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

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**Abstract**

Species distribution models frequently have issues with cross-seasonal transferability, with species distribution models created using breeding season data frequently not reflecting habitat use 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 for prioritizing habitat management. We demonstrated a potential application of this framework through an analysis of multi-season habitat use of American woodcock in Pennsylvania. We modeled woodcock breeding and migratory habitat throughout Pennsylvania using random forest classifiers and integrated the predictions of both models into a single tool 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 their seasonal management priorities. Multi-season distribution models like this one allow us to overcome issues with a 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.

**Introduction**

Species distribution models are frequently used to convert data about species occurrence and habitat associations into tools to assist conservation decision-making (Miller 2010). However, species distribution models are known to have issues with spatial transferability, where models may not be reflective of animal distributions in other parts of their range (spatial transferability; Randin et al. 2006), or for predicting species distributions into the future (temporal transferability; Dobrowski et al. 2011). We posit that an additional subcategory of temporal transferability exists, called cross-seasonal transferability, for species which have differing habitat use between seasons or life stages. Wildlife science has a long history of bias towards studying animals during the breeding season, which neglects the value of non-breeding habitat for survival and carry-over effects into the breeding season (Norris & Marra 2007). By building species distribution models which focus solely on the breeding season, we disregard habitat requirements during other portions of the year which may be essential to a species’ persistence.

Migratory birds are potentially vulnerable to issues of cross-seasonal transferability, as they 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, which frequently results in birds using fundamentally different types of habitat in each season (Rice et al. 1980, Allen et al. 2020, Stanley et al. 2021). Despite differences in habitat, there are circumstances in which breeding, wintering, and migratory habitat may occur in the same region, especially for short-distance migrants (ex. American woodcock, Figure 1). Managing in regions with seasonal overlap would necessitate creating separate distribution models for each season, and approaches to incorporate 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 & 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 custom built SDSS that are accessible via a web browser and can be easily used by decision makers with little additional training (Sugumaran & 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 might 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.

Here we demonstrate a SDSS framework for users 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 extensive overlap among migratory, breeding, and wintering ranges (Fig. 1), and fundamentally different habitat requirements among seasons (Myatt and Krementz 2007, Allen et al. 2020). Pennsylvania provides breeding habitat for an estimated 2.3% of the global woodcock population (52,400 birds), but it potentially provides migratory stopover habitat for a much larger proportion of woodcock that breed throughout the northeastern United States and eastern Canada (30.5%, 684,500 birds; Kelley et al. 2008). Therefore, managing for woodcock habitat in both the 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 priorities. We used a multi-season habitat modeling framework to predict the distribution of migratory and breeding habitats, which we combine in a SSDS for 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. Seasonal ranges were delineated by eBird’s Status and Trends project (Fink et al. 2022) using citizen science data. Migration routes illustrate potential connections between eastern (dashed line), central (solid line), and western (dotted line) population segments. Migration routes were originally proposed by Glasgow (1958) and were later reproduced by Moore et al. (2019). Inset illustrates multiple migration routes intersecting with the breeding range in the state of Pennsylvania.

**Methods**

*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 through 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. Singing Ground Survey routes were randomly distributed (Clark 1970), while Pennsylvania surveys were located purposefully near state gamelands or in areas where managers believe woodcock occupancy 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.

*Migratory season data*

We delineated woodcock occupancy 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 evening flights (Sheldon 1960), and on night roosts using spotlights and dip nets (Rieffenberger and Kletzly 1966, McAuley et al. 1993). We attached 4g, 5g, and 6.3g PinPoint GPS Argos transmitters (Lotek Wireless Inc., Newmarket, Ontario, CA) to captured woodcock. Transmitters recorded 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 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 that were > 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 combined woodcock stopover locations, which demonstrated woodcock presence, with 10,000 locations randomly distributed throughout Pennsylvania, which we considered pseudoabsence locations.

*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 habitat associations, 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 a 500m, 1km, 5km, and 10km radius 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 a 90m resolution, and then calculated the appropriate configuration metric within a 500m, 1km, 5km, and 10km radius of each pixel.

We evaluated several potential modeling techniques fit to a smaller subset of woodcock occurrence data using MaxEnt (Phillips et al. 2006), random forest classification (Breiman 2001), classification and regression trees (Brieman 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. After finding that the random forest classifier had the highest AUC, we 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), using 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 account for 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 & Wiener 2002). We assessed the accuracy of our random forest models using a k-fold cross validation approach to create separate training and testing datasets for each fold. We used 10 folds for the breeding season model but only 5 folds for the migratory season model to accommodate for small sample size in the migratory 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 the predictions of each fold together.

To avoid overwhelming the species distribution models with highly correlated or irrelevant variables, we selected a final model for each analysis using a three-step backwards variable-selection approach using the R package VSURF (Genuer et al. 2019), where each step produced a more parsimonious model. The first step eliminated variables which had a lower variable importance than a threshold value determined based on the guidelines provided in Genuer et al. (2015), removing variables that were irrelevant to the model. The second step retained only the variables in the analysis which led to the smallest out-of-bag error rates when training the model, effectively eliminating variables which had some relevance but were not critical for prediction. The third step used an stepwise process to add variables to a model, only including a variable if doing so would 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 models created from these reduced sets of variables using AUC to assess their predictive accuracy and used the set of variables with the highest AUC to create the final predictive layer for each model.

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

|  |  |  |
| --- | --- | --- |
| **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 |

*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). We elected to use hex plots to visually identify trends between covariates and predictive layers. To create hex plots, we sampled covariate values and predicted migratory and breeding season suitability at 10,000 randomly distributed points throughout Pennsylvania. We visually inspected those hex plots to identify relationships between the most important covariates, determined using the variable selection approach described above, and the associated predictive layer.

To highlight regional differences in the distribution of breeding and migratory habitat, we created a figure demonstrating how season-specific habitat suitability varies by ecoregion within Pennsylvania. We generated 10,000 randomly-distributed locations and sampled breeding and migratory habitat suitability at each of those points, and then created box-and-whisker plots of seasonal habitat suitability for each EPA level 3 ecoregion in Pennsylvania.

*Spatial Decision Support System*

To facilitate user choice in the importance of breeding and migratory season habitat to local management, we created a SDSS in the Shiny ecosystem (Chang et al. 2021) that allows users to assign weights to each seasonal layer in 10% increments (ex. 20% migratory and 80% breeding season), and combine them into a single multi-season layer (Fig. 2). The weighting was conducted on a pixel-by-pixel basis

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. *pw* therefore provides a simple weighted average based on user-defined weightings for each season.

Practitioners using a SSDS will often benefit from features customized to their management applications. In the case of the Pennsylvania Game Commission, a state wildlife management agency, one primary goal is to increase availability of woodcock habitat on state-managed gamelands. Thus, our tool required functionality to compare habitat suitability among gamelands. We used four metrics for comparison: average pixel value, total habitat, % high quality, and % medium quality, which were calculated using the weighted averages of the breeding and migratory season predictive layers.

Each prioritization metric was configured to answer a specific question for management applications. Average pixel value, or the mean of all pixels within a state gameland, tended to favor small gamelands that were predominantly composed of woodcock habitat, and was intended to demonstrate where a small amount of habitat management might have the largest returns for woodcock populations. Total habitat was average pixel value multiplied by the acreage of the gameland, which favored larger gamelands that might not be entirely composed of woodcock habitat but might contain a large amount of woodcock habitat in aggregate by virtue of their size. Total habitat could be used to determine which gamelands would have the highest impact if they were managed for woodcock. Percent high quality habitat was the percentage of cells within a gameland greater than the 33rd percentile of all pixels 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 by the tool), the user can 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 which is publicly available with the SDSS at www.woodcock.shinyapps.io/W-PAST.



Figure 2. Conceptual diagram of the decisions users can make 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 the statewide predictive layer and gameland prioritization metrics, which allow the user to compare the suitability of gamelands for woodcock management.

**Results**

We deployed transmitters on 463 woodcock from fall 2017 to spring 2021, with 82 individuals recording GPS locations at 113 migratory stopovers in Pennsylvania. Breeding season survey data were available for 770 locations along 77 American Woodcock Singing Ground Survey routes and 800 locations along 80 Pennsylvania Game Commission survey routes. The most predictive (AUC = 0.83) breeding season model 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). No variables at the finest landscape scale (0.5km), or in the suite of moisture variables, were included in the most informative model. Graphs of habitat suitability for each covariate showed strong, non-linear relationships with several of the most informative variables (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 (AUC=0.78) migratory model 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. While 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, the most informative migratory model included all available small-scale landscape covariates. Because of the influence of covariates at a 500m–1km scale, the migratory model provided predictions with much more spatial variation than the breeding season model, despite identical pixel resolutions of 90m (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, 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 in VSURF (Genuer et al. 2019) 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

Description automatically generated

Figure 3. Comparison of relationships between landscape variables and habitat suitability for breeding and migratory season models. 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.

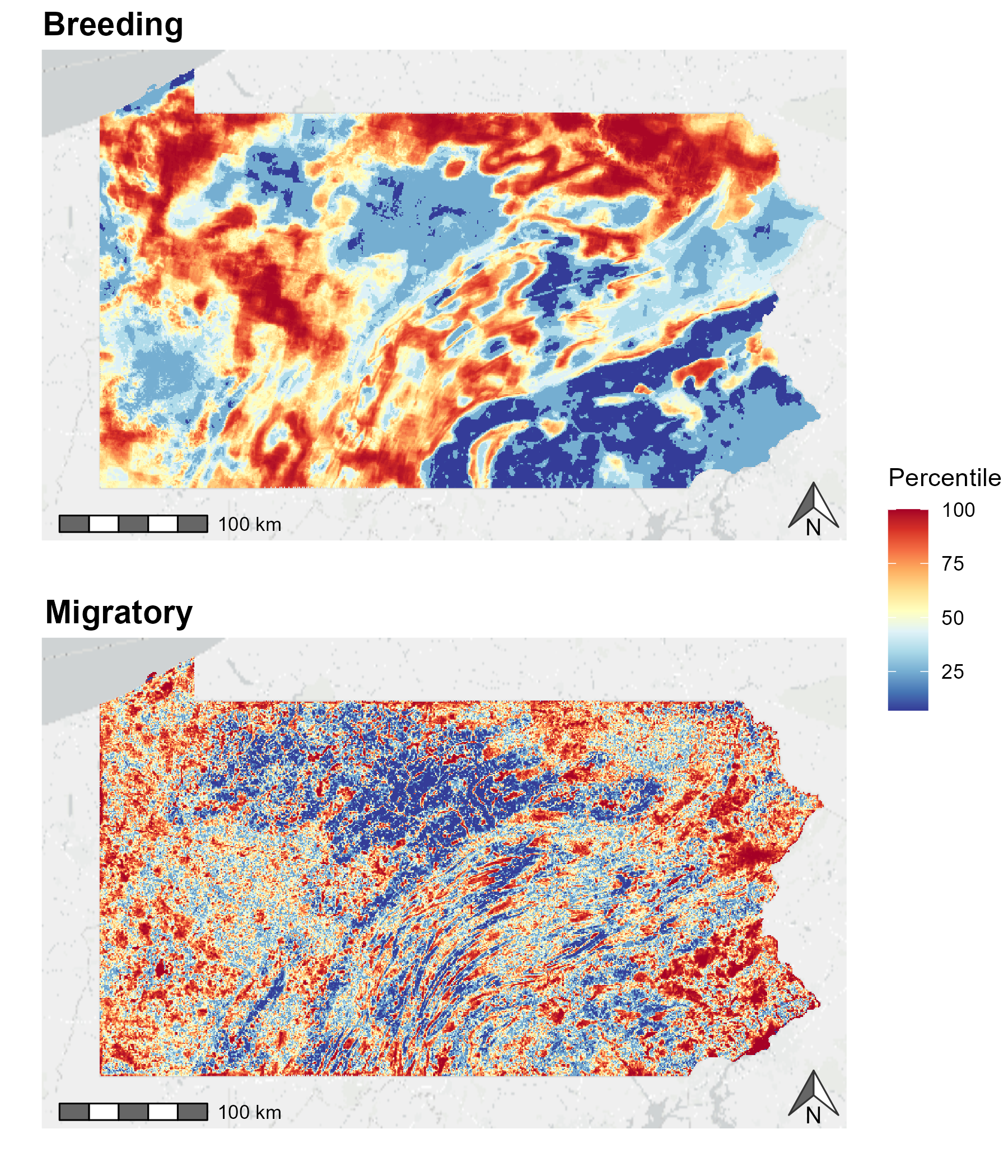


Figure 4. Breeding and migratory predictive habitat suitability layers suggest that woodcock select habitat at different scales in different seasons. Certain areas which are not productive for breeding season habitat management, such as southeastern Pennsylvania, may be productive for migratory habitat 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.

**Discussion**

We aimed to demonstrate integration of multiple species distribution models into a single SDSS, creating a tool that we have termed a multi-season distribution model. We constructed an example SDSS that emphasized the importance of practitioner input in management prioritization tools, by allowing user choice in the weighting of breeding and migratory habitat based on the user’s seasonal management objectives. This approach demonstrates how multi-season distribution models may allow users to overcome issues with low cross-seasonal transferability in species distribution models and prioritize management in a way that conserves habitat for an animal throughout all stages of its life cycle.

We demonstrate the necessity of an approach that incorporates cross-seasonal transferability by showing that American woodcock occur in distinctly different habitat during the breeding and migratory seasons in Pennsylvania, and associate with different spatial scales between seasons. During the breeding season, woodcock habitat suitability is 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 at which migratory birds select for habitat, managers may need to adjust the scale of their 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 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. The refuge is modeled as having high migratory habitat suitability for woodcock, demonstrating how urban wildlife refuges may provide crucial migratory stopover habitat in heavily urbanized areas.

The 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 low breeding season suitability of the Northern Piedmont, Middle Atlantic Coastal Plain, and the Eastern Great Lakes Lowlands ecoregions, despite high 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.

We believe that this multi-season distribution model framework, encompassing multiple seasonal distribution models, is particularly well suited to migratory bird management due to its flexibility in application of multiple data sources. One of the benefits of this type of analysis is that the breeding and migratory seasons can easily use separate 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, including the Breeding Bird Survey and Project Feederwatch (Robbins et al. 1986, Bonter and Greig 2021), 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 may have to 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 for the management of many migratory bird species.

**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.

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