*Multi-seasonal species distribution models better facilitate habitat conservation for a migratory bird*

Liam A. Berigan1, Amber M. Roth1, 2, Alexander C. Fish1, Lisa M. Williams3, Kenneth R. Duren3, Scott Bearer3, Kevin Wenner3, Phillip Kasper3, Erik J. Blomberg3

1 Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, 5755 Nutting Hall, ME 04469, USA

2 Department of Wildlife, Fisheries, and Conservation Biology and School of Forest Resources, University of Maine, 5755 Nutting Hall, ME 04469, USA

3 Pennsylvania Game Commission. 2001 Elmerton Avenue, Harrisburg, PA 17110, USA

Keywords (max 6): American woodcock, full annual cycle, migratory birds, transferability, species distribution model, habitat suitability model

**Abstract**

Species distribution models have issues with cross-seasonal transferability when data collected during a single season do not reflect habitat relationships across other seasons. This issue can be addressed using spatial decision support systems, which allow users to incorporate multiple season-specific distribution models into a single tool to facilitate conservation decisions. We demonstrated a potential application of this framework through an analysis of multi-season habitat use for a migratory bird, the American woodcock (*Scolopax minor*), in Pennsylvania, USA. We modeled woodcock breeding and migratory habitat distributions in Pennsylvania, USA, using random forest classifiers, and integrated the predictions of both models into a single decision support system using a Shiny application. The Shiny application accepts user input through breeding and migratory season weights, allowing users to customize the tool based on area-specific management priorities. We found low cross-seasonal transferability between breeding and migratory season models, with Pearson correlations of 0.15 at a pixel-scale and 0.39 at a local management area scale, indicating that conservation of breeding habitat alone is unlikely to result in efficient conservation of migratory habitat for woodcock. Woodcock breeding and migratory habitat is also unevenly distributed at a regional scale, with 3 Pennsylvania ecoregions having low breeding suitability but high migratory suitability. Creating a multi-season distribution model for woodcock management highlighted important migratory areas that may otherwise be overlooked due to a lack of breeding season occupancy, such as urban greenspaces. Flexibility in data sources and ability to compensate for low cross-seasonal transferability in distribution models make multi-season distribution modeling ideal for the study of birds and other migratory taxa.

**1 Introduction**

Species distribution models are frequently used to assist conservation decision-making (Miller, 2010), however, they are known to have issues with transferability. For example, models developed in one area may not be reflective of animal distributions in other parts of their range (spatial transferability; Randin et al., 2006), or may fail to project species distributions into the future due to changing conditions (temporal transferability; Dobrowski et al., 2011). We posit that an additional subcategory of spatiotemporal transferability exists, called cross-seasonal transferability, for situations where species habitat associations differ among seasons or life stages, resulting in animals using fundamentally different space throughout the year. For example, wildlife science has a long history of bias towards studying animals during the breeding season, which may neglect the value of non-breeding habitat for survival and ignore carry-over effects into the breeding season (Norris and Marra, 2007). By building species distribution models which focus solely on occurrence data collected during breeding, we may disregard portions of a species’ distribution that are essential to persistence.

Spatial decision support systems (SDSS; Hopkins and Armstrong, 1985) may provide a useful mechanism to circumvent issues of cross-seasonal transferability by combining distribution models from multiple seasons of the full annual cycle during the decision-making process. SDSS utilize user-friendly, interactive toolsets to guide users through making a set of spatial prioritization decisions (Sugumaran and Degroote, 2010). SDSS frequently come as extensions of existing geographic information systems (McConnell and Burger, 2011), but the learning curve and costs associated with professional geographic information systems can often be an impediment to reaching the intended user base (Harper, 2006). The widespread adoption of interactive online mapping tools, such as leaflet (Agafonkin, 2022) and ArcGIS Online (ESRI, 2023), has greatly expanded the capacity to custom build SDSS that are accessible via a web browser and can be easily used by decision makers with little additional training (Sugumaran and Sugumaran, 2007). SDSS provide an interface which allows users to interact with multiple spatial data layers, such as species distribution models. In circumstances where species distribution models have low cross-seasonal transferability, SDSS can compensate by incorporating multiple season-specific species distribution models into the decision-making process.

Migratory birds are clearly sensitive to issues of cross-seasonal transferability through use of different geographic areas throughout their annual cycle, coarsely divided into breeding, wintering, and migratory seasons (Marra et al., 2015). Resource requirements frequently differ among these three seasons, often resulting in bird use of fundamentally different habitat types (Allen et al., 2020; Rice et al., 1980; Stanley et al., 2021). However, there are circumstances in which breeding, wintering, and migratory habitat may occur within the same region, especially for short-distance migrants, which are generally defined as those migrating less than 2000 km (Rappole, 2013). Examples of short-distance migrants include wintering waterfowl, such as common eider (*Somateria mollissima*), where more northern breeding populations overwinter in the same regions that more southern populations breed (Goudie et al., 2020), and nomadic finch species such as pine siskin (*Spinus pinus*), which migrate, breed, and overwinter in the same regions despite differential resource requirements among seasons (Dawson, 2020). An SDSS approach that combines season-specific species distribution models into a single predictive layer could be particularly useful to avoid issues of cross-seasonal transferability when managing such species.

We demonstrate a SDSS framework to spatially-prioritize habitat management while accommodating the cross-seasonal transferability necessary to capture multiple seasons of a migratory bird’s full annual cycle. Our case study is focused on American woodcock (*Scolopax minor*;hereinafter woodcock) in the state of Pennsylvania, USA. Woodcock are short distance migrants with considerable overlap among migratory, breeding, and wintering ranges (Myatt and Krementz, 2007; Fig. 1), but fundamentally different habitat requirements among seasons (Allen et al., 2020). We aimed to develop a SSDS tool to aid conservation practitioners considering trade-offs between managing for breeding and migratory season habitat in Pennsylvania. Our specific objectives for the SDSS were to 1) maximize predictive accuracy of habitat classifications within each season, 2) combine seasonal models into a single prioritization layer using user-specified weights, and 3) evaluate suitability and providing relative rankings of local management areas.



Figure 1. Seasonal ranges and hypothetical migration routes of American woodcock in eastern North America. Seasonal ranges were delineated by eBird’s Status and Trends project (Fink et al., 2022) using citizen science data. Migration routes illustrate potential connections among eastern (dashed line), central (solid line), and western (dotted line) population segments. Migration routes were originally proposed by Glasgow (1958) and later reproduced by Moore et al. (2019). Inset illustrates multiple migration routes intersecting with the breeding range in the state of Pennsylvania.

**2 Methods**

*2.1 Study area*

We modeled woodcock habitat distribution throughout the state of Pennsylvania, which provides breeding habitat for an estimated 2.3% of the global woodcock population (52,400 birds) and provides stopover habitat during spring and fall migration for woodcock breeding throughout the northeastern United States and eastern Canada, which accounts for nearly 1/3rd of the global woodcock population (30.5% of global woodcock, 684,500 birds; Kelley et al., 2008). Pennsylvania also contains some wintering habitat for woodcock, which is negligible compared to breeding and stopover habitat (Fig. 1). Pennsylvania is composed of 11 U.S. Environmental Protection Agency (EPA) level 3 ecoregions (Omernik and Griffith, 2014), which reflect the topological gradient from Pennsylvania’s ridge-and-valleys in the central portion of the state to the coastal lowlands along the edge of Lake Erie. Less mountainous areas in Pennsylvania tend to be heavily agricultural (ex. Northern Piedmont ecoregion, 38% agricultural; Jin et al., 2019), with development primarily concentrated around the two largest cities, Philadelphia (pop. 1,600,000; U.S. Census Bureau, 2021) and Pittsburgh (pop. 300,000). Mountainous areas, such as the North Central Appalachians ecoregion, remain in mostly contiguous forest cover (84% forest; Jin et al., 2019).

Woodcock in Pennsylvania are managed by the Pennsylvania Game Commission, a state wildlife management agency, which regulates hunting and manages habitat for wildlife. The Pennsylvania Game Commission owns more than 600,000 hectares of land, referred to hereafter as state gamelands, which are managed primarily for wildlife and to provide hunting and trapping opportunities for the public (Pennsylvania Game Commission, 2023). Managing woodcock habitat for both breeding and migratory seasons are priorities for the Pennsylvania Game Commission, which requires tools to prioritize management projects on state gamelands.

*2.2 Breeding and migratory season data*

To model woodcock habitat distribution during the breeding and migratory seasons, we used separate data sources that described woodcock occupancy during each of those time periods. For the breeding season (March–May), we used survey data collected as part of the federally-coordinated American Woodcock Singing Ground Survey (Seamans and Rau, 2020) and additional state-level monitoring conducted by the Pennsylvania Game Commission. Both state and federal surveys consisted of 5.76 km routes with 10 evenly spaced points, where observers listened for woodcock songs during their crepuscular breeding display. Observers recorded counts of all males singing during 2-minute intervals shortly after dusk. We used survey data collected from 2016–2020, and distilled records to presence or likely absence at each point based on detection of at least one male during the 5-year period. Male woodcock are often assumed to display near female nesting habitat, and so male displays are likely an indicator of male and female presence at the scale of application (McAuley et al., 2020).

We delineated woodcock occurrence during the migratory season using GPS-tracking data from the Eastern Woodcock Migration Research Cooperative, a collaboration of 42 federal, state, provincial, non-profit, and university partners throughout the United States and Canada (www.woodcockmigration.org). We captured woodcock at 34 sites in Quebec, Ontario, Nova Scotia, Maine, Vermont, New York, Rhode Island, Pennsylvania, Maryland, West Virginia, Virginia, North Carolina, South Carolina, Georgia, Alabama, and Florida using mist nets during mornings and evening flights (Sheldon, 1960), or using spotlights and dip nets at night (McAuley et al., 1993; Rieffenberger and Kletzly, 1966). We attached 4g, 5g, or 6.3g PinPoint GPS Argos transmitters (Lotek Wireless Inc., Newmarket, Ontario, CA) to captured woodcock. Transmitters recorded GPS locations at 12–60m accuracy and were programmed to record diurnal locations every 1–3 days. Transmitters, bands, and attachment materials never exceeded 4% of a bird’s body weight, and all capture and handling were conducted with methods approved by the University of Maine Institutional Animal Care and Use Committee (Protocol # A2020-07-01).

We used woodcock location data to identify stopover locations, defined as any place where a migrant bird can land and survive until the next migratory flight (Mehlman et al., 2005). We consider woodcock to be migrating after they have made their first >16.1 km movement in fall or spring, and to complete their migration after they have made their last >16.1 km movement in the respective season. The >16.1 km threshold was chosen as it roughly divides the bimodal distribution of log-standardized step lengths, presumably distinguishing between local- and long-distance movements (Blomberg et al., In review). Because woodcock migrate at night, we considered all diurnal locations between migratory initiation and termination to be stopovers. We grouped successive locations within 3 km into a single stopover, based on our observations that movements <3 km tended to be recursive rather than directional, and removed all but one location from each stopover from the analysis to reduce pseudoreplication and spatial autocorrelation of closely clustered locations. We also generated 10,000 locations randomly distributed throughout Pennsylvania, which we considered pseudoabsence locations.

*2.3 Species distribution modeling*

We constructed separate species distribution models for migratory and breeding seasons to accommodate differences in habitat associations and data sources. Each model used explanatory variables with presumed relevance to woodcock habitat associations (McAuley et al., 2020), with suites of variables including land use/land cover, forest successional class, topography, region, and soil moisture (Table 1). We additionally calculated landscape metrics from the landscapemetrics package (Hesselbarth et al., 2019) in program R (R Core Team, 2022), which represented landscape composition and configuration. To generate composition metrics, we resampled the National Land Cover Dataset to a 90m resolution, and then calculated the percent of each cover type within 500m, 1km, 5km, and 10km radii for each pixel. For configuration metrics, we used the National Land Cover Dataset to create a binary forest/non-forest layer, which we resampled to 90m resolution, and then calculated each configuration metric within 500m, 1km, 5km, and 10km radii of each pixel.

We conducted a pilot evaluation of several potential modeling techniques fit to a subset of woodcock occurrence data, including using MaxEnt (Phillips et al., 2006), random forest classification (Breiman, 2001), and boosted regression trees (Elith et al., 2008). All models were fit using the R package SDMtune (Vignali et al., 2020). We compared model outputs using area-under-the-curve (AUC), a common metric of predictive accuracy for classification models (Fielding and Bell, 1997). The random forest classifier had the highest AUC among modeling approaches, and we therefore used random forest techniques for all subsequent models (Table A.1).

For the breeding season model, we used a random forest classifier designed for clustered data (Wang and Chen, 2016), and applied survey route as a clustering variable to compensate for spatial autocorrelation among points on the same survey route. As federal survey routes were randomly distributed (Clark, 1970) and state surveys were distributed opportunistically, we included survey type (state vs federal) as an explanatory variable to accommodate differences in route distribution. For the migratory season, we used a traditional random forest classification model, written using the randomForest package in R (Liaw and Wiener, 2002). We assessed the accuracy of all models using a k-fold cross validation approach, where separate training and testing datasets were randomly sampled for each fold. We sampled folds at a survey route level for the breeding season model to accommodate autocorrelation within survey routes and prevent data leakage between the training and testing datasets. We used 10 folds for the breeding season model (90% training, 10% testing), but only 5 folds for the migratory season model (80% training, 20% testing) to accommodate the smaller sample size of the stopover dataset. We averaged AUCs for each of the folds to produce a mean AUC for each model and created predictive layers at 90m resolution that averaged predictions across folds.

To avoid overwhelming final predictive models with highly correlated or uninformative variables, we used the R package VSURF (Genuer et al., 2022) to implement a three-step backwards variable-selection approach, where each step produced a more parsimonious model. The first step eliminated irrelevant variables with lower variable importance than a defined threshold value (determined based on guidelines in Genuer et al., 2015). The second step retained only variables with the smallest out-of-bag error rates when training the model, effectively eliminating variables with some relevance but not critical for prediction. The third step used a stepwise process to test whether each included variable led to an out-of-bag error decrease that was larger than a defined threshold value, effectively removing redundant variables from consideration (Genuer et al., 2015). We compared predictive accuracy of models created from each step using AUC, and retained the model from the step that produced the highest AUC to create a final predictive layer for each season.

We normalized the predictive layer for each season on a percentile scale, indicating whether a given pixel had a greater likelihood of woodcock occupancy than the corresponding percentage of other pixels in the state; for example, a value of 0.65 indicates that the pixel contains habitat that is more suitable than 65% of other pixels statewide. We termed these habitat suitability layers, with habitat suitability defined as a bounded, continuous index representing the degree to which a given site possesses the habitat components required for species occupancy (U.S. Fish and Wildlife Service, 1996). We occasionally refer to these habitat suitability layers as representing habitat distribution, which we define as the geographic distribution of habitat on the landscape, or as a representation of where areas of greater suitability occur or are absent.

Table 1. Explanatory variables used to model woodcock distributions in Pennsylvania, USA. Suites indicate conceptual grouping of variables into classes relevant to woodcock occurrence.

|  |  |  |
| --- | --- | --- |
| **Suite** | **Covariate** | **Source** |
| Land use/land cover | Land use/land cover | National Land Cover Dataset (Jin et al., 2019) |
| Forest successional class | Forest successional class | LANDFIRE (USGS and USDA, 2020) |
| Topography | Elevation | USGS (2000) |
| Slope | Derived from elevation |
| Region | EPA level 3 ecoregions | Omernik and Griffith (2014) |
| Soil moisture | Soil drainage | Web soil survey (NRCS, 2021) |
| Topographic wetness index | Derived from elevation (Fink, 2013) |
| Landscape composition  (0.5, 1, 5, and 10km scales) | % Forest | Derived from National Land Cover Dataset using landscapemetrics (Hesselbarth et al., 2019) |
| % Agricultural |
| % Developed |
| Landscape configuration  (0.5, 1, 5, and 10km scales) | Aggregation index | Derived from National Land Cover Dataset using landscapemetrics (Hesselbarth et al., 2019) |
| Cohesion |
| Edge density |

*2.4 Analysis of covariate relationships and comparative distribution of seasonal habitat*

Random forest techniques do not provide easily interpretable covariate relationships, leaving the user to determine how covariates might influence the outcomes of the model (Breiman, 2001). While we were not interested in exploring woodcock-habitat relationships per se, we nevertheless wanted to understand how environmental variables contributed to model predictions. We also sought to highlight regional differences in the distribution of breeding and migratory habitat among ecoregions. To depict these differences, we sampled covariate values, ecoregion type, and model-predicted suitability at 10,000 randomly distributed points throughout Pennsylvania. We used hex plots to visualize trends between covariates and predictions for each season, and visualized variation among each EPA level 3 ecoregion in Pennsylvania using box-and-whisker plots.

We used two metrics to evaluate cross-seasonal transferability between breeding and migratory season species distribution models, to better understand the utility of a multi-season modeling approach. The first was a Pearson correlation coefficient between the breeding and migratory season layers, calculated using the R package terra (Cohen et al., 2009; Hijmans, 2022), which measured the correlation between breeding and migratory suitability on the scale of individual pixels (90 m). The second metric measured the Pearson correlation between the total breeding habitat and the total migratory habitat provided by each gameland (described below in section 2.5), illustrating the co-occurrence of breeding and migratory habitat at the scale of the average state gameland (1992 ha).

*2.5 Spatial Decision Support System*

We created a SDSS in the Shiny ecosystem (Chang et al., 2022), named the Woodcock Priority Area Siting Tool (W-PAST), to facilitate local woodcock management planning. The SDSS allowed users to assign weights to each seasonal habitat suitability layer in 10% increments (ex. 20% migratory and 80% breeding season), and then combined seasonal predictions into a single multi-season layer (Fig. 2). The weighting was conducted on a pixel-by-pixel basis as a simple weighted average where *pw* indicates the value of the weighted pixel value, *wm* the weight of importance for migratory habitat, *wb* the breeding season weight, *pm* the migratory pixel value, and *pb* the breeding season pixel value.

Practitioners often benefit from SSDS features customized to their management applications. In the case of the Pennsylvania Game Commission, a primary goal was to increase availability of woodcock habitat on state-managed gamelands, requiring functionality within the tool to compare habitat suitability among gamelands. We built four comparison metrics into the SDSS that were calculated using the weighted averages of the breeding and migratory season predictive layers: average pixel value, total habitat, % high quality, and % medium quality. Average pixel value was the arithmetic mean of all pixels within a state gameland, which tended to favor small gamelands predominantly composed of woodcock habitat and was intended to demonstrate where a small amount of habitat management could increase local woodcock populations. Total habitat was average pixel value multiplied by the acreage of the gameland, which favored larger gamelands that contained relatively large amounts of woodcock habitat in aggregate by virtue of their size. Total habitat could be used to determine which gamelands would provide the most habitat in aggregate if they were managed for woodcock. Percent high quality habitat was the percentage of cells within a gameland that had values greater than the 33rd percentile of all pixel values in the state, and percent medium quality was the percentage of cells falling between the 66th and 33rd percentile. These percentile-based metrics allowed users to quantify the proportion of a gameland which might be suitable for woodcock management. By multiplying the percent high or medium quality by the gameland acreage (also provided in the tool), the user could also derive the acreage in each gameland that could be managed for woodcock effectively. Further instructions for using these metrics in management are included in a user manual, publicly available with the SDSS at www.woodcock.shinyapps.io/W-PAST.



Figure 2. Conceptual diagram of user decision options in the Woodcock Priority Area Siting Tool (W-PAST). Users can choose the weighting of migratory and breeding season habitat at 10% increments based on management priorities. The resulting weights are used to generate a statewide predictive layer and gameland prioritization metrics, which allow the user to compare the suitability of gamelands for woodcock management.

**3 Results**

We collected data from 328 migrant woodcock marked with GPS transmitters throughout the eastern portion of the woodcock’s range between fall 2017 and spring 2021. Eighty-two individuals (25%) recorded GPS locations at 113 stopovers in Pennsylvania. Breeding season survey data were available for 770 locations along 77 federal American Woodcock Singing-Ground Survey routes and 800 locations along 80 Pennsylvania Game Commission state survey routes. The most predictive breeding season model (AUC = 0.83) was the result of the second variable selection step, in which all variables with low predictive capacity were removed. This model was heavily informed by landscape variables at 5 and 10 km scales (Table 2), and no variables at the finest spatial scale (0.5 km) or in the suite of soil moisture characteristics were included in the most informative model. Graphs of habitat suitability for each covariate showed strong, non-linear relationships (Fig. 3). Suitability was highest for landscapes with 0–25% developed land area, 0–50% agricultural land area, and aggregation index values of 80–100, all at the 10km scale. At the 5km scale, the breeding season model also showed high suitability in landscapes with 30–100% forest cover (Fig. 3).

The most predictive migratory model (AUC=0.78) was the full model, including all landscape, land cover, geographic, and soil moisture covariates (Table 2). Likely due to the wide array of covariates influencing the model, individual covariate graphs do not show clear visual patterns between migratory habitat suitability and any one covariate. However, the migratory model illustrated greater tolerance of migrant woodcock for developed and dis-aggregated landscapes at a 10 km scale than the breeding season model (Fig. 3). The two models were also distinguished by the scale at which covariates influenced habitat suitability; the most informative breeding season model was not influenced by any landscape covariates at the 500 m scale, and only 1 landscape covariate at the 1 km scale, whereas the most informative migratory model included all available small-scale landscape covariates. Because of the influence of covariates at 500 m and 1 km scales, the migratory model predicted much more spatial variation in habitat distribution than the breeding season model, despite identical pixel resolutions (Fig. 4).

Breeding season habitat was not evenly distributed among ecoregions (Fig. 5A), with mean habitat suitability values ranging from 22.9–86.0%. Migratory habitat was more evenly distributed among ecoregions, with mean habitat suitability values ranging from 46.5–87.5%. Most of the difference between the distribution of migratory and breeding season habitat was in the Northern Piedmont, Middle Atlantic Coastal Plain, and Central Appalachians ecoregions, which had mean breeding season habitat suitability values of <30% and mean migratory season habitat suitability values of >60% (Fig. 5B). Breeding and migratory habitat rarely co-occurred at a pixel level, with a Pearson correlation coefficient of 0.15 between the breeding and migratory season predictive layers. Breeding and migratory habitat were slightly more likely to co-occur on gamelands, with a Pearson correlation coefficient of 0.39 between the total breeding habitat and total migratory habitat provided by gamelands.

Table 2. Variables selected via backwards variable selection using the R package VSURF (Genuer et al., 2022) for the migratory and breeding season models. The migratory model employs the full set of variables, while the breeding season model uses a subset of variables inclined towards coarse resolution landscape variables.

|  |  |  |
| --- | --- | --- |
| Suite | Migratory | Breeding |
| Landscape (500m) | Aggregation Index, Cohesion, Edge Density, % Forest, % Agricultural, % Developed |  |
| Landscape (1km) | Aggregation Index, Cohesion, Edge Density, % Forest, % Agricultural, % Developed | % Agricultural |
| Landscape (5km) | Aggregation Index, Cohesion, Edge Density, % Forest, % Agricultural, % Developed | Cohesion, % Forest, % Agricultural, % Developed |
| Landscape (10km) | Aggregation Index, Cohesion, Edge Density, % Forest, % Agricultural, % Developed | Aggregation Index, Cohesion, % Agricultural, % Developed |
| Land Cover | Forest, Successional Class |  |
| Geography | Elevation, Slope, Ecoregions | Elevation, Ecoregions |
| Soil Moisture | Drainage, Topographic Wetness Index |  |

A picture containing chart

Description automatically generated

Figure 3. Comparison of relationships between landscape variables and habitat suitability for breeding and migratory season models of American woodcock in Pennsylvania, USA. During the breeding season, woodcock habitat suitability is highest in highly aggregated landscapes with ~75% forest and ~25% agricultural cover. During the migratory season, however, woodcock become far more tolerant of landscapes that are unsuitable during the breeding season, including landscapes with higher proportions of developed cover. Habitat suitability is displayed on a percentile scale, indicating whether a certain pixel was more suitable for woodcock occupancy than the corresponding percentage of other pixels in the state.

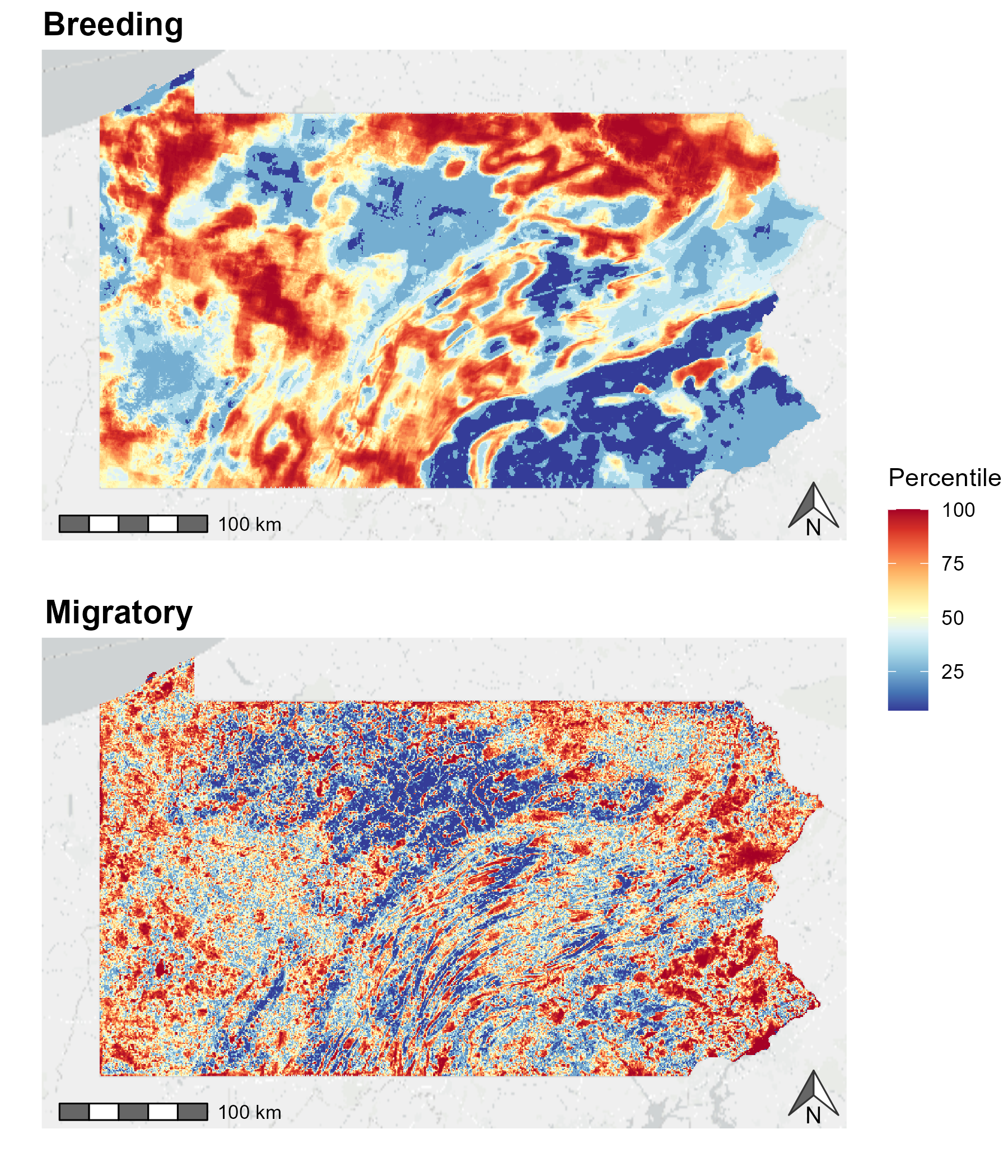


Figure 4. Breeding and migratory predictive habitat suitability layers suggest that woodcock select habitat at finer scales during the migratory season. Certain areas which are not appropriate for breeding season habitat management, such as southeastern Pennsylvania, may be appropriate for migratory habitat management. Percentile indicates whether a certain pixel was more suitable for woodcock occupancy than the corresponding percentage of other pixels in the state; for example, a value of 0.65 indicates that the pixel contains habitat that is more suitable than 65% of other pixels statewide.



Figure 5. Breeding and migratory season habitat suitability for woodcock (5A) by EPA level 3 ecoregion (5B) in Pennsylvania (Omernik and Griffith, 2014). Three ecoregions, Northern Piedmont, Middle Atlantic Coastal Plain, and Eastern Great Lakes Lowlands, had mean breeding season habitat suitability values of <30% and mean migratory season habitat suitability values of >60%. Habitat suitability is calculated based on randomly sampled locations within each ecoregion and uses a percentile scale, indicating whether a certain pixel was more suitable for woodcock occupancy than the corresponding percentage of other pixels in the state. Box plots, arranged in the same order as the figure legend, indicate the median and interquartile range while whiskers extend to the largest/smallest value within 1.5 times the interquartile range.

**4 Discussion**

We found that models of woodcock habitat distribution exhibited poor cross-seasonal transferability between distribution models, with low correlation between breeding and migratory habitat models at multiple spatial scales (Pearson correlation at pixel-level: 0.15, gameland-level: 0.39). As such, management focused on breeding habitat alone is unlikely to maximize conservation of migratory habitat for this species. We demonstrated a potential solution to increase cross-seasonal transferability through the integration of multi-season species distribution models into a single SDSS tool. The SDSS emphasizes the importance of user input by allowing choice in the weighting of breeding and migratory habitat to meet local management objectives and encourages users to make informed decisions regarding the importance of habitat during these stages.

Regional differences between the breeding and migratory models underscore the importance of multi-season distribution models in delineating regional priorities for migratory bird management. For the woodcock model, we found relatively low breeding season suitability within the Northern Piedmont, Middle Atlantic Coastal Plain, and the Eastern Great Lakes Lowlands ecoregions, despite high migratory suitability. User-weighted prioritization of seasonal habitat might allow managers in regions in which woodcock breeding habitat is scarce to instead prioritize migratory habitat management. On the other hand, a manager of an area that provides breeding habitat in a region where breeding habitat is scarce might decide that their most effective decision would be to prioritize breeding habitat as much as possible. We posit that there might be several effective management strategies based on the information provided in multi-season distribution models, and the incorporation of user-specified weights empowers users to consider multiple possible management decisions and customize the information provided to inform their management strategy.

We showed that American woodcock occurred in distinctly different habitat during the breeding and migratory seasons in Pennsylvania and were associated with different spatial scales between seasons. During the breeding season, woodcock habitat suitability was dependent primarily on covariates at 5- and 10-km scales, while during the migratory season habitat suitability was additionally dependent on covariates at 500-m and 1-km scales. This pattern supports past observations that migratory birds select habitat at a finer scale during migration (Stanley et al., 2021). Due to these differences in the scale, managers may need to adjust management to match the scale of the season of interest (Fattorini et al., 2020). For example, woodcock management for breeding season habitat in Pennsylvania might focus on conserving broad swaths of habitat on large public lands, such as Pennsylvania state gamelands. As the predictive layer is fairly uniform across even large state gamelands, performing habitat management at that scale would likely be effective. However, the migratory model had a much finer spatial resolution, and was much more likely to predict smaller pockets of habitat in areas not traditionally targeted by wildlife management agencies, such as urban areas or landscapes more heavily dominated by agriculture and privately-owned lands (McCance et al., 2017). Differences in the spatial scale of habitat associations among seasons demonstrate the necessity of modeling occupancy for each season separately and to ensure that management supports the habitat requirements at appropriate scales for animals throughout the full annual cycle.

Multi-season distribution modeling may also highlight areas of potential for conservation that are not traditionally managed for wildlife habitat due to a lack of breeding season occupancy. Woodcock were more tolerant of developed land cover during the migratory season than the breeding season, and the migratory season model predicted use of highly developed areas such as suburban Philadelphia and Pittsburg. This corresponds with findings of Buler and Dawson (2014), who found that migratory birds heavily used urban greenspaces during stopover, perhaps due to attraction to high levels of artificial light at night (McLaren et al., 2018) and lack of other stopover options. One implication is that, in addition to management for woodcock at smaller spatial scales, practitioners may need to consider management of urban greenspaces for migratory birds. Opportunities for urban habitat conservation might come through partnerships with public and private landowners, such as park authorities and utility companies, to conserve migratory habitat in urban greenspaces (Cerra, 2017). Another opportunity for urban habitat conservation might be the Urban National Wildlife Refuge program (USFWS, 2023), which has dual roles in preserving wildlife habitat and expanding access to natural areas for historically excluded communities. Pennsylvania is host to one Urban National Wildlife Refuge, John Heinz National Wildlife Refuge at Tinicum, located in the Philadelphia suburbs. Our model predicted high migratory habitat suitability for woodcock within this refuge, demonstrating how urban wildlife refuges may provide crucial stopover habitat in heavily urbanized areas.

A multi-season distribution model framework is particularly well suited to migratory bird management due to its flexibility in application of multiple data sources, which is particularly useful for species that are studied using separate techniques and surveys during each season. While there are several surveys for examining bird distribution during the breeding and wintering seasons (e.g. Bonter and Greig, 2021; Robbins et al., 1986), examining bird habitat use during the migratory period continues to be a challenge. Individually-marked birds with GPS transmitters are the gold standard for this type of analysis, as stopover locations can be separated from breeding and wintering locations for each tagged bird. However, GPS transmitters are still too large to attach to many small migratory birds, and the low number of stopovers attained per individual (mean = 1.4, sd = 0.6 in this study) combined with the considerable price of these transmitters may make attaining a large sample size a financial difficulty for most study species. The use of citizen science data collected during migration, such as the eBird data collection platform (Sullivan et al., 2009), may provide a more generalizable way to collect stopover location data, but certain assumptions must be made to distinguish true migratory locations from early breeding/wintering season arrivals. Decisions on seasonal management priorities can also be informed by other data sources and models, such as multi-season survival models to determine whether breeding or migratory habitat has a greater role in limiting survival or migratory corridor models to identify high densities of migrants (Cohen et al., 2022). SDSS provide a framework for blending these multi-season datasets and models to improve management and conservation decision making for migratory birds.

Non-avian taxa are also likely to find benefits from the application of multi-season distribution models. Seasonally differing habitat use within a region is common among altitudinal migrants, including ungulates (Boyce, 1991; Mauer, 1998), and partial migrants ranging from large mammals to insects (Chapman et al., 2011). Cross-seasonal transferability issues which arise from these habitat differences can be addressed through a multi-season distribution modeling framework, allowing flexibility in data sources and facilitating user choice in seasonal prioritization.

**CRediT authorship contribution statement**

LA Berigan, AM Roth, LM Williams, KR Duren, S Bearer, K Wenner, P Kasper, and EJ Blomberg contributed to the conceptualization of this study and design of the methodology. KR Duren acquired funding for the creation of W-PAST, while EJ Blomberg and LM Williams acquired funding for the expansion of the Eastern Woodcock Migration Research Cooperative (EWMRC) into Pennsylvania. LA Berigan and AC Fish curated the GPS data and LM Williams curated the survey data used in this study. LA Berigan conducted the formal analysis and built the W-PAST tool. LA Berigan, AM Roth, and EJ Blomberg wrote the original draft of the manuscript, and all authors contributed to revisions and editing.

**Declaration of competing interest**

The authors have no conflicts of interest to declare.

**Supplementary material**

Appendix A. AUC scores from pilot evaluation of modeling techniques.

**Data availability**

The code used in this analysis is publicly available at github.com/EWMRC/AMWO-seasonal-weighted-SDM. Data are available from the corresponding author upon reasonable request.

**Acknowledgements**

We thank the 42 state, federal, university, and non-profit collaborators who have provided funding and/or logistic support to the EWMRC, a full list of whom is available at woodcockmigration.org. In addition to their collaboration with the EWMRC, the Pennsylvania Game Commission provided woodcock survey data for this analysis and funded the creation of W-PAST. We would also like to thank Rebecca Rau and the U.S. Fish and Wildlife Service for their administration of the American Woodcock Singing-Ground Survey, which provided breeding season data for this analysis.

**References**

Agafonkin, V., 2022. Leaflet.js. https://leafletjs.com/ (accessed 4.27.2023).

Allen, B.B., McAuley, D.G., Blomberg, E.J., 2020. Migratory status determines resource selection by American Woodcock at an important fall stopover, Cape May, New Jersey. The Condor 122, duaa046.

Blomberg, E.J., Fish, A.C., Berigan, L.A., Roth, A.M., Rau, R.D., Balkcom, G., Carpenter, B., Costanzo, G., Duguay, J.P., Graham, C.L., Harvey, B., Hook, M., Howell, D.L., Maddox, S., McWilliams, S., Meyer, S.W., Nichols, T.C., Pollard, J.B., Roy, C., Sausville, D., Slezak, C., Stiller, J., Tetreault, M., Washington, D., Weik, A., Williams, L., In review. The phenology of spring migration by male American woodcock and its relevance to continental population monitoring. Journal of Wildlife Management.

Bonter, D.N., Greig, E.I., 2021. Over 30 years of standardized bird counts at supplementary feeding stations in North America: a citizen science data report for Project FeederWatch. Frontiers in Ecology and Evolution 9, 619682.

Boyce, M.S., 1991. Migratory behavior and management of elk (Cervus elaphus). Applied Animal Behaviour Science 29, 239–250.

Breiman, L., 2001. Random forests. Machine learning 45, 5–32.

Buler, J.J., Dawson, D.K., 2014. Radar analysis of fall bird migration stopover sites in the northeastern US. The Condor: Ornithological Applications 116, 357–370.

Cerra, J.F., 2017. Emerging strategies for voluntary urban ecological stewardship on private property. Landscape and Urban Planning 157, 586–597.

Chang, W., Cheng, J., Allaire, J.J., Sievert, C., Schloerke, B., Xie, Y., Allen, J., McPherson, J., Dipert, A., Borges, B., 2022. shiny: Web Application Framework for R.

Chapman, B.B., Brönmark, C., Nilsson, J.-Å., Hansson, L.-A., 2011. The ecology and evolution of partial migration. Oikos 120, 1764–1775.

Clark, E.R., 1970. Woodcock status report, 1969. U.S. Fish and Wildlife Service, Laurel, MD.

Cohen, E.B., Buler, J.J., Horton, K.G., Loss, S.R., Cabrera-Cruz, S.A., Smolinsky, J.A., Marra, P.P., 2022. Using weather radar to help minimize wind energy impacts on nocturnally migrating birds. Conservation Letters 15, e12887.

Cohen, I., Huang, Y., Chen, J., Benesty, J., Benesty, J., Chen, J., Huang, Y., Cohen, I., 2009. Pearson correlation coefficient. Noise reduction in speech processing 1–4.

Dawson, W.R., 2020. Pine Siskin (Spinus pinus), version 1.0, in: Poole, A.F. (Ed.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.

Dobrowski, S.Z., Thorne, J.H., Greenberg, J.A., Safford, H.D., Mynsberge, A.R., Crimmins, S.M., Swanson, A.K., 2011. Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. Ecological Monographs 81, 241–257. https://doi.org/10.1890/10-1325.1

Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. Journal of animal ecology 77, 802–813.

ESRI, 2023. ArcGIS Online. https://www.arcgis.com/.

Fattorini, N., Lovari, S., Watson, P., Putman, R., 2020. The scale-dependent effectiveness of wildlife management: A case study on British deer. Journal of Environmental Management 276, 111303.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental conservation 24, 38–49.

Fink, C.M., 2013. Dynamic Soil Property Change in Response to Natural Gas Development in Pennsylvania. (Thesis). Pennsylvania State University.

Fink, D., Auer, T., Johnston, A., Strimas-Mackey, M., Ligocki, S., Robinson, O., Hochachka, W., Jaromczyk, L., Rodewald, A., Wood, C., Davies, I., Spencer, A., 2022. eBird Status and Trends. https://doi.org/10.2173/ebirdst.2021

Genuer, R., Poggi, J.-M., Tuleau-Malot, C., 2022. VSURF: Variable Selection Using Random Forests.

Genuer, R., Poggi, J.-M., Tuleau-Malot, C., 2015. VSURF: an R package for variable selection using random forests. The R Journal 7, 19–33.

Glasgow, L.L., 1958. Contributions to the knowledge of the ecology of the American woodcock, Philohela minor (Gmelin), on the wintering range in Louisiana (Dissertation). Texas A&M University, College Station , Texas.

Goudie, R.I., Robertson, G.J., Reed, A., Billerman, S.M., 2020. Common Eider (Somateria mollissima), version 1.0, in: Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.

Harper, E., 2006. Open-source technologies in web-based GIS and mapping (Thesis). Northwest Missouri State University, Maryville, Missouri.

Hesselbarth, M.H.K., Sciaini, M., With, K.A., Wiegand, K., Nowosad, J., 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography 42, 1648–1657.

Hijmans, R.J., 2022. terra: Spatial Data Analysis. https://CRAN.R-project.org/package=terra.

Hopkins, L.D., Armstrong, M.P., 1985. Analytic and cartographic data storage: a two-tiered approach to spatial decision support systems, in: Proceedings of Seventh International Symposium on Computer-Assisted Cartography. Washington, DC: American Congress on Surveying and Mapping.

Jin, S., Homer, C., Yang, L., Danielson, P., Dewitz, J., Li, C., Zhu, Z., Xian, G., Howard, D., 2019. Overall methodology design for the United States national land cover database 2016 products. Remote Sensing 11, 2971.

Kelley, J.R., Williamson, S., Cooper, T.R., 2008. American Woodcock Conservation Plan: a summary of and recommendations for woodcock conservation in North America. US Fish & Wildlife Publications 430.

Liaw, A., Wiener, M., 2002. Classification and Regression by randomForest. R News 2, 18–22.

Marra, P.P., Cohen, E.B., Loss, S.R., Rutter, J.E., Tonra, C.M., 2015. A call for full annual cycle research in animal ecology. Biology letters 11, 20150552.

Mauer, F.J., 1998. Moose migration: northeastern Alaska to northwestern Yukon territory, Canada. Alces: A Journal Devoted to the Biology and Management of Moose 34, 75–81.

McAuley, D.G., Keppie, D.M., Whiting Jr., R.M., 2020. American Woodcock (Scolopax minor), version 1.0, in: Poole, A.F. (Ed.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.

McAuley, D.G., Longcore, J.R., Sepik, G.F., 1993. Techniques for Research into Woodcocks: Experiences and Recommendations, in: Proceedings of the Eighth American Woodcock Symposium. U.S. Fish and Wildlife Service, p. 5.

McCance, E.C., Decker, D.J., Colturi, A.M., Baydack, R.K., Siemer, W.F., Curtis, P.D., Eason, T., 2017. Importance of urban wildlife management in the United States and Canada. Mammal Study 42, 1–16.

McConnell, M., Burger, L.W., 2011. Precision conservation: a geospatial decision support tool for optimizing conservation and profitability in agricultural landscapes. Journal of Soil and Water Conservation 66, 347–354.

McLaren, J.D., Buler, J.J., Schreckengost, T., Smolinsky, J.A., Boone, M., Emiel van Loon, E., Dawson, D.K., Walters, E.L., 2018. Artificial light at night confounds broad-scale habitat use by migrating birds. Ecology Letters 21, 356–364.

Mehlman, D.W., Mabey, S.E., Ewert, D.N., Duncan, C., Abel, B., Cimprich, D., Sutter, R.D., Woodrey, M., 2005. Conserving stopover sites for forest-dwelling migratory landbirds. The Auk 122, 1281–1290.

Miller, J., 2010. Species distribution modeling. Geography Compass 4, 490–509.

Moore, J.D., Andersen, D.E., Cooper, T.R., Duguay, J.P., Oldenburger, S.L., Stewart, C.A., Krementz, D.G., 2019. Migratory connectivity of American Woodcock derived using satellite telemetry. The Journal of Wildlife Management 83, 1617–1627.

Myatt, N.A., Krementz, D.G., 2007. Fall migration and habitat use of American woodcock in the central United States. The Journal of wildlife management 71, 1197–1205.

Norris, D.R., Marra, P.P., 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. The Condor 109, 535–547.

NRCS, 2021. Web Soil Survey. https://websoilsurvey.nrcs.usda.gov/ (accessed 12.08.2021).

Omernik, J.M., Griffith, G.E., 2014. Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environmental Management 54, 1249–1266. https://doi.org/10.1007/s00267-014-0364-1

Pennsylvania Game Commission, 2023. Pennsylvania State Game Lands [WWW Document]. URL https://www.pgc.pa.gov/HuntTrap/StateGameLands/Pages/default.aspx (accessed 7.12.23).

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecological modelling 190, 231–259.

R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M., Guisan, A., 2006. Are niche-based species distribution models transferable in space? J Biogeography 33, 1689–1703. https://doi.org/10.1111/j.1365-2699.2006.01466.x

Rappole, J.H., 2013. The avian migrant: the biology of bird migration. Columbia University Press.

Rice, J., Anderson, B.W., Ohmart, R.D., 1980. Seasonal Habitat Selection by Birds in the Lower Colorado River Valley. Ecology 61, 1402–1411. https://doi.org/10.2307/1939049

Rieffenberger, J.C., Kletzly, R.C., 1966. Woodcock night-lighting techniques and equipment. WH Goudy, compiler. Woodcock research and management 33–35.

Robbins, C.S., Bystrak, D., Geissler, P.H., 1986. The Breeding Bird Survey: its first fifteen years, 1965-1979. Patuxent Wildlife Research Center, Laurel, MD.

Seamans, M.E., Rau, R.D., 2020. American Woodcock Population Status, 2020. U.S. Fish and Wildlife Service, Laurel, MD.

Sheldon, W.G., 1960. A method of mist netting woodcocks in summer. Bird-banding 31, 130–135.

Stanley, C.Q., Dudash, M.R., Ryder, T.B., Shriver, W.G., Serno, K., Adalsteinsson, S., Marra, P.P., 2021. Seasonal variation in habitat selection for a Neotropical migratory songbird using high-resolution GPS tracking. Ecosphere 12, e03421.

Sugumaran, R., Degroote, J., 2010. Components of SDSS II, in: Spatial Decision Support Systems: Principles and Practices. CRC Press, Boca Raton, FL, USA, pp. 145–190.

Sugumaran, V., Sugumaran, R., 2007. Web-based Spatial Decision Support Systems (WebSDSS): evolution, architecture, examples and challenges. Communications of the Association for Information Systems 19, 40.

Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D., Kelling, S., 2009. eBird: A citizen-based bird observation network in the biological sciences. Biological conservation 142, 2282–2292.

U.S. Census Bureau, 2021. 2020 Decennial Census. Washington, D.C., USA. data.census.gov.

U.S. Fish and Wildlife Service, 1996. U.S. Fish and Wildlife Service Service Manual, 870 FW 1.

USFWS, 2023. Urban Wildlife Conservation Program. https://www.fws.gov/program/urban-wildlife-conservation (accessed 6.27.23).

USGS, 2000. 7.5 minute digital elevation models (DEM) for Pennsylvania (30 meter). U.S. Geological Survey, Reston, VA. http://www.pasda.psu.edu/.

USGS, USDA, 2020. LANDFIRE 2.0.0 Successional Class Layer. U.S. Geological Survey and U.S. Department of Agriculture, Reston, VA and Washington, DC. http://landfire.cr.usgs.gov/viewer/.

Vignali, S., Barras, A.G., Arlettaz, R., Braunisch, V., 2020. SDMtune: An R package to tune and evaluate species distribution models. Ecology and Evolution 10, 11488–11506. https://doi.org/10.1002/ece3.6786

Wang, J., Chen, L.S., 2016. MixRF: A Random-Forest-Based Approach for Imputing Clustered Incomplete Data. https://github.com/randel/MixRF.