*Joint life-stage-specific species distribution models better facilitate habitat conservation for a short distance migratory bird*

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**Introduction**

Species distribution models are frequently used to convert data about species occurrence and habitat associations into tools suitable for assisting conservation decision-making. By predicting the occurrence of habitat conditions which are suitable for the occupancy of one or more species of interest, species distribution models have allowed users to address issues ranging from conservation planning to ecological hypothesis testing (cite tk). The debut of remote sensing data, including multispectral satellite imagery and derivative datasets, has made it easier than ever to predict species distributions over massive spatial scales (cite tk), especially using new advances in prediction using advanced classification techniques (cite tk). However, species distribution models are known to have issues with transferability (cite tk), where species distribution models may not be reflective of animal distributions at other places or times. Species for which habitat use changes between seasons or life stages are especially prone to having issues with the transferability of distribution models through time, which can lead to underestimation of habitat requirements unless habitat is modeled in multiple seasons or life stages.

Migratory birds are potentially vulnerable to issues with transferability of species distribution models, as they frequently use different habitat during their breeding, wintering, and migratory stages (cite tk). During the migratory stage, birds are dependent on stopover sites, defined as any place where a bird can land and survive until the next migratory flight (Mehlman 2005). As survival during migration is believed to limit populations for many species of birds (Sillett and Holmes 2002, Rockwell et al. 2017, Robinson et al. 2020), conserving stopover habitat is assumed to be important for slowing bird declines (Faaborg et al. 2010). Resource requirements during stopover are frequently different from those during the breeding and wintering seasons (Allen et al. 2020, Stanley et al. 2021), which can result in birds using fundamentally different types of habitat during stopover than other times of the year (cite tk). Despite these differences in habitat, migratory stopover sites can often overlap with breeding or wintering ranges, especially for short-distance migrants (Fig 1). Therefore, we may encounter circumstances in which a bird species is dependant on habitat conservation for two or more stages of the full annual cycle in the same region. This would necessitate creating separate distribution models for each of those stages, and finding a way to best incorporate both of those models into decisions regarding spatial prioritization of land for conservation.

Decision support tools may provide a useful mechanism to combine distribution models from multiple stages of the full annual cycle and allow users to consider them both during the decision-making process. Decision support tools have a long history in conservation, tracing back at least to the debut of Marxan and its predecessors in the 1990s and early 2000s (cite tk). Like Marxan, many decision support tools focus on the problem of spatial prioritization of conservation, putting them in a class of tool called spatial decision support systems (cite tk). Spatial decision support systems (SDSS) utilize user-friendly, interactive toolsets to guide users through the process of making a set of spatial prioritization decisions. SDSS frequently come as extensions of existing geographic information systems, such as ArcMap (cite tk), but the learning curve and costs associated with professional geographic information systems can often be an impediment to reaching the intended user base. The widespread adoption of interactive online mapping tools, such as the leaflet javascript library (cite tk) and ArcGIS Online, has greatly expanded the potential for custom built SDSS that are accessible via a web browser and can be easily used by decision makers with little additional training (cite tk).

SDSS have several advantages as a distribution method for species distribution models. First, SDSS allow us to walk users through the process of using the species distribution model as it was intended. This can be a useful way to ensure that users comply with the constraints of the species distribution model and adhere to appropriate uses, especially given that overextension of species distribution models is a major issue in conservation (cite tk). Second, SDSS allow us to incorporate additional data that can be used to make management decisions, such as management area boundaries and land use/land cover data. The additional layers incorporated into SDSS could easily be extended to include multiple single-season distribution models, allowing the user to plan their habitat management based on species distribution throughout the full annual cycle.

Here we demonstrate how a SDSS can be used to provide a framework for users to spatially prioritize land for conservation based on multiple stages of a migratory bird’s full annual cycle. Our case study focuses on American woodcock (*Scolopax minor*;hereinafter woodcock) in the state of Pennsylvania, USA. Woodcock are short distance migrants that have extensive overlap of their migratory, breeding, and wintering ranges (Fig. 1), and are known to use fundamentally different habitat during different stages of their life cycle (Myatt and Krementz 20tk, Allen et al. 2020). Pennsylvania provides breeding habitat for an estimated tk% of all woodcock throughout their range (cite SGS tk), but it potentially provides migratory stopover habitat for a much larger contingent of birds breeding throughout New England (estimated tk% of woodcock) and maritime Canada (estimated tk% of woodcock). Therefore, managing for woodcock habitat in both the breeding and migratory seasons have been identified as priorities by the Pennsylvania Game Commission. We demonstrate a tool for balancing those priorities using a multi-season habitat modeling framework to combine migratory and breeding habitat suitability models into a single decision support tool for habitat prioritization. By identifying areas that provide both migratory and breeding habitat, users could improve full annual cycle conservation and more efficiently allocate management resources with a straightforward prioritization framework and online tool.



Figure 1. Seasonal ranges and migratory routes of American Woodcock. Migratory routes are from 534 woodcock tagged primarily in the eastern management region (cite tk) and are not indicative of migratory routes in the central management region. Large portions of the mid-Atlantic United States host woodcock habitat during multiple seasons, including breeding, wintering, and migration, although woodcock habitat use changes between seasons (cite tk).

**Methods**

*Breeding season species distribution model*

We modelled distribution of woodcock habitat during the breeding season using spring survey data collected as part of the US Fish and Wildlife Service Woodcock Singing Ground Survey (Seamans and Rau 2020) and similar state-level survey data collected by the Pennsylvania Game Commission. These surveys consisted of 5.76 km survey routes with 10 evenly spaced points, where observers listened for woodcock calls during their crepuscular breeding display. Presence-absence was determined at each point based on whether male displays were visible during a 2 minute interval shortly after dusk. Singing Ground Survey routes were randomly distributed (Clark 1970), while Pennsylvania surveys were opportunistically distributed near state gamelands or in areas where managers believe woodcock occupancy is likely. We converted state and federal survey data from 2016 — 2020 to a presence-absence dataset based on detection of at least one male during the 5-year period. Presence-absence locations were then used as the response variable in the breeding season species distribution model.

We selected explanatory variables for the species distribution model with presumed relevance to woodcock habitat. These included variables representing land use/land cover (National Land Cover Dataset; Jin et al. 2019), forest successional class (LANDFIRE; U.S. Geological Survey and U.S. Department of Agriculture n.d.), elevation (U.S. Geological Survey 2000), slope, EPA level 3 ecoregions (Omernik and Griffith 2014), soil drainage (Natural Resources Conservation Service n.d.), and topographic wetness index (Fink 2013). We additionally added landscape metrics from the landscapemetrics R package (Hesselbarth et al. 2019) representing landscape composition (% forest, % agricultural, % developed) and configuration (aggregation index, cohesion, edge density). To generate these landscape metrics, we cropped a binary forest/non-forest layer derived from the National Land Cover Dataset to the extent of a circle of the given radius from each 90m pixel, and then ran the appropriate function from the landscapemetrics package on each cropped raster at 500m, 1km, 5km, and 10km scales.

Initially, we considered several modeling techniques for creating species distribution models. We ran prelimary models on a smaller subset of woodcock occupancy data using MaxEnt (cite tk), random forest (cite tk), classification and regression trees (cite tk), and neural networks (cite tk) in package tk (cite tk) to determine which modeling framework would be best suited for our data. We compared these models using area-under-the-curve (AUC; cite tk), 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 models going forward. For the breeding season species distribution model, we used a random forest classifier designed for clustered data (Wang and Chen 2016) to predict whether woodcock would be present or absent at survey points. We used survey route id as a clustering variable to compensate for autocorrelation between points on the same survey route. We also included survey type as an explanatory variable to account for the non-random distribution of state survey routes. To avoid overwhelming the model with highly correlated variables, we elected to use a backwards variable-selection approach (Genuer et al. 2019) to determine which variables to include in the final model using a three-step process, where each step produced a more parsimonious model. The first step eliminates variables that have little importance to prediction, the second step removes variables that have some relevance but are not critical for prediction, and third step eliminates variables that are redundant. We calculated AUC metrics to determine which step produced the most predictive model and carried that model forward to the final analysis. We used a k-fold cross validation approach with 10 folds to evaluate our final model, using 90% of the data in each fold as a training dataset and the remaining 10% as a testing dataset. We averaged AUCs for each of the 10 folds to produce a mean AUC for the final model. We then created predictive layers for each of the 10 folds and averaged those layers together to create a final predictive layer for the breeding season model.

*Migratory season species distribution model*

We used GPS data from the Eastern Woodcock Migration Research Cooperative (EWMRC) to designate woodcock migratory stopover sites throughout the state of Pennsylvania. The EWMRC is a collaboration of 34 federal, state, provincial, non-profit, and university partners throughout the United States and Canada that deployed transmitters on woodcock throughout the eastern portion of their range (www.woodcockmigration.org). We captured birds 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. Capture techniques included 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 tags (Lotek Wireless Inc., Newmarket, Ontario, CA) to captured woodcock. These tags record locations at 12 — 60m accuracy depending on cover type (Berigan, unpublished data), and were programmed to record locations every 1 — 3 days at 0900 or 1500 Eastern Time, outside of the woodcock’s nocturnal migration period. Transmitters, bands, and attachment materials never exceeded 4% of a bird’s body weight, and all capture and handling was conducted with methods approved by the University of Maine Institutional Animal Care and Use Committee (Protocol # A2020-07-01).

Our transmitters collected locations from the breeding, wintering, and migratory seasons. To filter this data to just the migratory locations, we delineated migratory movements for each bird on an individual basis. We determined that a woodcock had begun migration when it made its first movement > tk km, and it had completed migration after it made its final movement of that length. All diurnal locations between migratory initiation and termination we considered to be migratory stopover locations. Consecutive locations from the same individual that were within 3 km of each other were considered to be part of the same stopover, and all but the one of those locations, selected randomly, were removed from the analysis.

We used woodcock stopover locations, as well as 10,000 randomly distributed pseudoabsence locations, as the response variable for the migratory model. We used a similar methodology as the breeding season model to build the migratory model. As survey route groupings were not necessary for the migratory model, we replaced the mixed random forest model structure used in the breeding season model with a traditional random forest classification model, written using the tk package in R. We used the same backwards variable selection approach as we used in the breeding season model to select the explanatory variables to include in the final model.

Explanatory variables were the same as used in the breeding season model, although no clustering or survey type variables were necessary for the migratory season analysis. We then used these data to create a species distribution model using a random forest classifier (Vignali et al. 2020). We calculated an AUC value to evaluate the model and generated a migratory season predictive layer as described above for the breeding season section.

*Multi-season predictive layer*

To facilitate user choice in how and where to prioritize migratory and breeding season habitat, we created a decision making tool in the Shiny ecosystem (Chang et al. 2021) to allow users to manually assign weights to each seasonal layer and combine them into a single multi-season layer (Fig. 2). The user can choose the weighting of each layer in 10% increments (ex. 20% migratory and 80% breeding season). The weighting was conducted as follows on a pixel-by-pixel basis, with *pw* indicating the value of the weighted pixel value, *wm* indicating migratory weight, *wb* indicating breeding season weight, *pm* indicating migratory pixel value, and *pb* indicating breeding season pixel value.

Because our application was targeted at users in the Pennsylvania Game Commission, the application also shows the comparative suitability of Pennsylvania state gamelands for each weighted layer. We used four metrics for comparing the habitat suitability of gamelands. The first was average pixel value, which favored small gamelands which were predominantly composed of woodcock habitat. The second was average pixel value multiplied by the acreage of the gameland, which we titled landscape suitability index. Landscape suitability index favored large gamelands which might not be entirely composed of woodcock habitat but might contain a large amount of woodcock habitat in aggregate. The final metrics were the percent of the gameland which was of high quality, defined as all cells greater than the 33rd percentile of all pixels, or of medium quality, defined as all cells between the 66th and 33rd percentile.

The decision support tool also includes several features to facilitate effective use of the application. The tool redirects all users to a landing page on opening the application, which displays information on how the tool was created and its intended use. It also warns users that the spatial scale of the application is not suitable for micro-scale habitat management, as both the breeding and migratory season distribution models were built using landscape metrics that were calculated at multi-kilometer scales. The zoom function in the tool is also limited in how far it will zoom in to encourage users to avoid using the distribution model for a smaller scale than it was intended. We have also included a detailed manual on how to use the application, and a recording of a workshop for Pennsylvania Game Commission employees, to ensure that the uses of this decision support tool fit the assumptions that were made when making the component species distribution models. This layer is publicly accessible at www.woodcock.shinyapps.io/W-PAST.

Diagram

Description automatically generated

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 the various metrics compiled for state gamelands. Two state gameland metrics (landscape suitability index and average pixel value) are available as spatial layers; other metrics can be accessed by clicking on individual gamelands.

**Results**

We deployed transmitters on 463 woodcock from Fall 2017 — Spring 2021, with 82 individuals recording a total of 113 GPS locations at migratory stopovers in Pennsylvania. These data were used in conjunction with X Singing Ground Survey and X Pennsylvania Game Commission survey routes, with tk points per route, to create breeding and migratory season distribution models. The most informative breeding season model was the most constrained model, for which all unpredictive and autocorrelated variables had been removed. This produced a model with an AUC of 0.83, which was heavily informed by landscape variables at the 5 and 10 kilometer scales (Table 1). No variables at the finest landscape scale (500m) or in the suite of moisture variables were included in the most informative model. While random forest models do not provide coefficients that can be used to determine the impact of each covariate on the model, graphs of habitat suitability for each covariate showed strong, non-linear relationships with several of the most informative variables. Suitability was highest for landscapes at the 10km scale with 0 – 25% developed land area, 0 – 50% agricultural land area, and aggregation index values of 80 – 100. At the 5km scale, the breeding season model also showed high suitability for landscapes with 30 – 100% forest cover (Fig. 3).

The most informative migratory model was the full model, including all landscape, land cover, geographic, and moisture covariates (Table 1). This produced a model with an AUC of 0.78. 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 showed greater tolerance for developed and dis-aggregated landscapes at a 10km scale than the breeding season model (Fig. 3). The two models are also distinguished by the scale at which covariates influence 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. This caused the migratory model to provide predictions at a finer spatial scale than the residential species distribution map (Fig. 4).

Breeding season habitat was not evenly distributed between 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%.

|  |  |  |
| --- | --- | --- |
| 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 |  |

Table 1. Variables selected via backwards variable selection in VSURF 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.

![Chart, scatter chart

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

A map of the world

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

Chart

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Figure 5. Migratory and breeding season habitat suitability for woodcock in Pennsylvania, broken out by EPA level 3 ecoregion (Omernik and Griffith 2014). Most of the difference between the distribution of migratory and breeding season habitat was in the Northern Piedmont, Middle Atlantic Coastal Plain, and Eastern Great Lakes Lowlands ecoregions, which had mean breeding season habitat suitability values of < 30% and mean migratory season habitat suitability values of >60%.

**Discussion**

Our goal during this study was to demonstrate how decision support tools can facilitate the integration of multiple distribution models into a single decision-making framework. For our case study, we show that American woodcock occur in distinctly different habitat during the breeding and migratory seasons in Pennsylvania. A breeding habitat only approach would have overlooked stopover habitat for woodcock in southeastern Pennsylvania, where there is little breeding habitat but considerable migratory traffic. By including information about both seasons, with the ability to customize seasonal weights, users can decide the extent to which they believe each seasonal habitat is a priority for their management, and determine which sites are best suited for management based on that prioritization.

We found that woodcock select habitat at radically different scales between seasons, demonstrating that management in multiple seasons is also likely to need to be multi-scalar. The two models produced predictive layers with very different spatial resolutions, largely due to the role of different covariate relationships during each of the two seasons. During the breeding season, woodcock habitat suitability is dependent primarily on variables at 5 and 10 km scales, while during the migratory period 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). With widespread differences in the scale at which migratory birds select for habitat, managers may also need to adjust the scale of their management to match the scale of the intended season. 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 the most efficient. However, the migratory model had a much finer spatial resolution, and was much more prone to having small “pockets” of habitat in areas not well suited to wildlife management, such as urban areas. Habitat management for migratory habitat would likely want to match this spatial scale, focusing on the preservation of greenspaces that might be too small to be managed for breeding season habitat. Urban greenspaces, such as parks and wooded backyards, might be important sources of migratory habitat that have traditionally not been focused on by wildlife managers. By acknowledging that the spatial scale of selection changes between seasons, we can tailor our migratory bird management to the appropriate scale to ensure that our conservation efforts are the most successful.

The regional differences between the breeding and migratory models underscore the importance of multi-season distribution models in delineating regional priorities for 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. The common thread here is that there might be several effective management strategies based on the information provided in seasonal distribution models. By providing these models as a part of a decision support tool, where the user can actively choose how much to weight each model, we empower the user to make those management decisions and customize the information provided to match their management strategy.

We believe that this decision support tool framework, encompassing multiple seasonal distribution models, is particularly well suited to migratory bird management due to its flexibility in data sources. One of the benefits of this type of analysis is that the breeding and migratory periods can easily use separate data streams, 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 determine where the highest densities of migrants are passing through. With this added context, multi-season habitat suitability models could provide a valuable tool for the management of many migratory bird species.

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