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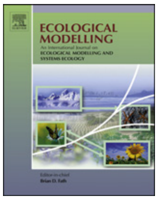

Integration of distance, direction and habitat into a predictive migratory movement model for blue-winged teal (*Anas discors*)

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ABSTRACT

Historically, the migration of birds has been poorly understood in comparison to other life stages during the annual cycle. The goal of our research is to present a novel approach to predict the migratory movement of birds. Using a blue-winged teal case study, our process incorporates not only constraints on habitat (temperature, precipitation, elevation, and depth to water table), but also approximates the likely bearing and distance traveled from a starting location. The method allows for movement predictions to be made from unsampled areas across large spatial scales. We used USGS' Bird Banding Laboratory database as the source of banding and recovery locations. We used recovery locations from banding sites with multiple within-30-day recoveries were used to build core maximum entropy models. Because the core models encompass information regarding likely habitat, distance, and bearing, we used core models to project (or forecast) probability of movement from starting locations that lacked sufficient data for independent predictions. The final model for an unsampled area was based on an inverse-distance weighted averaged prediction from the three nearest core models. To illustrate this approach, three unsampled locations were selected to probabilistically predict where migratory blue-wing teals would stopover. These locations, despite having little or none data, are assumed to have populations. For the blue-winged teal case study, 104 suitable locations were identified to generate core models. These locations ranged from 20 to 228 within-30-day recoveries, and all core models had AUC scores greater than 0.80. We can infer based on model performance assessment, that our novel approach to predicting migratory movement is well-grounded and provides a reasonable approximation of migratory movement.

1. Introduction

Despite vast amounts of research conducted on birds, migration ecology is poorly understood relative to the other life stages during the migratory birds' annual cycle (Bairlein, 2008). In 1979, Gauthreaux (1979) called for a modern synthesis of bird migration, which without, he argued, we would be incapable of properly identifying and monitoring critical stopover habitat or assessing population dynamics of threatened and endangered species. As our needs for understanding migration remain the same, or are perhaps even more critical, we still have yet to reach a full synthesis on bird migration (Hutto, 1998, 2000). The primary goal of this research is to present a method that will advance our ability to model the migratory movement of birds based on habitat requirements, directionality, and distance. Our long-term goal is use modeling to explore connectivity between breeding and nonbreeding habitat, to identify key stopover areas, and to forecast potential impacts of climate and land-use change on migration systems.

The lag in knowledge gained regarding bird migration relative to breeding and wintering ecology is largely due to the intrinsic difficulties associated with studying migration. There has been significant work in migration ecology in the last thirty years (Faaborg et al., 2010); key advances owing largely to innovations in technology, i.e. radio/satellite telemetry, GPS, and isotope analysis. However, modern technologies remain expensive, and thus greatly reduce the feasible sample size. These technologies have provided valuable information about fine-scale movement of individual birds, but lack the ability to extrapolate this knowledge to an entire population or to individuals in different areas.

Alternatively, research has been conducted where comprehensive surveys count migratory birds at a key stopover location. The Prairie Pothole Region (PPR) is one example (Earnst, 1994; De Leon and Smith, 1999; Naugle et al., 2001). The PPR is critical habitat for waterfowl; millions of migratory birds use the PPR as stopover habitat, while other birds rely on it for nesting sites (Williams et al., 1999). Conservation of migratory waterfowl, which rely on this area, requires extensive knowledge about the ecology of the PPR.

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However, we need to know from where these birds are coming, where they are going, and what ranges in migratory distance and direction they are capable of traveling.

Recently, there have been a few well-constructed attempts to spatially model migratory bird movement, specifically to determine their migratory pathway. Tankersley and Orvis (2003) explored potential migration pathways of neotropical birds across the United States. They determined location of optimal stopover habitat, defining habitat requirements from previous research, and then established connections of stopovers based on a fixed distance and bearing. In 2008, Downs and Horner (2008) developed a network approach to investigate potential migration pathways, which attempts to find the optimal path (i.e., path with fewest stops) across the landscape. The nodes in the network are all delineated freshwater wetlands in the study extent, and, as with the 2003 study, the distance is predefined.

Our research advances upon the foundation of the above studies by predefining neither distance nor any other predictor variable. This approach has significant advantages, because distance traveled by a bird will impact its habitat selection. Migratory birds are likely to continue flying in search of better habitat, or vice versa, select less suitable habitat if distance traveled is great (Moore and Aborn, 2000; Alerstam, 2001). By not fixing distance traveled, our model is more likely to capture some of this interplay between distance and habitat.

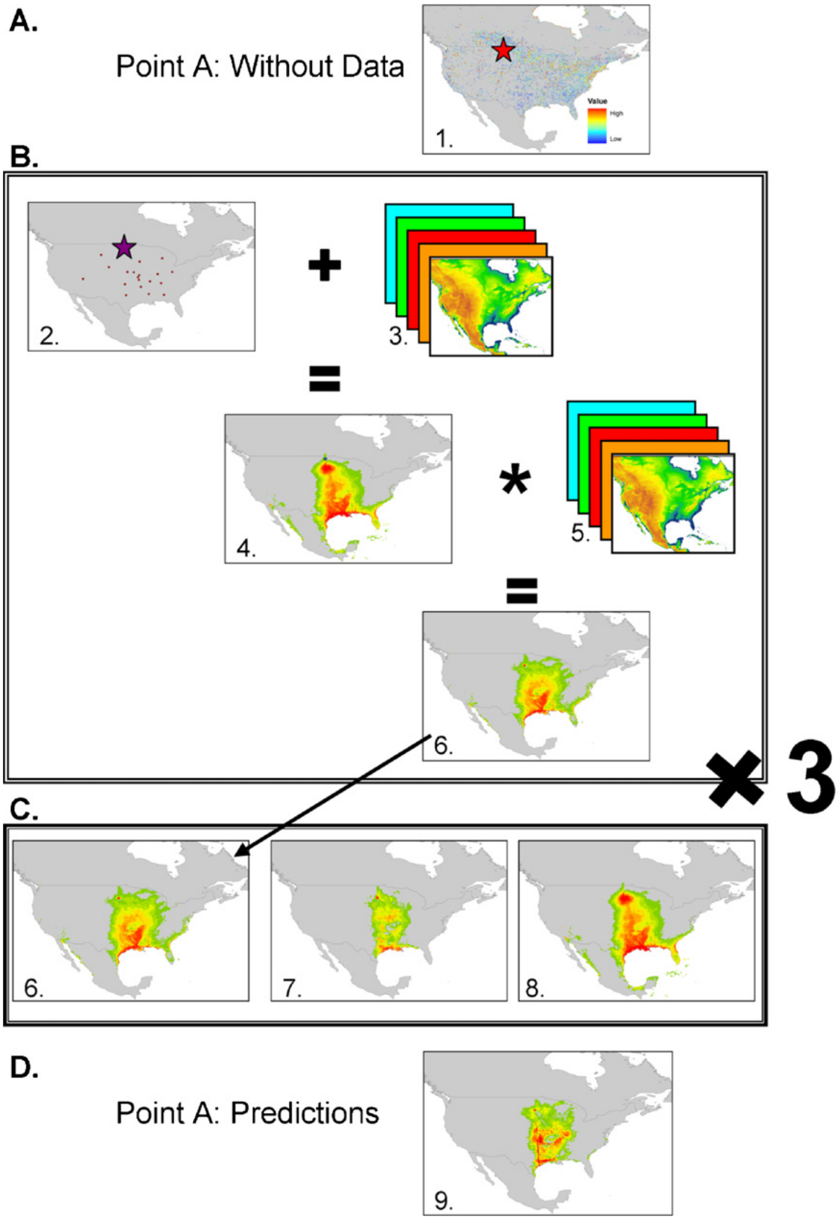

Fig. 1. Graphical representation of the approach to predict movement from an undersampled point. Part A: the point denoted with a red star is a hypothetical location where there is either no banding data or the available data is insufficient to create a core model. Part B: this portion is repeated three times; once for each of the closest three banding location with sufficient recoveries. Inset 2 depicts the location of the banding site (purple star) with multiple within-30-day recoveries (small red circles). The recoveries are used as the dependent variables with the independent variables (inset 3) to create a MaxEnt model of predicted movement (inset 4). With the ancillary variables (inset 5) recalculated for the undersampled point, the core model (used to create predictions in inset 4) is used to project the probabilities for the undersampled point (inset 6). Part C: the predictions from the first closest core model (inset 6) and the two next closest core models (inset 7 and 8) are averaged together weighted by the inverse distance to undersampled point. Part D: inset 9 depicts the final averaged prediction of movement from undersampled point. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

We used banding data from the Bird Banding Laboratory (BBL) dataset. Because the BBL has a large sample size (over 3 million game bird bands recovered) and large spatial extent (United States, and, although less comprehensive, Mexico and Canada) (Buckley et al., 1998), this is an ideal data set to accomplish the goals of this work.

The main goal of our research is to present a novel method, which may provide a means to predict migration movement of birds. Predicted movement from one area to another is contingent on habitat selection criteria, and likely distance and bearing of travel. The described approach allows for predictions to be made from any starting or stopover location, including areas that might have little or no sample data.

2. Methods

The main goal of this research is to develop a method by which to predict movement of a migratory bird from a source location to its next migration stopover (or to, perhaps, its final destination). This endeavor, essentially, has two main lines of analysis. The first is creating models to determine the predicted probabilities of movement from source areas that have been thoroughly sampled. These models will be referred to as the core models for the entire process. The second, and the real obstacle for this area of research, is predicting movement to a destination from source areas where there has been inadequate levels of sampling to reasonably predict migration movement. To accomplish our goal, the models developed for well-sampled areas (core models) were used to predict for less-than-ideally-sampled areas (undersampled point prediction).

2.1. Development of core models from well-sampled areas

The BBL is a long-term data set, started in 1902, which records the banding location of a bird and all its subsequent recoveries (Gustafson and Hildenbrand, 1999). To illustrate the approach of this study, blue-wing teal (*Anas discors*) fall migration was used as the test case. Blue-wing teal was selected based on its relative high levels and consistency of sampling.

Initially, the BBL data was filtered to include only birds that were recovered within 30 days of being banded. For the remaining portion of this text, "recovery" will reference only to individuals recaptured within 30 days of being banding. Selecting these recoveries was necessary to increase the likelihood that the individuals' travel was not confounded by multi-season or foraging movement (Kölzsch and Blasius, 2008). Additionally, only birds that moved from their original location were included. This avoided including birds that may not have begun their migration. Because all incidents are recorded to a 10 min (approximately 16 km) grid, how many recoveries each grid cell had was calculated. All grid cells that have above 20 recoveries were considered appropriate locations to build core models.

The ancillary variables used to model the destination probability from the selected source location are temperature, precipitation, elevation, depth to water table (DWT), distance, and direction. All variables were resampled to the BBL's 10 min grid spanning the extent of the contiguous United States, Mexico and Canada. At 30 s resolution (1 km), the average temperature and precipitation from WorldClim was utilized (Cameron et al., 2005). The 3 s (90 m) Shuttle Radar Topography Mission (SRTM) Elevation Data Set was used for elevation. The DWT data layer is a simulated data set that reliably predicts the location of natural wetlands by finding the long-term stable solution of the balance between the climate driven fluxes (precipitation and evapotranspiration) and geologic/topographic water fluxes (riverine and groundwater movement) (Fan et al., 2007). The DWT has been shown to be an accurate predictor variable for migratory waterfowl habitat (Kreakie et al., submitted for publication).

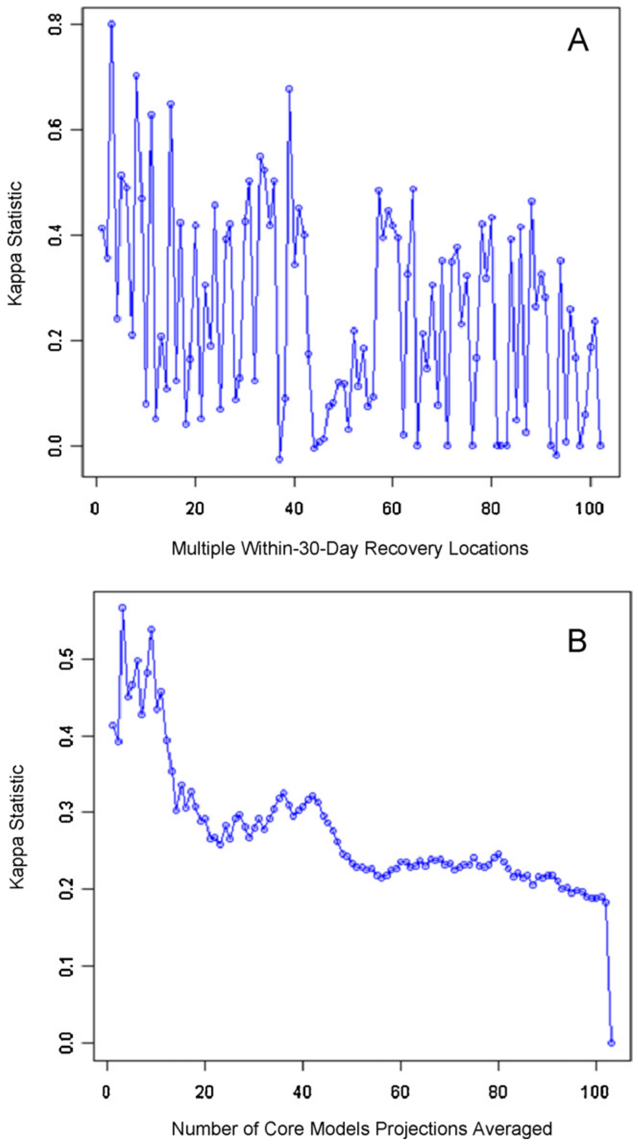

Fig. 2. Line graphs of method assessment. A: kappa statistic comparing the test location prediction to predictions made for the test location from the other 103 core model locations. The 103 core models are arranged with increasing geographical distance from the test location. B: kappa statistic comparing the test location to increasing numbers of averaged predictions made from core model.

The above ancillary variables remained constant in all our models, whereas distance and bearing varied according to source location. Distance and bearing were both calculated in R (R Development Core Team, 2011) using the "geosphere" package (Hijmans et al., 2011). To determine the distribution of distance traveled from a specific source location, great-circle distance was calculated between the source location and all potential destination cells (i.e., to all other 10 min grid cells in the study area). This process was repeated for direction, but to calculate the bearing between source point and all potential destination cells. These two variables were created for each prediction made from a single source location.

The probability of migration to a destination location was modeled using a maximum entropy algorithm executed in MaxEnt version 3.3.2 (Dudik et al., 2004; Phillips et al., 2006). MaxEnt is typically used in ecology for creating species distribution models,

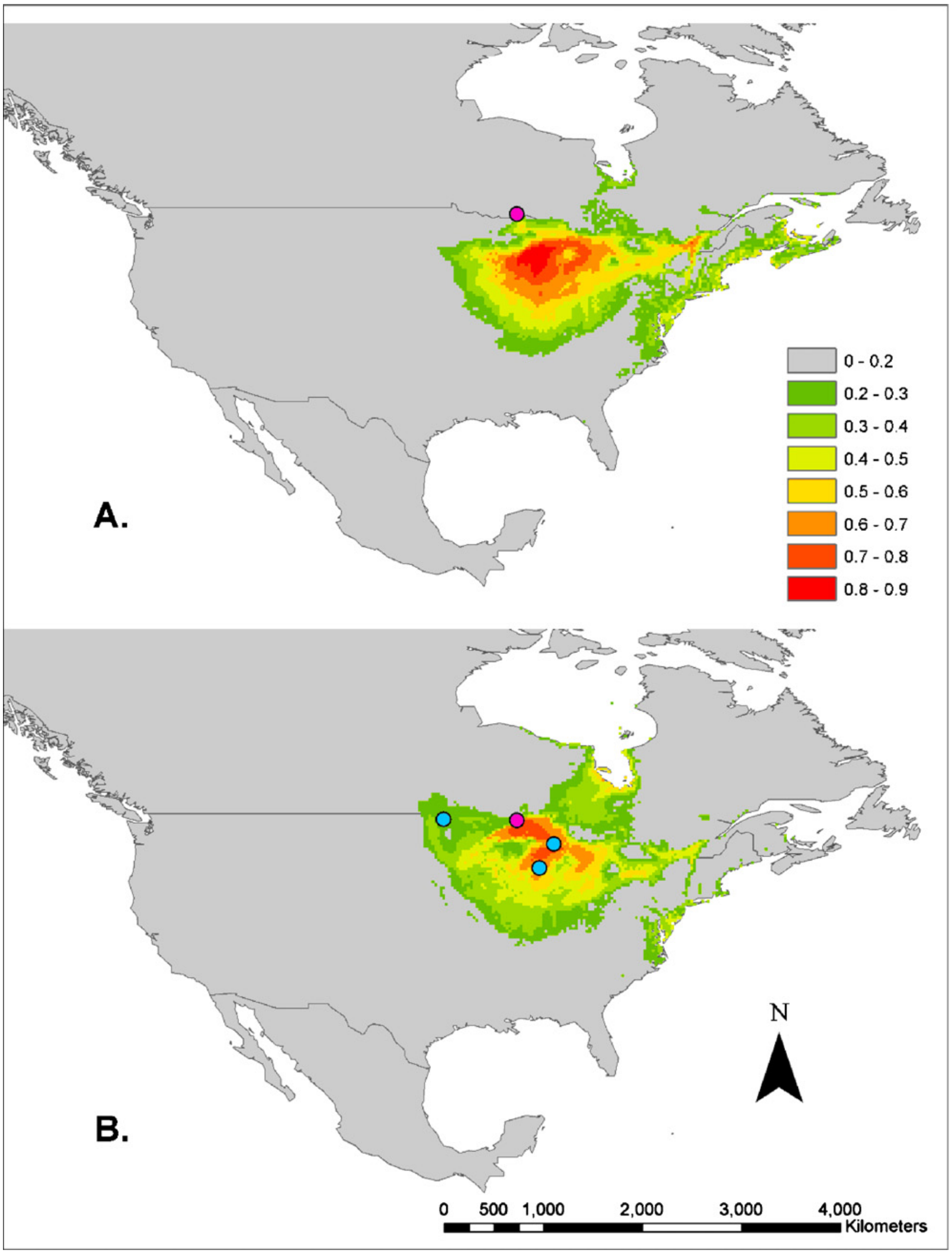

Fig. 3. Maps of predictive blue-winged teal movement from Ontario, Canada (48.42,−89.25), which is marked with the red dot in each map. (A) is the predictive movement surface created with 44 within-30-day recovery locations. (B) is the probability surface created using the method introduced in this text; essentially treating this point as if it had no survey data. Core models from the three locations marked with blue dots were used to project for the point of interest in Ontario. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

and our desired results our not exceedingly different from that of a species distribution model. Instead of creating predictions based only on the distribution of habitat measures, our approach includes consideration of the migratory distance and direction of appropriate habitat. In essence, MaxEnt "estimate(s) the target distribution by finding the distribution of maximum entropy (i.e., that is closest to uniform) subject to the constraint that the expected value of each feature under this estimated distribution matches its empirical average" (Phillips et al., 2004). MaxEnt was also selected over other approaches due to several of its attributes. It requires presence-only data, therefore it is not necessary to have known absences or create artificial absences (Elith et al., 2006, 2011). MaxEnt has been shown to model accurately despite varying sample sizes (Wisz et al., 2008). Even though the BBL is a large data set, it was subsetted substantially to obtain desired data sets.

2.2. Development of undersampled point prediction and the final prediction

To predict movement from an area that does not have adequate recovery numbers for independent modeling, we relied on projections from core models created in the previously described approach (Fig. 1). For undersampled locations, the nearest, in geographical space, core model was located. This nearest core model was used to project predictions for the undersampled point. The undersampled point predictions were created by retaining all the environmental independent variables, except the distance and direction were changed to correspond to the new source location. This process was repeated a total of three times with predictions made from the three closest core model locations. The three predictions were then averaged together weighted by the inverse distance to the specified point, which was used as the final prediction.

2.3. Assessment of model performance

The MaxEnt model for each of the core source locations was created by using only the within-30-day recovery locations as the dependent variable. Only the recoveries were used because we want to know where a bird is likely to migrate if it were to start at the source location. The recoveries were split into 70% training data and 30% test data, and the split was randomized ten times. A total of 10,000 background points, which were also randomized ten times, were used to produce the receiver operating characteristic (ROC) plot and calculate the area under the curve (AUC) score. The AUC score was used to determine acceptability of a model and to compare different models.

As previously stated, the final prediction for an unsampled area is based on the average predictions of the three nearest core model locations. The decision to use three models was determined by comparing the performance of increasing numbers of core model projections averaged together to the predictions for a point with adequate within-30-day sample data. For clarification, first we selected a core model location and model movement predictions for this point (from now on referred to as the test location). Then we selected the next core model that was spatially the closest to the test location and projected movement predicted for the test location. The test location predictions and the projected predictions from the next closest core model were compared using a Kappa statistic. Kappa statistic measures the agreement between two data sets; a kappa statistic of 1.0 is prefect agreement and 0 is no agreement (Landis and Koch, 1977; Bell and Fielding, 1997). Kappa statistic indicates how closely the forecasted predictions are to the prediction from actual data. This process was repeated by creating projected predictions from the next closest core model for the test location.

The above process for assessing the modeling methods for unsampled locations is not ideal, yet it is presently the only method available. Ideally, one would prefer to completely independent data to test the method, but this data is lacking. Therefore, we were required to use model prediction from the test location as comparison data set. Because we were required to compare model output to model output, this should be taken into account was reviewing the conclusions. However, the AUC scores of the core models were all well above the threshold of acceptable, and should be considered resonable points of reference. At least until independent movement data is available to validate the full method (Fig. 1).

3. Results

There were 104 locations that had over 20 within-30-day recoveries of blue-winged teal. The number of recoveries for each core model location ranged from 20 to 228. Models preformed nearly equally regardless of number of recovery locations. The model with 228 recovery points had an AUC of 0.983, and the model with 21 recovery points, the least, had an AUC of 0.965 (Supplemental Fig. 1A). Additionally, both the bearing and distance predictor variables significantly contributed to the AUC scores of the core model (Supplemental Fig. 1B and C).

As a means of assessment for undersampled area predictions, we compared the outputs from a test location that had adequate sampling and then used our method to create projections for this area as if it did not have any sample data. The test location is in Thunder Bay, Ontario, Canada (48.42,−89.25), and had a total of 44 blue-winged teal birds recovered within 30 days of banding. The MaxEnt model was constructed with 44 recovery locations and had an AUC score of 0.962. All 103 other core model locations were used to project predictions for this test location. Kappa statistics, which describe the accuracy of the core model projected predictions to the predictions from actual data, ranged from 0 to 0.7978 (Fig. 2A). Generally, the core models closest to the test location performed best. We tested the agreement between increasing numbers of core model projected predictions averaged together weighted by inversed distance to the test location (Fig. 2B), and determined three to be optimal.

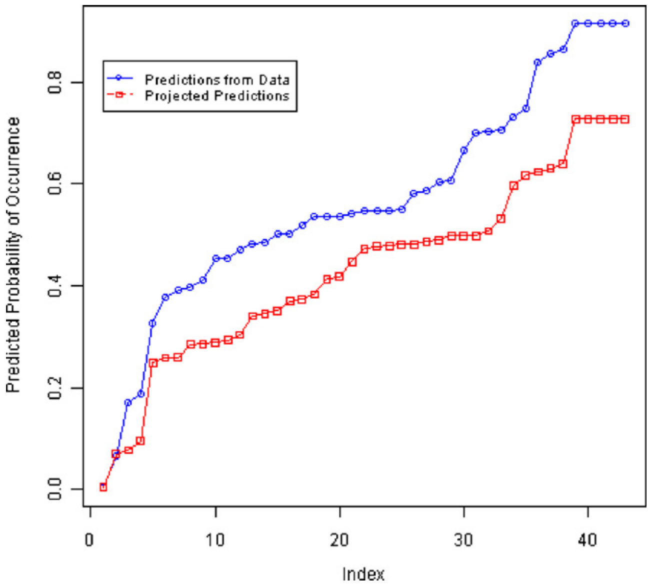

Fig. 4. Line graphs of predicted probability of occurrence for recovery points. The blue line represents the sorted values of predicted probability from the model created with actual date (Fig. 3A). The red line represents the sorted value of predicted probability averaged from the three projected models for the test point (Fig. 3B). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Fig. 3A maps the predictions for the test location based on actual within-30-day recovery data from this point. Fig. 3B used the three closest core model locations: (1) eastern Montana, USA (48.48, −95.92) with 30 recovery locations, (2) Upper Peninsula, Michigan, USA (46.25, −85.92) with 30 locations, and (3) eastern Wisconsin, USA (44.08, −87. 92) with 23 locations.

Additionally, we examined the predicted probability of occurrence for recovery points used to create the MaxEnt prediction in Fig. 3A (Fig. 4). For the same recovery point locations, the values of predicted probability of occurrence were then compared to the values of projected predicted probability in Fig. 3B. This comparison provides us with a way to compare the predicted probability of occurrence for actual data points between the two methods presented in this research. Clearly, the method that relies on averaging the three closest core models closely mirrors the model predictions created with actual recovery data. The projected predicted probability is however less than the predicted values from actual data, as anticipated. The method used to create predictions for location that lack sample data closely mirrors the predictions made by the model created with actual data, but is conservative in its predictions of likely occurrence.

Our method was then applied to three locations with no recovery data, and where it was considered highly likely to be blue-wing teal habitat (Kreakie et al., submitted for publication). The first location was immediately south of Winnipeg, Manitoba (49.31, −97.34) (Fig. 5A). This location's predictions are focused in the Mississippi flyway and have an upper probability of predicted occurrence around 0.72. The second model was built for a location in eastern Montana (48.37, −105.86) in the Prairie Pothole Region (Fig. 5B). Its results, with highest predicted probability of occurrence about 0.71,

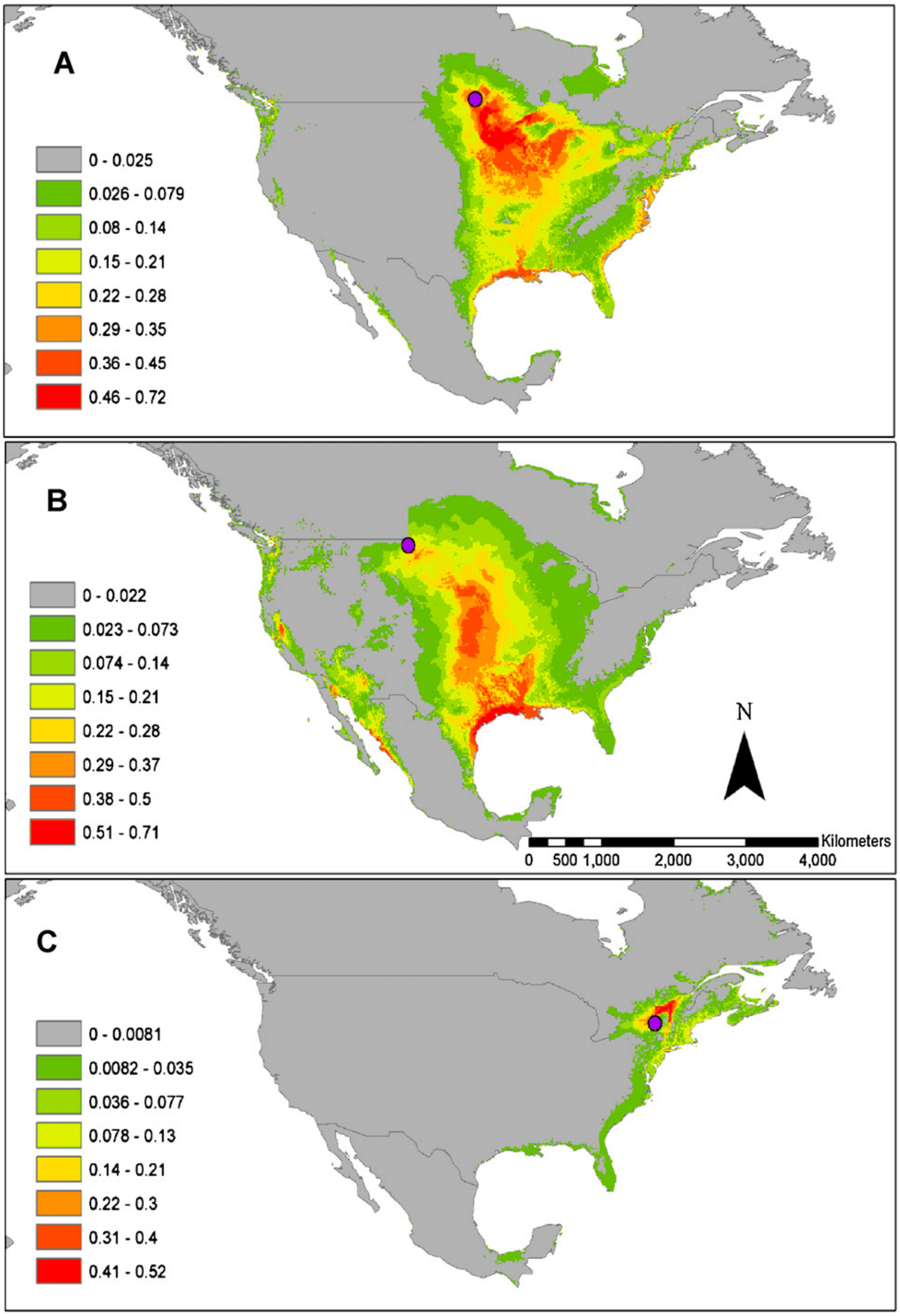

Fig. 5. Maps of predictive blue-wing teal movement from three different source locations. (A) has a start location (purple dot) in Manitoba, Canada. (B) is in Montana, USA, and (C) in New York, USA. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

predicted a main corridor of migration through the Great Plains and eventually merging into the Mississippi flyway. The final location is in the Ha-De-Ron-Dah Wilderness Area in the New York Adirondacks (43.76, −75.21) (Fig. 5C). This projection depicts less distance traveled and is concentrated in the Adirondacks and along the Atlantic Flyway. It projected 0.52 as the high end of its predicted probability of occurrence.

4. Discussion

The intent of this project is to present a novel method of predicting migratory bird movement and to explore its validity and outputs with a blue-winged teal case study. The inclusion of habitat measures, distance, and bearing make it possible to create probabilistic predictions based on the ecology, physiology, and behavior of a species. Each species is ecologically constrained by its suitable stopover habitat. Determining species distributions is, perhaps, the traditional manner in which MaxEnt is used in ecology; it defines the probability distribution of environmental variables. Beyond habitat needs of a species, there are physiological considerations that influence the optimal distance flown by birds between stopover locations. Clearly, migration has a predefined final destination, and this behavioral factor is accounted for by the inclusion of bearing.

Conceivably the largest contribution of this approach is the inclusion of both distance and habitat in determining the predicted movement. Given that migration is extremely costly to the animal in terms of resources and mortality, optimal migration theory illustrates that birds should attempt to accomplish migration with the minimal number of stopovers (Desholm, 2003; Fujita et al., 2004). Since migration has a high caloric demand, physiology prevents individuals from making the journey in one step. This means that birds should attempt to maximize the distance they fly between stopovers while attempting to select optimal habitat for refueling and predator-avoidance. Stopover locations that are too close to one another will increase the overall cost of migration. While flying past optimal habitat to maximize the distance between stopovers, the bird risks not finding suitable habitat before resources are depleted. The interaction between optimizing distance and habitat selection during migration is directly incorporated in this method.

This method is fundamentally comprised of two main parts: (1) construction of the core models for banding sites that have adequate within-30-day recoveries and (2) using the core models to project probabilities for sites that lack sampling. Model assessment of each of these parts entails different approaches. Core model assessment relied on the use of AUC scores (Supplemental Fig. 1). Each core model performed well, and can be interpreted as a reliable prediction of real-world events. We demonstrated that the addition of bearing and distance added to the accuracy of the predictions. Based on these results, it can be inferred that our approach for modeling migration movement from locations with numerous within-30-day recoveries is well founded. However, there are a large number of locations without the data necessary to directly predict movement, and must rely on the second part of our method.

The assessment of the predictions for undersampled location is not as forthright as the core model validation procedure. To illustrate the validation of undersampled location predictions, the predictions made from a core model as test data set were used. Then various projected predictions were created for the test location, and compared to the original predictions. In Fig. 2A, kappa statistics compare all core models projected predictions to the actual data predictions for the test location. Clearly, as the distance from the test location increase the kappa statistic decreases. For this point, projected predictions' accuracy decrease as distance between the core model location and projection point location increases. Instead of relying on a single projected prediction, we tested the validity of using multiple projected predictions for the final prediction. This agreement between the actual data predictions and averaged projected predictions spikes at three. These results show that the closest core models have the highest accuracy, and that three predictions averaged together is the strongest.

Although the predictions are not identical, and we have no way to know which is superior, they do share some key similarities. The areas in each map that have high predicted probability of being stopover habitat for this source location have the same spatial extent. This includes the complexity of the shape to the high probability area. For example, both results include areas around the Hudson Bay and up into the St. Lawrence River.

Even though the predictions are all made for the same species, this method makes it possible to examine regional differences in migrations routes due to the inclusion of distance and bearing in modeling (Fig. 5). The maps for Manitoba (Fig. 5A) and Montana (Fig. 5B) depict similar predictions along the Central and Mississippi Flyways. However, those individuals leaving from Montana have a more diffuse predicted path, which includes some portions along the Pacific Flyway. This is obviously due to the relative proximity to this area compared to the source location in Manitoba. The source location in New York (Fig. 5C) is even further east, and nearly completely abandons the Mississippi Flyway in favor of the Atlantic. The ability to predict regional movement of migratory birds will be critical for their long-term conservation (Haig et al., 1998).

The BBL data has many attributes that contribute to usefulness in migration study: for example, the large spatial extent of banding sites, the near global recording of recoveries, and the long time span of the study. Nonetheless, there are data considerations that should be kept in mind while interpreting the output. Since the occurrence of banding sites that have sufficient within-30-day points to build a core is rare, they are not evenly distributed across the landscape. If the three core models used to create the averaged prediction for a site are all exceedingly distant from the prediction site, the results should be carefully reviewed. It is likely that the habitat selection would not change for migrating birds within a species. Although clearly the average distance and bearing traveled would vary regionally for migrating birds.

The need for increased understanding about migration is no less important than in 1979 when Gauthreaux called for a modern synthesis of bird migration. The field has advanced in the last 30 years, but not sufficiently to address his original concerns and definitely not enough to help mediate modern concerns. The method outlined in this text will allow for us to begin to explore step-wise movement across the landscape and identify key stopover locations. Stopover habitat is of critical importance to migratory birds (Alerstam et al., 1990; Alerstam and Hedenström, 1998; McWilliams et al., 2004). It has been estimated that some individuals spend as much of 90% of their migration actually resting and refueling in stopovers (Schaub et al., 2001). Typically, these habitats are wetlands, which are extremely sensitive landscape features (Fretwell et al., 1996). Wetlands are exposed to multiple anthropogenic pressures; such as water divergence, land use change, sedimentation/erosion, and rapid climate change. It is critical to understand how birds use these habitats as they move between their breeding and wintering ground to ensure their long-term conservation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2011.10.019.

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