*Joint breeding and migratory season species distribution models better facilitate habitat conservation for a migratory bird*

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Target: Biological Conservation

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

**Abstract**

Species distribution models frequently have issues with cross-seasonal transferability if 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 prioritize habitat management. We demonstrated a potential application of this framework through an analysis of multi-season habitat use by American woodcock in Pennsylvania, USA. We modeled woodcock breeding and migratory habitat distributions in Pennsylvania 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 the user to customize the tool based on area-specific management priorities. Multi-season distribution models like this one allow us to overcome lack of cross-seasonal transferability by incorporating multiple season-specific species distribution models into a single management prioritization framework. This framework is best suited for taxa which radically shift their habitat use throughout the full annual cycle, such as migratory birds.

**1 Introduction**

Species distribution models are frequently used to tools to assist conservation decision-making (Miller, 2010), however, they are known to have issues withtransferability. 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 as a result of changing conditions (temporal transferability; Dobrowski et al., 2011). We posit that an additional subcategory of temporal transferability exists, called cross-seasonal transferability, for situations where species habitat associations differ fundamentally among seasons or life stages, resulting in the species 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.

Migratory birds are one group of organisms that are clearly sensitive to issues of cross-seasonal transferability through use different geographic areas throughout their annual cycle that can be 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 in the same region, especially for short-distance migrants (ex. American woodcock, Fig. 1). Conserving birds in regions with seasonal overlap may therefore necessitate separate distribution models for each season, and approaches to incorporate these multiple models into the management decision process.

Spatial decision support systems (SDSS) may provide a useful mechanism to combine 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. SDSS frequently come as extensions of existing geographic information systems such as ArcMap (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 and ArcGIS Online (Agafonkin, 2022; 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 also be used to compensate by incorporating multiple season-specific species distribution models into the decision-making process. An SDSS approach could allow species distribution models from different seasons to be combined into a single predictive layer using user-specified weights. For example, a user might want to primarily conserve breeding habitat for a species and conserve migratory habitat as a secondary objective. Using an SDSS, the user could weight a breeding season species distribution model to 70% and a migratory season species distribution model to 30% and output a single predictive habitat layer that prioritized management areas according to the user’s seasonal management objectives.

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). Pennsylvania provides breeding habitat for an estimated 2.3% of the global woodcock population (52,400 birds), and stopover habitat for nearly 1/3 of woodcock migrating throughout the northeastern United States and eastern Canada (30.5%, 684,500 birds; Kelley et al., 2008). Managing woodcock habitat for both breeding and migratory seasons have been identified as priorities by the Pennsylvania Game Commission, and our goal was to develop a SSDS tool to aid managers considering trade-offs between those two priorities. We used a multi-season modeling framework to predict the distribution of migratory and breeding habitats, which we combine in a SSDS to facilitate habitat prioritization. By identifying areas that might meet joint objectives to conserve habitat during multiple seasons, users could improve full annual cycle conservation and more efficiently allocate management resources



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 Breeding season data*

To model woodcock habitat suitability in Pennsylvania 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 calls during their crepuscular breeding display. Observers marked woodcock as present at each point based on whether male displays were recorded during 2-minute intervals shortly after dusk. Federal survey routes were randomly distributed (Clark, 1970), while state surveys were located purposefully near state gamelands or in areas where managers believe woodcock occurrence was likely. We used survey data collected from 2016–2020, and distilled records to presence or likely absence based on detection of at least one male during the 5-year period.

*2.2 Migratory season data*

We delineated woodcock occurance 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 morning and evenings (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 migratory stopover locations, defined as any place where a migrant bird can land and survive until the next migratory flight (Mehlman et al., 2005). We determined whether a bird was actively migrating based on when the bird started and ceased making movements > 16.1 km in the spring or fall. Because woodcock migrate at night, we considered all diurnal locations between migratory initiation and termination to be stopovers. After a visual inspection of recursive movement patterns, we decided that locations from the same bird within 3km reflected a single stopover decision by a migrating woodcock. To reduce pseudoreplication and spatial autocorrelation of closely clustered locations, we selected one location randomly from each cluster of points within 3km and removed the remainder from the analysis. 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 to accommodate differences in habitat associations and data sources between seasons. Each model used explanatory variables with presumed relevance to woodcock occurrence, 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), classification and regression trees (Breiman et al., 1984), and neural networks (Hopfield, 1982). 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. The random forest classifier had the highest AUC among modeling approaches, and we therefore used random forest techniques for all subsequent models.

For the breeding season model, we used a random forest classifier designed for clustered data (Wang and Chen, 2016), and applied survey route id as a clustering variable to compensate for spatial autocorrelation among points on the same survey route. We also included survey type (state vs federal) as an explanatory variable to accommodate the non-random distribution of state survey routes. 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 (XX%) and testing (XX%) datasets were randomly sampled each fold. We used 10 folds for the breeding season model, but only 5 folds for the migratory season model 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 add variables to each model, only retaining variables if doing so lead to an appreciable decrease in the model’s out-of-bag error. This effectively removed 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.

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 using 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 spatial 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 sought to understand how environmental variables contributed to model predictions. We sampled covariate values and model-predicted suitability at 10,000 randomly distributed points throughout Pennsylvania, and used hex plots to visualize trends between covariates and predictions for each season.

To highlight regional differences in the distribution of breeding and migratory habitat, we evaluated variability in season-specific habitat suitability values among ecoregions within Pennsylvania. We generated 10,000 randomly-distributed locations and sampled breeding and migratory habitat suitability at each of those points, and visualized variation among each EPA level 3 ecoregion in Pennsylvania using box-and-whisker plots.

*2.5 Spatial Decision Support System*

We created a SDSS in the Shiny ecosystem (Chang et al., 2022) to facilitate user choice in the importance of breeding and migratory season habitat to local 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), which 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 state wildlife management agency, 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 comparsion 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 produce large returns for local woodcock. 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 have the greatest relative impact 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 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 deployed transmitters on 463 woodcock from fall 2017 to spring 2021, and 82 individuals recorded GPS locations at 113 migratory 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 (0.5km) or in the suite of 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 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 10km 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 500m scale, and only 1 landscape covariate at the 1km scale, whereas the most informative migratory model included all available small-scale landscape covariates. Because of the influence of covariates at a 500m and 1km 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. 5), 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%.

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 |
| Moisture | Drainage, Topographic Wetness Index |  |

A picture containing chart

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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.

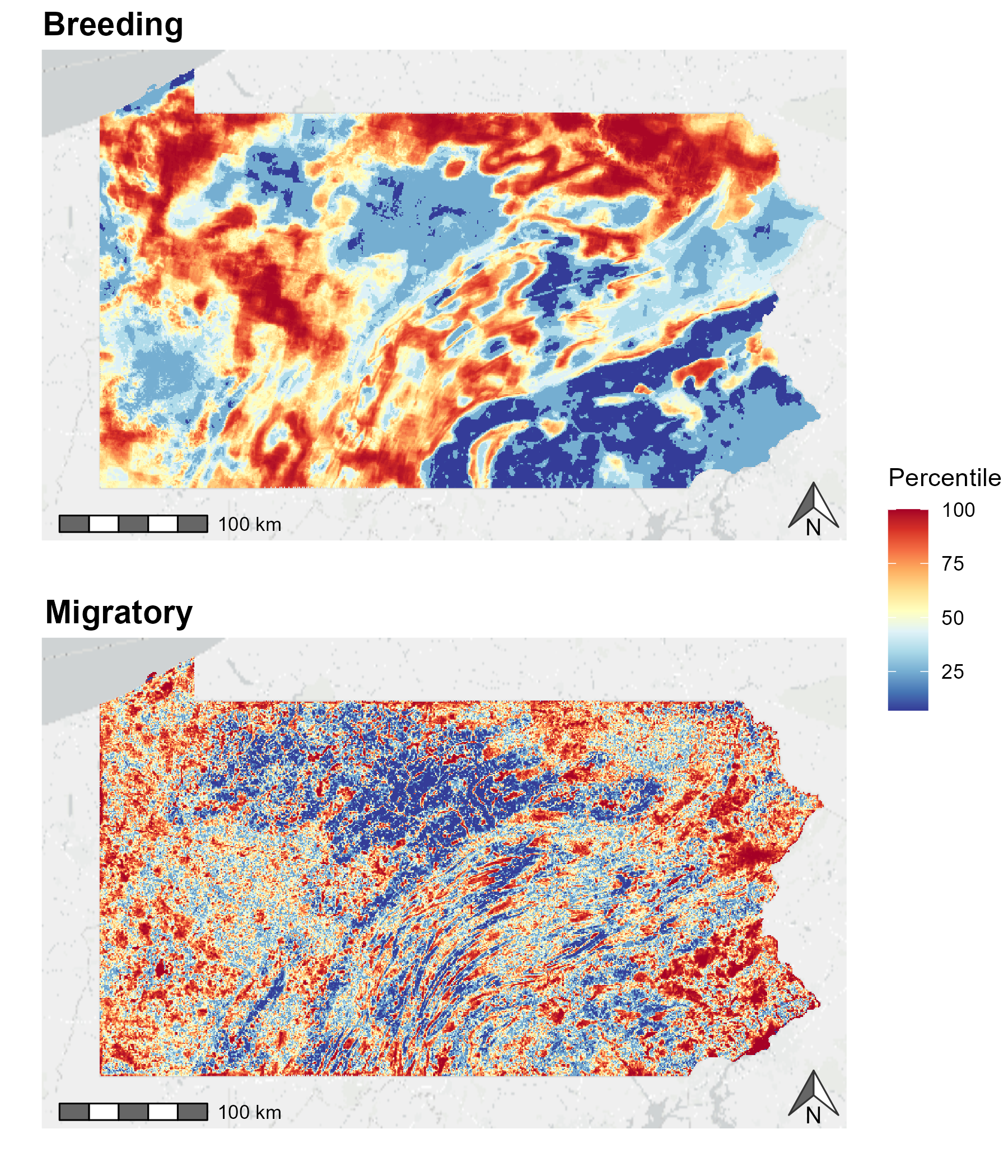


Figure 4. Breeding and migratory predictive habitat suitability layers suggest that woodcock select habitat at different scales in different seasons. Certain areas which are not productive for breeding season habitat management, such as southeastern Pennsylvania, may be productive for migratory habitat management. Percentile indicates whether a certain pixel was more suitable for woodcock occupancy than the corresponding percentage of other pixels in the state.



Figure 5. Breeding and migratory season habitat suitability for woodcock by EPA level 3 ecoregion 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 demonstrated an integration of multi-season species distribution models into a single SDSS tool. The SDSS emphasizes the importance of practitioner input in management prioritization by allowing user choice in the weighting of breeding and migratory habitat to meet local management objectives. This approach allows users to overcome issues with low cross-seasonal transferability in species distribution models and prioritize management in a way that conserves habitat across stages of the life cycle. It also accommodates clear regional differences in relative availability of seasonal habitat in the state.

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 500m and 1 km scales. This pattern supports past observations that migratory birds select habitat at a finer scale during the migratory season (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. 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 prone to having small pockets of habitat in areas not traditionally targeted by wildlife management agencies, such as urban areas. Differences in the spatial scale of habitat associations between seasons demonstrate the necessity of modeling occupancy for each season separately, to ensure that management supports the habitat requirements of 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. 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, presumably 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. Another opportunity for urban habitat conservation might be the Urban National Wildlife Refuge program, 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 migratory stopover habitat in heavily urbanized areas.

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, however these areas had much greater migratory suitability. This is one example of a circumstance in which a user-weighted prioritization of seasonal habitat might be particularly effective. Managers in regions in which woodcock breeding habitat is scarce might instead decide to prioritize migratory habitat management, for example, allowing managers to play to their regions’ strengths. 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 move would be to prioritize breeding habitat as much as possible. These examples demonstrate that there might be several effective management strategies based on the information provided in multi-season distribution models. By incorporating practitioner input through user-specified weights of each seasonal model, we empower users to consider multiple possible management decisions and customize the information provided to inform their management strategy.

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 migratory passerines, 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 migratory 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 should also be informed by other data sources, such as full annual cycle survival models to determine whether breeding or migratory habitat has a greater role in limiting survival, and migratory corridor models to identify high densities of migrants (Cohen et al., 2022). With this added context, multi-season distribution models will provide valuable support tools for the conservation of many migratory birds.

**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 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.

**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 would like to 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

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.

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.

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

Breiman, L., Friedman, J., Olshen, R., Stone, C., 1984. Classification and regression trees. Wadsworth Int. Group 37, 237–251.

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.

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.

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.

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

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

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. https://CRAN.R-project.org/package=VSURF

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.

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.

Hopfield, J.J., 1982. Neural networks and physical systems with emergent collective computational abilities. Proceedings of the national academy of sciences 79, 2554–2558.

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.

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.

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

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

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

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, Maryland.

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, 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.

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

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