and geographic region may influence the resulting productivity of species breeding in or near a newly managed site. Using spatially-explicit models of productivity may provide a useful avenue for predicting post-management productivity of multiple species (in our case, woodcock and warblers) prior to implementation. Such a proactive approach may ultimately affect the decision to implement management, the targeted species for which management is being implemented, or the type of management depending on the management's stated goals and desired outcomes. Despite a growing body of literature documenting poor success in achieving conservation goals using multi-species approaches (Burnett and Roberts, 2015; Hiers et al., 2016; Carlisle et al., 2018a), threatened and declining species continue to be regularly incorporated into community- and ecosystem-level management strategies. Notably, endangered species that are included in multi-species management plans may be more likely to exhibit declining population trends than species with individualized management plans (Clark and Harvey, 2002). Successful multi-species management outcomes remain uncommon, and instances where successful outcomes are reported rarely provide evidence of synchrony between landscape management and demographic responses of multiple species (Rubinoff, 2001; Suter et al., 2002).

The results from our study area in the northwestern portion of both species' breeding distributions suggest the need for similar investigations of landscape-productivity associations between these two species more broadly across their overlapping breeding ranges. Management intended to benefit both woodcock and warblers may be more effective if it prioritizes one species over the other at spatial scales typical of individual management actions with the goal of producing highly productive populations of both species regionally. Alternatively, productivity of both species could be locally optimized to produce a landscape conferring moderate productivity for both woodcock and warblers without maximizing productivity of either species. We argue that either strategy is preferable to implementing a multi-species management approach and relying on the unsubstantiated assumption of symmetric, increased productivity in both species following management, which our models suggest is an unlikely outcome in our study area. In reality, managers are often tasked with creating and maintaining landscapes that support populations of numerous species. The fact that associated species may exhibit opposing responses to cover-type management might encourage managers to carefully consider potential tradeoffs resulting from management decisions, especially when the area available for implementing management is limited. Our results suggest that neither woodcock nor warblers may be effective umbrella species for the other and it is likely unproductive to continue management for these species under such an assumption. Our results do not preclude other species from serving as effective umbrellas or benefitting from umbrella-species management even within young-forest systems. Understanding the relationships between the demographic rates of entire communities of co-occurring species and the shared cover-type features and general landscape heterogeneity at relevant scales could help identify groups of species that respond similarly to the same cover-type management. Until such information is available, failing to acknowledge uncertainty in the outcomes of management implementation puts managers at risk of unintentionally negatively affecting associated species in the community, which may lead to a decrease in the perceived value of science-based management (Simpfendorfer et al., 2011). This may further limit the ability of mangers to garner resources and implement adaptive management strategies in the future. Therefore, the identification of species that can be managed together based on relationships among occurrence, population demography, and landscape attributes will be necessary for successful management.

Acknowledgments

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Johnson, D. Page, J. Lehman, and W. Brininger for assisting with data collection in the field and T. Cooper for logistical support. We are especially grateful to D. Dustin and E. Johnson and their dogs for their assistance finding woodcock nests and broods. Golden-winged warbler data (http://hdl.handle.net/11299/167309) were collected as part of the study by Peterson (2014) and Peterson et al. (2016a) during a project funded by the U.S. Fish and Wildlife Service and U.S. Geological Survey through Research Work Order No. 87 at the Minnesota Cooperative Fish and Wildlife Research Unit and Minnesota Department of Natural Resources following Protocol #1004A80575, approved by the University of Minnesota Institutional Animal Care and Use Committee. We are grateful for logistical support provided by P. Blackburn, W. Brininger, W. Faber, W. Ford, J. Loegering, M. McDowell, H. Saloka, and R. Vallender. We thank L. Arnold, S. Barlow, D. Bradshaw, J. Bruggman, R. Carr, M. Dawson, L. Deets, J. Feura, A. Fish, R. Franta, C. Gesmundo, A. Jensen, M. Johnson, J. Lehman, T. McAllister, D. McNeil, E. Pokrivka, R. Poole, A. Rehmann, J. Refsnider, R. Refsnider, N. Seeger, E. Sinnot, and B. Vernasco for assistance with golden-winged warbler field data collection. We thank J. Fieberg for providing valuable assistance that aided in the development and validation of productivity models for both woodcock and warblers. We appreciate K. Adkins, A. Chalfoun, K. Goebel, N. Hill, and three anonymous reviewers for providing comments that improved this manuscript. Photo of American woodcock courtesy of Flickr/Fyn Kynd. Photo of golden-winged warbler courtesy of J. Lehman. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government or the University of Minnesota.

Appendix A

A.1. Description of study site

The dominant tree species at Tamarac NWR 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*). A mix of management strategies including timber harvest, shearing, and prescribed fire, combined with varied and often poor soil types, resulted in the maintenance of forest cover types in early successional stages throughout portions of Tamarac NWR. Across the region (northern Minnesota), commercial forestry practices on both public and private lands maintain diversity in forest structure (Tavernia et al., 2016). Additional data used to inform warbler models came from study sites at Rice Lake National NWR, in Aitkin County, Minnesota, USA (46.53° N, 93.34° W) and Sandilands Provincial Forest in Manitoba, Canada (49.64° N, 96.25° W). These additional study sites had similar cover types and landscape compositions to Tamarac NWR (Peterson et al., 2016a) and no significant changes to the vegetation in the study area occurred over the period of the study.

A.2. Definitions of landscape variables

Peterson et al. (2016a) and Kramer et al. (in press) classified land cover manually using 1-m resolution digital aerial photographs (2009; Minnesota Department of Natural Resources) in Arc 10.1 Geographic Information System (GIS) software (Environmental Systems Research Institute, Redlands, CA). They defined “mature forest” as stands with canopies > 20 m and average canopy closure > 60% (Brohman and Bryand, 2005). We classified areas dominated by vegetation from 1 to 3 m tall as “shrublands”. In the study area, these stands ranged from 5 to 15 years post-harvest, were 1–30 ha, and were composed of shrubs, forbs, grasses, and patches of saplings. 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. Less common cover-type categories included “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 was not considered an important cover type for breeding woodcock or warblers in our study. Peterson et al. (2016a) and Kramer et al. (in press) investigated the importance of an additional component for edge density (i.e., length of edge within a specified area) by identifying edges between mature forest (i.e., deciduous forest and forested wetland) and shrubland (i.e., upland shrubland and wetland shrubland) as the edges between these cover types are reported to be important to woodcock and edges are known to influence avian nest survival rates (Chalfoun et al., 2002; Meunier et al., 2006) and juvenile survival rates (Peterson et al., 2016a).

A.3. Life history of study species

Both woodcock and warblers have a nesting period of ~25 days, which includes the laying and incubation periods. In warblers, this 25-day nest-survival period also includes the nestling period in which recently hatched warblers remain in the nest and are cared for by both parents. The juvenile survival period for each species was defined by their respective life history and behaviors. The start of the juvenile survival period was defined as the date that juveniles left the nest (i.e., hatching for woodcock, and fledging for warblers). Juvenile woodcock become capable of flight and begin to travel greater distances from their nesting areas ~15 days post-hatching (Daly, 2014). Kramer et al.'s (in press) model of juvenile woodcock survival rate consisted of one survival period (from hatching to 15 days post-hatching) because there was no association between age and survival rate in juvenile woodcock (Daly, 2014). Warblers are flightless and limited in their mobility upon departing the nest and for several days thereafter. Consequently, a significant portion of juvenile warbler mortality occurs during the first few days after leaving the nest and the survival rate of juvenile warblers is associated with different landscape factors in the early and late juvenile survival period (Peterson, 2014; Peterson et al., 2016a; Peterson et al., 2016b; Streby et al., 2016). Therefore, Peterson et al. (2016a) split the juvenile survival period of warblers into early (i.e., days 1–3 after fledging) and late (i.e., days 4–8 after fledging) periods, which combined to account for 86% of all fledgling warbler mortalities in their study (Peterson et al., 2016a; Streby et al., 2016). Overall, ~8% (2/25) of juvenile woodcock mortality and ~14% (11/81) of juvenile warbler mortality was directly attributed to exposure. In a number of cases (n = 3), determining the proximate cause of mortality (e.g., predation versus exposure and subsequent consumption by a scavenger) was difficult for radio-marked juvenile woodcock in Daly's (2014) study. Thus, it is unclear how weather and predation may have interacted to influence juvenile woodcock mortality (Kramer et al., in press).

A.4. Statistical independence of juvenile woodcock and warblers

Juvenile woodcock within the same brood were treated as independent experimental units because there was no evidence of dependence among juveniles in the same broods (K. Daly and D. Andersen reanalyzed the data in Daly et al., 2015 using Winterstein's third Chi-squared goodness-of-fit test [Winterstein, 1992]; average P-value of 50 iterations was P = 0.32 [Daly et al., in press]). Golden-winged warblers exhibit near-obligate brood

division in which the social parents of a brood provision and care for a subset of their recently fledged brood resulting in the formation of two stable sub-broods (Peterson et al., 2016b). Sub-broods rarely occur together after fledging (Peterson et al., 2016b). Therefore, juvenile golden-winged warblers from different sub-broods were considered independent experimental units and a single juvenile was randomly selected from the small number of sub-broods in which > 1 juvenile was monitored (2% of all sub-broods; Peterson, 2014, Peterson et al., 2016a).

Table A.1
A cover types and impact radii included in models of productivity for American woodcock (2011 − 2012) and golden-winged warblers (2010 − 2012) breeding at Tamarac National Wildlife Refuge, Minnesota, USA. Possible relationships between survival rate and cover types were investigated separately for each survival period (i.e., nesting and juvenile period for woodcock; nesting, early juvenile, and late juvenile periods for warblers) at different radii (see main text for details). The radius and polynomial function that explained the most variation in survival rate for each cover type in each survival period are presented. Cover types that failed to explain meaningful variation in survival rate (at any radius) compared to the intercept-only model were not included in our analysis and those uninformative parameters are denoted as "N/A".

Landscape variable	American woodcock			
	Nest survival rate		Juvenile survival rate (days 1–15)	
	Scale (m)	Polynomial function	Scale (m)	Polynomial function
Mature forest	500	Linear	500	Linear
Edge	N/A	N/A	N/A	N/A
Forested wetland	N/A	N/A	N/A	N/A
Grassland	500	Linear	N/A	N/A
Wetland shrubland	N/A	N/A	250	Linear
Upland shrubland	500	Linear	1 000	Linear

Landscape variable	Golden-winged warblers					
	Nest survival rate		Early juvenile survival rate (days 1–3)		Late juvenile survival rate (days 4–8)	
	Scale (m)	Polynomial function	Scale (m)	Polynomial function	Scale (m)	Polynomial function
Mature forest	N/A	N/A	25	Linear	25	Linear
Edge	50	Linear	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

Table A.2
Model rankings, weights, and log-likelihoods of all possible combinations of cover-type covariates (at the appropriate impact radius) that explained meaningful variation in American woodcock survival during nesting or juvenile survival periods at Tamarac National Wildlife Refuge, Minnesota, USA from 2011–2012. Reconstructed from Kramer et al. (in press).

Model	ΔAIC_c	k	ω	$-2 * \text{Log-likelihood}$
Woodcock nest survival rate models				
Upland Shrubland 500 + Grassland 500[a]	0.00	3	0.38	140.0
Mature Forest 500 + Upland Shrubland 500 + Grassland 500	0.70	4	0.27	138.6
Grassland 500	1.59	2	0.17	143.6
Mature Forest 500 + Grassland 500	3.37	3	0.07	143.4
Upland Shrubland 500	4.21	2	0.05	146.2
Mature Forest 500	4.89	2	0.03	147.0
Intercept[c]	5.34	1	0.03	149.4
Mature Forest 500 + Upland Shrubland 500	5.86	3	0.02	145.8
Woodcock juvenile survival rate models (day 1–15)				
Upland Shrubland 1 000 + Wetland Shrubland 250[b]	0.00	3	0.71	170.8
Mature Forest 500 + Upland Shrubland 1 000 + Wetland Shrubland 250	2.00	4	0.26	170.8
Wetland Shrubland 250	8.46	2	0.01	181.2
Mature Forest 500 + Wetland Shrubland 250	9.20	3	0.01	180.0
Mature Forest 500 + Upland Shrubland 1 000	10.29	3	0.00	181.0
Upland Shrubland 1 000	10.47	2	0.00	183.2
Mature Forest 500	10.66	2	0.00	183.4
Intercept[c]	11.66	1	0.00	186.4

[a] Best-supported nest survival rate model AIC_c was 146.11.
[b] Best-supported juvenile survival rate model AIC_c was 176.81.
[c] Null juvenile survival rate model.

Table A.3
Model rankings, weights, and log-likelihoods of all possible combinations of cover-type covariates (at the appropriate impact radius) that explained meaningful variation in golden-winged warbler survival rates during nesting or juvenile survival periods at Tamarac National Wildlife Refuge, Minnesota, USA from 2010–2012. Reconstructed from Peterson et al. (2016a).

Model	ΔAIC_c	k	ω	$-2 * \text{Log-likelihood}$
Warbler nest survival rate models				
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Grassland 200 + (Grassland 200)^2 + Wetland Shrubland 200 + Forested Wetland 175 + Coniferous Forest 50[a]	0.00	10	0.43	787.1
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Grassland 200 + (Grassland 200)^2 + Wetland Shrubland 200 + Forested Wetland 175	1.72	9	0.18	790.9
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Grassland 200 + (Grassland 200)^2 + Wetland Shrubland 200 + Coniferous Forest 50	3.49	9	0.08	792.6
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Grassland 200 + (Grassland 200)^2 + Forested Wetland 175 + Coniferous Forest 50	4.12	9	0.05	793.3
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Wetland Shrubland 200 + Forested Wetland 175 + Coniferous Forest 50	4.42	8	0.05	795.6
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Grassland 200 + (Grassland 200)^2 + Wetland Shrubland 200	4.97	8	0.04	796.2
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Grassland 200 + (Grassland 200)^2 + Coniferous Forest 50	5.51	8	0.03	796.7
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Wetland Shrubland 200 + Forested Wetland 175	5.62	7	0.03	798.8
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Forested Wetland 175 + Coniferous Forest 50	5.92	7	0.02	799.1
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Grassland 200 + (Grassland 200)^2 + Forested Wetland 175	6.04	8	0.02	797.2
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Grassland 200 + (Grassland 200)^2	7.23	7	0.01	800.5
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Forested Wetland 175	7.33	6	0.01	802.6
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Wetland Shrubland 200 + Coniferous Forest 50	7.49	7	0.01	800.7
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Coniferous Forest 50	7.56	6	0.01	802.8
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3 + Wetland Shrubland 200	8.51	6	0.01	803.8
Age + Grassland 200 + (Grassland 200)^2 + Wetland Shrubland 200 + Forested Wetland 175 + Coniferous Forest 50	8.70	7	0.01	801.9
Age + Shrubby Edge 50 + (Shrubby Edge 50)^2 + (Shrubby Edge 50)^3	8.82	5	0.01	806.1
Age + Grassland 200 + (Grassland 200)^2 + Wetland Shrubland 200 + Forested Wetland 175	9.13	6	< 0.01	804.4
Age + Grassland 200 + (Grassland 200)^2 + Wetland Shrubland 200 + Coniferous Forest 50	10.64	6	< 0.01	805.9
Age + Wetland Shrubland 200 + Forested Wetland 175 + Coniferous Forest 50	10.81	5	< 0.01	808.1
Age + Grassland 200 + (Grassland 200)^2 + Wetland Shrubland 200	10.99	5	< 0.01	808.3
Age + Wetland Shrubland 200 + Forested Wetland 175	11.06	4	< 0.01	810.4
Age + Grassland 200 + (Grassland 200)^2 + Forested Wetland 175 + Coniferous Forest 50	11.72	6	< 0.01	807.0
Age + Forested Wetland 175 + Coniferous Forest 50	12.09	4	< 0.01	811.4
Age + Grassland 200 + (Grassland 200)^2 + Forested Wetland 175	12.33	5	< 0.01	809.6
Age + Grassland 200 + (Grassland 200)^2 + Coniferous Forest 50	12.36	5	< 0.01	809.6
Age + Forested Wetland 175	12.54	3	< 0.01	813.9
Age + Wetland Shrubland 200 + Coniferous Forest 50	12.82	4	< 0.01	812.1
Age + Grassland 200 + (Grassland 200)^2	12.89	4	< 0.01	812.2
Age + Wetland Shrubland 200	13.01	3	< 0.01	814.3
Age + Coniferous Forest 50	13.06	3	< 0.01	814.4
Age + Intercept[d]	13.43	2	< 0.01	816.8
Warbler juvenile survival rate models (days 1–3)				
Age + Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3 + Grassland 200 + Coniferous Forest 50 + (Coniferous Forest 50)^2[b]	0.0	10	0.11	320.0
Age + Mature Forest 25 + Grassland 200 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3 + Coniferous Forest 50 + (Coniferous Forest 50)^2	0.3	10	0.10	320.4
Age + Grassland 200 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3 + Coniferous Forest 50 + (Coniferous Forest 50)^2	0.4	9	0.09	322.6
Age + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3 + Grassland 200 + Coniferous Forest 50 + (Coniferous Forest 50)^2	1.0	9	0.07	323.0
Age + Mature Forest 25 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3 + Coniferous Forest 50 + (Coniferous Forest 50)^2	1.1	9	0.07	323.2
Age + Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3 + Grassland 200 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3 + Coniferous Forest 50 + (Coniferous Forest 50)^2	1.1	13	0.07	314.8
Age + Mature Forest 25 + Grassland 200 + Coniferous Forest 50 + (Coniferous Forest 50)^2	1.1	7	0.06	327.4
Age + Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3 + Coniferous Forest 50 + (Coniferous Forest 50)^2	1.2	9	0.06	323.2
Age + Mature Forest 25 + Coniferous Forest 50 + (Coniferous Forest 50)^2	1.3	6	0.06	329.6
Age + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3 + Grassland 200 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3 + Coniferous Forest 50 + (Coniferous Forest 50)^2	1.6	12	0.05	317.4
Age + Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3 + Coniferous Forest 50 + (Coniferous Forest 50)^2	2.4	12	0.03	318.2
Age + Grassland 200 + Coniferous Forest 50 + (Coniferous Forest 50)^2	2.4	6	0.03	330.3
Age + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3 + Coniferous Forest 50 + (Coniferous Forest 50)^2	3.0	8	0.03	327.2
Age + Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3 + Grassland 200	3.1	8	0.02	327.2
Age + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3 + Coniferous Forest 50 + (Coniferous Forest 50)^2	3.9	8	0.02	328.0
Age + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3 + Grassland 200	4.0	7	0.02	330.2
Age + Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3	4.0	7	0.02	330.2
Age + Coniferous Forest 50 + (Coniferous Forest 50)^2	4.4	5	0.01	334.8

(*continued on next page*)

Table A.3 (*continued*)

Model	ΔAIC_c	k	ω	$-2 * \text{Log-likelihood}$
Age + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3 + Coniferous Forest 50 + (Coniferous Forest 50)^2	4.5	11	0.01	322.4
Age + Mature Forest 25	4.6	4	0.01	337.0
Age + Mature Forest 25 + Grassland 200	4.8	5	0.01	335.2
Age + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3	5.5	6	0.01	333.8
Age + Mature Forest 25 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3	5.5	7	0.01	330.8
Age + Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3 + Grassland 200 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3	5.6	11	0.01	323.4
Age + Mature Forest 25 + Grassland 200 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3	5.6	8	0.01	329.8
Age + Grassland 200 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3	5.9	10	0.01	326.0
Age + Grassland 200	6.3	4	< 0.01	338.6
Age + Grassland 200 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3	6.3	7	< 0.01	332.6
Age + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3 + Grassland 200 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3	6.4	10	< 0.01	326.4
Age + Intercept[d]	7.2	3	< 0.01	341.6
Age + Mature Forest 25 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3	7.4	6	< 0.01	335.8
Age + Shrubby Edge 200 + (Shrubby Edge 200)^2 + (Shrubby Edge 200)^3 + Forested Wetland 125 + (Forested Wetland 125)^2 + (Forested Wetland 125)^3	7.8	9	< 0.01	329.8
Warbler juvenile survival rate models (days 4–8)				
Grassland 175 + (Grassland175)^2[c]	0.0	4	0.30	89.1
Mature Forest 25 + Grassland 175 + (Grassland175)^2	2.0	5	0.11	89.0
Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3 + Grassland 175 + (Grassland175)^2	2.2	7	0.10	85.2
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3	2.6	5	0.08	89.7
Shrubby Edge 200 + (Shrubby Edge 200)^2 + Grassland 175 + (Grassland175)^2	3.0	6	0.07	88.1
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Grassland 175 + (Grassland175)^2	3.1	7	0.06	86.1
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Mature Forest 25	4.2	6	0.04	89.3
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Mature Forest 25 + Grassland 175 + (Grassland175)^2	4.6	8	0.03	85.5
Mature Forest 25 + Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3 + Grassland 175 + (Grassland175)^2	4.9	8	0.03	85.8
Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + Grassland 175 + (Grassland175)^2	4.9	7	0.03	87.9
Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3	5.3	5	0.02	92.4
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + Grassland 175 + (Grassland175)^2	5.6	9	0.02	84.5
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Shrubby Edge 200 + (Shrubby Edge 200)^2	5.9	7	0.02	88.8
Shrubby Edge 200 + (Shrubby Edge 200)^2 + Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3 + Grassland 175 + (Grassland175)^2	5.9	9	0.02	88.9
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3	6.0	8	0.01	84.9
Shrubby Edge 200 + (Shrubby Edge 200)^2	6.9	4	0.01	87.8
Mature Forest 25	6.9	3	0.01	96.0
Shrubby Edge 200 + (Shrubby Edge 200)^2 + Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3	6.9	7	0.01	98.1
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2	7.4	8	0.01	90.4
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3 + Grassland 175 + (Grassland175)^2	7.4	10	0.01	88.3
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Mature Forest 25 + Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3	7.5	9	0.01	84.3
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + Grassland 175 + (Grassland175)^2	7.6	10	0.01	86.4
Intercept[d] (constant survival rate)	7.7	3	0.01	84.5
Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3	7.9	8	0.01	99.1
Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3 + Grassland 175 + (Grassland175)^2	8.1	10	0.01	89.0
Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2	8.6	5	< 0.01	85.4
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3	9.6	10	< 0.01	96.8
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Mature Forest 25 + Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3 + Grassland 175 + (Grassland175)^2	9.8	11	< 0.01	86.6
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3	10.2	11	< 0.01	84.9
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Mature Forest 25 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3 + Grassland 175 + (Grassland175)^2	11.6	13	< 0.01	86.3
Wetland Shrubland 300 + (Wetland Shrubland 300)^2 + (Wetland Shrubland 300)^3 + Shrubby Edge 200 + (Shrubby Edge 200)^2 + Forested Wetland 400 + (Forested Wetland 400)^2 + (Forested Wetland 400)^3 + Grassland 175 + (Grassland175)^2	11.6	12	< 0.01	82.1

[a] Best-supported nest survival rate model AIC_c was 809.6.
[b] Best-supported early period juvenile survival rate model AIC_c was 340.5.
[c] Best-supported late period juvenile survival rate model AIC_c was 97.2.
[d] Null model.

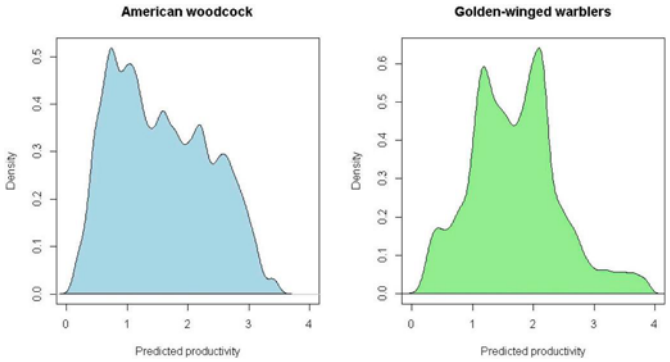

Fig. A.1. Kernel density plots of the relative frequency of predicted productivity estimates of American woodcock (blue; n = 83 389, bandwidth = 0.07381; 2011–2012) and golden-winged warblers (green; n = 50 185, bandwidth = 0.07395; 2010–2012) at the nest-site scale (i.e., 1 m^2) over the entire 900-ha study area (Tamarac National Wildlife Refuge, Minnesota, USA).

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