*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 an incredibly popular technique for converting scientific knowledge about species distributions 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 that ever to predict species distributions over massive spatial scales (cite tk), especially using new advances in prediction using advanced classification techniques (cite tk). However, despite advances in species distribution modeling, these models are still only as useful as they are interpretable. When used in a management context, a species distribution model is frequently only one source of information that is being used to make decisions. This model might be used in combination with land ownership data, other management priorities, and even other species distribution models to arrive at an optimal land management strategy. To aid interpretation of our species distribution models, it is in our best interests to supply these models as a part of decision support tools, which can assist users in interpreting the species distribution model in the context of additional data which is used in conservation decision-making.

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 in conservation 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) focus on creating easy to use, interactive toolsets which 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 price barrier 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 stick 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 showcase multiple species distribution models, or even multiple distribution models from the same species in circumstances where habitat changes between seasons or life stages. This could be especially important for migratory species, for which survival often depends on the conservation of habitat during several migratory stages (cite tk).

Migratory birds, in particular, require breeding, wintering, and stopover habitat. While this habitat is frequently distributed across multi-regional or international scales (Rosenberg et al. 2016), migratory stopover sites can often overlap with breeding or wintering ranges, especially for short-distance migrants. Migratory stopover sites are 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). These 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 abilities to acquire large-scale observational data (Lin et al. 2020). These technologies provide spatial data that can be used to create stopover habitat distribution models, which can be used in conjunction with breeding and wintering habitat distribution models to ensure that habitat for a species is conserved during all stages of the migratory 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.

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 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. 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. Survey route id was used 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 under 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 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 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).

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. 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 Shiny application (Chang et al. 2021) to 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 Commission.

**Results**

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%.

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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 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. The lack of correlation between breeding 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 goal during this study was 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 was 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 dependance of birds on highly forested areas during the breeding season but not the migratory season. 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.

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.

**Literature cited**

Allen, B. B., D. G. McAuley, and E. J. Blomberg. 2020. Migratory status determines resource selection by American Woodcock at an important fall stopover, Cape May, New Jersey. The Condor 122:1–16. <https://academic.oup.com/condor/article/doi/10.1093/condor/duaa046/5910724>. Accessed 22 Apr 2021.

Bonter, D. N., and E. I. Greig. 2021. Over 30 Years of Standardized Bird Counts at Supplementary Feeding Stations in North America: A Citizen Science Data Report for Project FeederWatch. Frontiers in Ecology and Evolution 9. <www.frontiersin.org>.

Buler, J. J., and D. K. Dawson. 2014. Radar analysis of fall bird migration stopover sites in the northeastern U.S. The Condor 116:357–370. Oxford Academic. <https://academic.oup.com/condor/article/116/3/357/5153136>. Accessed 31 Dec 2021.

Chang, W., J. Cheng, J. J. Allaire, C. Sievert, B. Schloerke, Y. Xie, J. Allen, J. McPherson, A. Dipert, and B. Borges. 2021. shiny: Web Application Framework for R. <https://cran.r-project.org/package=shiny>.

Clark, E. R. 1970. Woodcock status report, 1969.

Fair, J. M., E. Paul, J. Jones, A. B. Clark, C. Davie, and G. Kaiser. 2010. Guidelines to the use of wild birds in research. Washington, D.C.

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

Genuer, R., J.-M. Poggi, and C. Tuleau-Malot. 2019. VSURF: Variable Selection Using Random Forests. <https://cran.r-project.org/package=VSURF>.

Hesselbarth, M., M. Sciaini, K. With, … K. W.-, and undefined 2019. 2019. landscapemetrics: an open‐source R tool to calculate landscape metrics. Wiley Online Library 42:1648–1657. Blackwell Publishing Ltd. <https://onlinelibrary.wiley.com/doi/abs/10.1111/ecog.04617>. Accessed 30 Jul 2021.

Jin, S., C. Homer, L. Yang, P. Danielson, J. Dewitz, and C. Li. 2019. Overall methodology design for the United States national land cover database 2016 products. Remote Sensing. <https://www.mdpi.com/593344>. Accessed 30 Jul 2021.

McAuley, D. G., J. R. Longcore, and G. F. Sepik. 1993. Techniques for research into woodcocks: experiences and recommendations. Pages 5–11 *in*. Proceedings of the Eighth American Woodcock Symposium, US Fish and Wildlife Service Biological Rep. Volume 16.

McLaren, J. D., J. J. Buler, T. Schreckengost, J. A. Smolinsky, M. Boone, E. Emiel van Loon, D. K. Dawson, and E. L. Walters. 2018. Artificial light at night confounds broad-scale habitat use by migrating birds. Ecology Letters 21:356–364. <http://doi.wiley.com/10.1111/ele.12902>. Accessed 22 Apr 2021.

Moore, F. R., editor. 2000. Stopover Ecology of Nearctic–Neotropical Landbird Migrants: Habitat Relations and Conservation Implications. Studies in.

Natural Resources Conservation Service. n.d. Web Soil Survey. United States Department of Agriculture. <https://websoilsurvey.nrcs.usda.gov/>. Accessed 8 Dec 2021.

Omernik, J. M., and G. E. Griffith. 2014. Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environmental Management 54:1249–1266. <www.epa.gov/wed/pages/ecoregions.htm>. Accessed 17 Nov 2021.

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

Robbins, C., D. Bystrak, and P. Geissler. 1986. The Breeding Bird Survey: its first fifteen years, 1965-1979. <https://apps.dtic.mil/sti/citations/ADA323126>. Accessed 9 Jan 2022.

Rodewald, P. G., and M. C. Brittingham. 2004. Stopover habitats of landbirds during fall: use of edge-dominated and early-successional forests. The Auk 121:1040–1055. Oxford University Press.

Seamans, M. E., and R. D. Rau. 2020. American woodcock population status, 2020. Laurel, MD, USA.

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

Stanley, C. Q., M. R. Dudash, T. B. Ryder, W. G. Shriver, K. Serno, S. Adalsteinsson, and P. P. Marra. 2021. Seasonal variation in habitat selection for a Neotropical migratory songbird using high‐resolution GPS tracking. Ecosphere 12:e03421. John Wiley & Sons, Ltd. <https://onlinelibrary.wiley.com/doi/10.1002/ecs2.3421>. Accessed 27 Mar 2021.

Sullivan, B., C. Wood, M. Iliff, R. Bonney, D. Fink, and S. Kelling. 2009. eBird: A citizen-based bird observation network in the biological sciences. Biological Conservation 142:2282–2292. <https://www.sciencedirect.com/science/article/pii/S000632070900216X?casa\_token=5yvlj7v6-x8AAAAA:M9CI5RTOM2a18BJgaB6LZ1039-0zMx6UqZgWs9y9xPJdHxZoVdqMBxv7oH1i7zL32Z9nlupkP2M>. Accessed 9 Jan 2022.

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

U.S. Geological Survey, and U.S. Department of Agriculture. n.d. LANDFIRE 2.0.0 Successional Class Layer. <http://landfire.cr.usgs.gov/viewer/>. Accessed 8 Dec 2021.

Vignali, S., A. G. Barras, R. Arlettaz, and V. Braunisch. 2020. SDMtune: An R package to tune and evaluate species distribution models. Ecology and Evolution 00:1–18.

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