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

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**Introduction**

The principle that animals frequently use different habitats as they shift among stages of their life or annual cycle has been a component of wildlife management dating back to Leopold (1933). Multi-stage habitat use has been incorporated into the management of animals ranging from white-tailed deer (Voigt et al. 1997) to greater sage-grouse (Fedy et al. 2012) and has been a popular focus of studies on migratory birds (Norris 2005, Marra et al. 2015). For the latter group, conservation throughout the full annual cycle is necessary to slow population declines, and recent migratory bird management plans advocate for international conservation of breeding, stopover, and wintering habitat (Rosenberg et al. 2016). Undertaking a range-wide approach to management is an important step in migratory bird conservation, but because multiple migration stages can be present in the same location, full annual cycle conservation can be a local issue as much as an international one. Much of a species’ migratory range, for example, can overlap with its breeding and wintering ranges, especially for short distance migrants or species with widespread breeding or non-breeding distributions (Fig. 1). Most regions that are typically considered to be part of a bird’s breeding range, for example, might be more accurately considered to be in the joint breeding and migratory range, and full annual cycle conservation in these areas would require consideration of both the breeding and migratory habitat requirements of that species.

During migration, birds use habitat at stopover sites, which Mehlman (2005) defines as any place where a bird can land and survive until the next migratory flight. The lowest quality stopover sites might provide the bare minimum required for a bird to rest, refuel, and avoid predation before continuing migration. However, sites with more abundant or higher quality resources can improve a migratory bird’s condition and can increase its probability of successfully completing migration. 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 an important step in slowing bird declines (Faaborg et al. 2010). Habitat selection during stopover is frequently different from habitat selection during the breeding and wintering seasons (Allen et al. 2020, Stanley et al. 2021), which can result in birds using habitat types during migratory stopovers that they normally would not use during other times of the year. Differences in seasonal space use can be tracked with some ease due to recent technological advances in radar (Larkin and Diehl 2012), animal tracking devices (Bridge et al. 2011), and eBird data (Lin et al. 2020). These technologies can provide spatial data that can be used to create stopover habitat distribution models, which can be compared and combined with breeding and wintering habitat distribution models in much the same way that multi-season habitat use is examined for other wildlife species.

Multi-season habitat suitability models require considerably more data that single-season models, and so in practice they are most likely to be useful when habitat use is considerably different between seasons. The first step in a multi-season modeling process would be to determine whether habitat use is different enough between the two seasons to justify a multi-season framework. Users should aim to determine whether the added benefit of multi-season modeling will outweigh the costs of this approach, including collecting data, creating a modeling framework, and teaching managers to use it. If data from multiple seasons is already available, we can create predictive habitat suitability layers for each season and determine whether management would be significantly different if one predictive layer was used as opposed to the other. If no such prior data exists, then we can make this determination based on preexisting research and determine whether additional data collection would be worthwhile. Many forest-dwelling, night-migrating bird species use similar migratory stopover sites (Moore 2000, Rodewald and Brittingham 2004), so the use of multi-species migratory stopover models such as that provided by Buler and Dawson (2014) could prove useful in determining whether a multi-season framework incorporating migratory habitat would be worthwhile. Here we demonstrate 1) how to determine if space use differs enough between seasons to make multi-season management worthwhile and 2) how to implement a multi-season habitat modeling framework by using spatially explicit, high-resolution migratory stopover data in combination with breeding season survey data to enable multi-seasonal management for a declining migratory bird species.

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). Pennsylvania provides both breeding habitat and stopover habitat for birds migrating to and from the northern extent of their range. However, Allen et al. (2020) suggests that woodcock stopover habitat often differs from habitat used during residential periods. Therefore, management for breeding habitat alone may not be enough to protect woodcock stopover habitat. To determine whether additional management for stopover habitat is necessary, we first model migratory and breeding season woodcock habitat in Pennsylvania and examine the overlap between the two. If there is significant spatial overlap between migratory and breeding habitat, then existing management strategies for woodcock in Pennsylvania (which historically were based on breeding data) may be adequate to provide migratory stopover habitat. If overlap is minimal, then a new framework that blends management of stopover and breeding habitat may be needed. We then demonstrate 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.

Map

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Figure 1. Breeding (red), wintering (cyan), and year-round (blue) range for American woodcock. The Z-coordinate shows the density of spring migratory movements through an area by GPS-tagged woodcock (Berigan et al. in prep). Much of the breeding and year-round range for woodcock also includes migratory corridors, and conservation for woodcock during both migratory and non-migratory seasons would be of primary concern in these areas.

**Methods**

*Breeding season species distribution model*

We created a breeding season species distribution model for woodcock in the state of Pennsylvania using federal Woodcock Singing Ground Surveys (Seamans and Rau 2020) and similar state-level surveys conducted by the Pennsylvania Game Commission. Singing Ground Surveys, which were originally established in 1968, consist of 5.76 km survey routes with 10 evenly spaced points. Presence-absence is determined at each point based on whether male displays were visible during a 2 minute interval shortly after dusk. Singing Ground Survey routes are randomly distributed throughout Pennsylvania, and the same routes are run annually when possible (Clark 1970). Pennsylvania Game Commission woodcock surveys are run using the same methodology, but these routes are placed 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 by marking each survey point as present if there were woodcock observed at that point at least once during the 5-year interval, and absent if they were not. Presence-absence locations were then used as the response variable in the breeding season species distribution model. The explanatory variables in the species distribution model included several suites of variables presumed to be relevant to woodcock habitat. These included variables representing land use/land cover (Jin et al. 2019), forest successional class (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 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. We ran each of these landscape metrics at 500m, 1km, 5km, and 10km scales. We then assigned the output value from the function to the appropriate 90m pixel. These were then used as explanatory variables in the species distribution model. The species distribution model 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. The survey route id was used as a clustering variable to compensate for autocorrelation between points on the same survey route. We also included the survey type as an explanatory variable in the analysis to account for bias in the state survey route allocation. 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 set of variables should be used in the final model. This approach uses a three-step process, with each step producing 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 the AUCs for the models produced by each of the three steps and used the set of variables produced by the step with the highest AUC in the final model. 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 together the AUCs calculated for each of the 10 folds to find the 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 has been deploying transmitters on woodcock since 2017 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 flight period. Transmitters, bands, and attachment materials never exceeded 4% of a bird’s body weight, and all bird capture was conducted in accordance with best practices for wildlife research (Fair et al. 2010).

Transmitters were deployed on 463 woodcock from Fall 2017 — Spring 2021, and 82 of those individuals recorded a total of 113 GPS locations at migratory stopovers in Pennsylvania. 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. Woodcock stopover locations, as well as 10,000 randomly distributed pseudoabsence locations, were used as the response variable for the migratory model. The 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 using the methodologies described in 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 Shiny application (Chang et al. 2021) that would allow users to manually assign weights to each and combine them into a single layer (Fig. 2). The user can choose the weighting of each layer in 10% increments (ex. 20% migratory and 80% breeding season). 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. This layer is publicly accessible at www.woodcock.shinyapps.io/woodcock\_weighted\_habitat.

A computer screen capture

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Figure 2. Shiny application used to jointly weight migratory and breeding season habitat for the Pennsylvania Game Commision.

**Results**

The most informative breeding season model was the third-step 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 show 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 residential 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 residential 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%.

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| --- | --- | --- |
| 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 residential 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 residential 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 residential season, including landscapes with higher proportions of developed cover.

A map of the world

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Figure 4. The lack of correlation between residential and migratory habitat suitability (measured on a percentile scale) indicates that single-season species distribution models will likely not reflect the suitability of a landscape for woodcock during other portions of the year.

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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 goals during this study were to establish whether migratory habitat suitability differed from breeding season habitat suitability and to demonstrate a framework that would allow for simultaneous management of habitat across multiple seasons. We found that migratory and breeding season habitat frequently occurred in separate areas (Fig. 4), which indicated that management based on single-season results likely wouldn’t encapsulate multi-season habitat needs. These differences are likely the result of differential selection patterns between the two seasons, which have been observed in woodcock (Allen et al. 2020) and other migratory bird species (Stanley et al. 2021). Here, we show that these differences in selection result in habitat distribution models that differ in spatial resolution and regional distribution, with implications for future habitat modeling efforts and for woodcock management.

Differences in spatial resolution between the two models is due largely 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 kilometer scales, while during the migratory period habitat suitability was dependent on covariates at 500 meter and 1 kilometer scales as well. This pattern supports past observations that migratory birds select habitat at a finer spatial scale during the migratory season (Stanley et al. 2021). In addition to a lower spatial resolution, the migratory model differentiated itself from the breeding season model with a higher tolerance for landscape factors that are traditionally avoided during the breeding season. Woodcock were far more likely to use developed landscapes at a 10 kilometer scale during the migratory season than the breeding season, which led to high migratory habitat suitability values in areas that would be hostile to woodcock during the breeding season, such as downtown Philadelphia. This corresponds with the results of Stanley et al. (2021) which found that wood thrush become generalists during migration and are more tolerant of certain habitat factors which would otherwise repel them during other seasons. Overall, our results show that woodcock use regions with a mix of forest and agricultural cover during the breeding season, but woodcock during the migratory season often choose sites based on a variety of local habitat characteristics. This speaks to the importance of multi-scalar modeling when investigating migratory bird habitat selection, especially across multiple seasons or life stages.

Differences in regional distribution is primarily encapsulated in low breeding season suitability of the Northern Piedmont, Middle Atlantic Coastal Plain, and the Eastern Great Lakes Lowlands ecoregions, despite high migratory suitability. These three ecoregions include the two largest metropolitan areas in Pennsylvania (Philadelphia and Pittsburgh), so avoidance of these areas during the breeding but not the migratory season makes sense considering the covariate relationships we observed. The Eastern Great Lakes Lowlands and Middle Atlantic Coastal Plain ecoregions are also the two smallest ecoregions on the map and include only one state gameland where management for woodcock migratory habitat could take place. However, these areas could still be demographically important during woodcock migration. Green spaces within urban areas have been noted to be magnets for migratory bird stopover during migration (Buler and Dawson 2014), presumably due to high artificial light at night (McLaren et al. 2018) and lack of other stopover opportunities. Despite the lack of state gamelands in these areas, wildlife agencies may find it beneficial to engage other land management partners in these areas (such as urban parks and private landowners) to conserve migratory habitat in urban greenspaces. It is also worth noting that the Philadelphia suburbs include John Heinz National Wildlife Refuge at Tinicum, an urban wildlife refuge managed by the U.S. Fish and Wildlife Service that is modeled as having high migratory habitat suitability for woodcock. In addition to the roles that urban wildlife refuges play in education and outreach, these refuges may also provide crucial migratory stopover habitat in areas that are otherwise not managed for wildlife.

Most ecoregions in Pennsylvania that provide breeding season habitat also provide migratory habitat, and so a regional priority map that was based on breeding season information alone would likely have been enough to result in migratory habitat conservation. However, at a local, site specific scale, breeding season and migratory habitat suitability was much more likely to differ. We surmise that, when used for site prioritization in this manner, modeling breeding season and migratory habitat suitability separately will likely be necessary to ensure that habitat is adequately protected during both seasons. To facilitate the incorporation of both migratory and residential habitat suitability into a single management framework, we used a Shiny tool to combine the two layers and left it up to the user to decide how these layers should be weighted. Leaving this decision to the user serves two purposes. First, it encourages discussion within the management agency regarding the agency’s priorities in conserving residential and stopover habitat, to meet both the objectives of their stakeholders and to achieve a stable woodcock population. Second, by allowing the user to make the weighting decision, we allow users to determine whether weighting should change based on regions. Some regions may be valuable as both stopover and residential habitat; in such a case, a balanced user weighting of the two layers may be a good way to determine which gamelands provide both types of habitat. Ecoregions such as the Northern Piedmont, Middle Atlantic Coastal Plain, and the Eastern Great Lakes Lowlands might provide only migratory habitat, and so a user weighting that favors migratory habitat might be best employed to determine where woodcock management would be best applied within that region. In addition, a map of migratory corridors for woodcock could be used to determine where woodcock are most likely to fly over the state and be used to determine the regions in which migratory habitat management would be most important (Berigan et al. in prep).

The analysis shown here provides a tool that can be used to manage multi-season woodcock habitat in the state of Pennsylvania and demonstrates a framework that can be applied to any of several migratory bird species. 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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