REPORT

APPLICATION OF A SPATIALLY EXPLICIT INDIVIDUAL-BASED MODEL TO CONSERVATION OF MIGRATING SONGBIRDS

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Executive Summary

1. How migratory songbirds respond to the landscapes through which they must pass is poorly understood. Migrants stopover in diverse landscapes during their migratory journey and must quickly and safely replenish up to half of their weight as fuel with little or no information about resources and sources of stress.

2. We conducted field experiments to assess the effects and relative influence of endogenous and exogenous factors on songbird movement during spring stopover in southcentral Louisiana (Kisatchie National Forest) and used the results of these experiments to parameterize a spatially explicit individual-based model of forest songbird movement and refueling ability in relation to landscape context during stopover.

3. In order to apply the model across the Gulf South region, we determined the generality of the behaviors observed in Kisatchie National Forest by comparing actual migrant behavior to simulated migrant behavior at a second site in another state spring 2011 (Leaf River Wildlife Management Area of De Soto National Forest, MS (30° 55' N 89° 02' W). De Soto National Forest was selected because the latitude is very similar to Kistachie National Forest and because it contains the hardwood, mixed and pine habitat characteristic of the region.

4. We applied the model to test the expectation that fuel deposition rate (FDR) would decrease in landscapes with less hardwood habitat and less habitat contagion, or spatial aggregation of habitat. We used a factorial design with three levels of two factors, the proportion and the contagion of hardwood habitat. We found FDR decreased as the amount of hardwood in the landscape decreased from 42 to 22 to 12 %. Counter to our expectation, FDR was higher in the landscapes with low contagion as compared to the landscapes with high contagion.

5. Quickly locating habitat with sufficient food resources may be the most important factor determining a successful migration and migrants that arrived in higher quality habitat types gained more mass. Therefore, differences in FDR may be most influenced by whether or not an individual experiences an initial searching cost after landing in poor quality habitat.

6. The model is a valuable tool for identifying features of landscapes that influence their fitness value for migratory songbirds. For example, the model can be used to derive the difference in FDR between (a) alternative landscapes, (b) in one landscape before and after the addition of suitable habitat (c) through time, or (d) as a consequence of habitat loss.

Introduction

Over half of all birds breeding in the forests of eastern North America migrate from more tropical wintering areas in the Caribbean, Mexico, and Central and South America (Rappole 1995). While it is presumed that the costs of migration are balanced by the benefits of exploiting seasonally abundant resources (Greenberg 1980), our inability to track the fates of individuals across the spatial and temporal extent of migratory routes has lead to a lack of empirical data on the demographic effects of the migratory period. Many long-distance intercontinental landbird migrant species are currently declining (Robbins et al. 1989, Askins et al. 1990, Marchant 1992, Berthold et al. 1998, Sokolov et al. 2001, Sauer et al. 2007) and migratory species appear to be declining faster than resident breeding species (Robbins et al. 1989, Askins et al. 1990, Sanderson et al. 2006) suggesting events outside of the breeding period may be limiting populations (Sillett and Holmes 2002, Newton 2006). However, the questions of when, where and how long-distance migratory passerine populations are regulated continue to focus primarily on events associated with the breeding and wintering phases of the migrant's annual cycle (e.g., Terborgh 1989, Sherry and Holmes 1995, Newton 2004). Still, billions of landbirds engage in annual migrations of hundreds to thousands of kilometers and along that journey they must adjust to unfamiliar habitats, find enough food, resolve often conflicting demands between predator avoidance and meeting energetic requirements, correct for orientation mistakes, and cope with adverse weather. Meanwhile, they may encounter wind turbines, tall structures, light pollution, non-native predators, and increasingly smaller patches of habitat. Therefore, rapid changes in landscape configuration, resource availability, air space, and climate due to unprecedented human activity may be inflating the risks associated with migration (Wilcove and Wikelski 2008), making it critical to incorporate the migratory period into studies of where, when and how migratory songbird populations are limited (Moore et al. 1995).

Migration is energetically costly (Blem 1980). Consequently, successful migration typically requires frequent stopover periods for refueling between flights, the duration of which cumulatively far exceed time spent in flight and largely determine the duration of the migratory period (Hedenström and Alerstam 1997, Alerstam 2003). Therefore, how well a migrant solves the problem of finding suitable habitat while avoiding predation in each stopover landscape will determine not only if she survives but also her subsequent reproductive success (Sandberg and Moore 1996, Smith and Moore 2003). Nevertheless, there is surprisingly little information about the influence of environmental factors on fuel deposition rates (FDR), recognized as the currency of migration, during stopover (Jenni and Schaub 2003, Schaub et al. 2008).

Incorporating the migratory period into comprehensive conservation strategies requires identifying and protecting important stopover sites (Mehlman et al 2005). However, prioritizing stopover sites for protection necessitates an understanding of their value to migrating songbirds. It is essential to establish how factors including landscape context translate into the refueling value of stopping over at a site. Forested areas across the eastern US are declining largely due to urban growth, timber harvesting and other development, particularly in coastal areas (Drummond and Loveland 2010). Here we examine how the abundance and configuration of suitable habitat in a landscape affect FDR of nocturnal migrants during stopover. The consequences of landscape composition and configuration have been well studied for breeding birds (e.g., Andrén 1994, Smith et al. 2011) but the effects of landscape context on songbirds during stopover remains poorly understood (Ktitorov et al. 2008).

Selection of a stopover site may be the greatest determinant of refueling rates (Schaub and Jenni 2001, Dunn 2002) suggesting that characteristics of sites, exclusive of their geography (Schaub and Jenni 2001), strongly influence FDR. The amount of hardwood forest cover positively influenced the distribution of spring migrants in Gulf South landscapes (Buler et al. 2007) and FDR for two songbird species in Europe were higher at sites with more forest cover (Ktitorov et al. 2008). Moreover, when suitable habitat is less fragmented, migrants may

increase FDR by reducing the energetic or time costs associated with an initial searching period prior to foraging (Alerstam and Lindstrom 1990, Alerstam and Hedenstrom 1998) and spending more time foraging successfully with less movement (see Graber and Graber 1983). We tested the expectations that FDR would be positively related to the amount of hardwood forest cover and the level of habitat contagion, a measure of spatial aggregation, in a landscape. Further, because safely finding suitable habitat in a timely manner is essential for a successful stopover, we expected FDR to be greater for migrants landing in hardwood habitat. We applied the constructed model to test these predictions about the influence of landscape context on FDR in a factorial experiment.

Our goal was to quantify the impacts of landscape pattern on migrating songbirds during stopover in Gulf South landscapes. Successful refueling during migration is influenced by a variety of factors and spatially explicit individual-based models are a tool uniquely suited to incorporating individual variability into behavioral responses to a changing environment (McLane et al. 2011). Previous work (Simons et al. 2000, Pearson and Simons 2002) demonstrated the predictive ability of models for this period when migrants are thought to be most at risk but no subsequent attempt has been made to build empirically derived individual-based models of stopover. To achieve our objective, we constructed a spatially explicit individual-based model of migratory songbirds moving through and refueling in heterogeneous landscapes. The specific objectives of this research were to build an empirically derived model about stopover ecology, calibrate and validate the model using field data, and use the model assess the impacts of change landscape pattern on migrant birds.

Methods

An individual-based model for stopover migrant behavior was developed to simulate the movement of virtual migrant birds on a raster map of forest habitats found the Gulf South region of the U.S. As birds move, they gain and lose energy, measured as body mass, according to the foraging opportunities presented by different habitat types. The research reported herein uses field data on radio-tagged birds to adjust the rates of body mass gain (FDR) and to modify the movement rules. The objective was to produce a more realistic and accurate model of stopover ecology for a common and representative migrant bird species then to use this model to assess the impacts of landscape pattern of habitats on migrant birds.

Derivation of model parameters from field data

We parameterized the model based on the results of field experiments conducted in Kistachie National Forest, LA (30° 57’ N 93° 08’ W) during the springs of 2007 and 2008. This site was chosen because a high density of spring migrants stopover there (Fischer et al. 2011) and it contains forest types characteristic of those found throughout the Gulf South region including longleaf pine savannas and bottomland hardwood forests (Evans 1994, Keddy 2009). I present the principal data collection methodologies and results here because they were used to parameterize the model and in the next section (model construction) we discuss how we applied them in the model.

We chose the red-eyed vireo (*Vireo olivaceus*) as a model species representative of canopy foraging songbirds of eastern North America (Cimprich et al. 2000). The red-eyed vireo is a long distance migrant wintering in South America and is one of the most common species breeding extensively in deciduous forests across Canada and eastern North America. We captured known migratory individuals, recently arrived across the Gulf of Mexico (captured at Johnson’s Bayou, LA, 29° 45’ N 93° 30’ W). On the day of capture we attached a radio-transmitter weighing less than 3 % of mean body mass to each bird (model BD-2A, Holohil, Ontario, Canada). The following morning, red-eyed vireos were released in one of six predetermined locations surrounded predominately by one of three habitat types: upland

longleaf pine (*Pinus palustris*) savanna (pine), bottomland hardwood forest (hardwood), and an intermediate between the two (mixed) in two landscapes. We continuously followed the movements of migrants from release until they left to continue migration. We simultaneously characterized the environment through which migrants were moving by measuring the distribution of food, avian predators and other migrants. We found predictable responses to endogenous and exogenous factors during stopover.

Movement during stopover varied with time since arrival at the stopover site and was most strongly influenced by energetic condition and habitat. Red-eyed vireos moved the furthest and fastest upon arrival at a stopover site during which time they selected hardwood and mixed habitat, characterized by greater food availability. Once in habitat characterized by more abundant food they also captured more food items when observed foraging. Moreover, migrants arriving in habitat characterized by less abundant food initially moved further and faster presumably while they were searching for food/ better habitat. Finally, red-eyed vireos without fuel reserves, under pressure to replenish fuel stores necessary to continue migration in a timely fashion, moved faster and further throughout stopover than migrants with fuel reserves.

Model structure

The model simulates the movement and energy status of songbirds during stopover. Each simulation follows one individual and predicts habitat associations, movement patterns and FDR. Movement rules depend on energetic status for a set of migrant characteristics in a heterogeneous landscape. Each daylight hour (12-hour days) for the duration of stopover the model migrant makes step-wise movement decisions through a heterogeneous landscape composed of 28.5 m square cells representative of habitat types of variable quality (Figure 1).

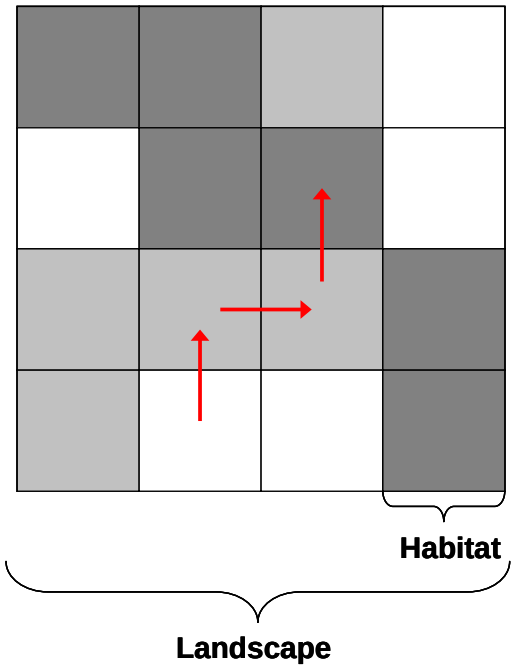

Figure 1. Graphical depiction of an individual-based model of a landscape where each shade of cell represents a habitat type and the arrow represents a model animal making stepwise movements.

The model structure reflects the behavior observed during field experiments. During each hour, the migrant moves a specified number of map cells. The number of cells crossed is

specific for the hour of the day and day of stopover as well as the bird's condition and habitat type occupied at the end of the previous hour. Energetic condition is updated based on the number of cells crossed and the habitat type of the last cell (see below for calculation of energetic gain). Migrants preferentially selected habitat with greater food abundance but did not bias their movements in a seasonally appropriate direction. Therefore, directionality of model migrants are determined by habitat (hardwood > mixed > pine > unforested) in the 24 surrounding cells. We used the 24 surrounding cells for three reasons. First, model migrant movement did not reflect observed migrant movement when I used the adjacent eight surrounding cells. Second, we considered the distance across two 28.5 m cells to be a distance across which migrants could reasonably assess resources whereas the distance across three cells was likely beyond a biologically reasonable range of perception. Finally, model migrant movement reflected observed movement when the 24 surrounding cells were used. When adjacent cells are of equal quality, the migrant preferentially selects those not previously visited and otherwise selects randomly among adjacent cells of equal or greater habitat quality. Migrants cannot revisit cells except when all surrounding cells having been visited. In this situation, migrants can pass through an adjacent cell that was previously visited if there is a cell across it that has not been previously visited.

Energetic costs are reflected in the proportion of each hour not spent foraging because the energetic cost of flying the relatively short distances moved during stopover is likely to be minimal (see Lindström 1991). The time not spent foraging is determined by the number of cells crossed which were calculated from the mean time it took observed migrants moving linearly, and not observed foraging, to move 28.5 m. We assume that foraging occurred in the last cell of the movement at each time-step and the energetic gain is based on the habitat type of that cell (see below for determination of habitat-specific rates). Therefore, prior to each movement the energetic condition index of each migrant is updated by adding mass change from the time spent foraging in the last cell of the movement as follows:

Foraging time= one hour - (number of cells crossed time to cross a cell)*
*Energetic condition = current condition + (foraging time*habitat specific mass change rate of the last cell of time step)*

We summarize the attributes of the model "migrant" and the landscape which must be specified for each simulation and the parameters generated from each simulation. The model migrant is initialized with a body mass in grams, a start location, and a set of movement values that vary with the hours of the day and day of stopover. The landscape is initialized with a set of gain values for the habitat types in the map. The start location can be selected at random by the modeling environment or specified as a cartesian coordinate in the map. Random start locations are selected from forested (hardwood, pine or mixed) cells migrants are not known to land in unforested habitat types (see Chernetsov 2006). The movement values are specified as a set of integers listing the number of map cells to move between hourly time steps. Movement distance is a function of habitat and body mass and depends on the day and hour of stopover.

The gain values are a vector of values corresponding to the habitat types in the landscape (hardwood, mixed, pine, unforested). Maximum FDR are determined by food availability, capture rates and digestive rates (Lindstrom 1991). Our experimental work found food availability was related to habitat type in Kisatchie National Forest. We used the observed difference in foraging success between habitat types (number of successful attacks per time spent foraging) to determine the relative foraging benefit of time spent in a pine, mixed or hardwood cell. The gain value of unforested habitat was assumed to be zero. Frank Moore's lab at The University of Southern Mississippi has been banding spring migrants near Johnson's Bayou for over 15 years. This site is adjacent to an ecological barrier and mean mass change rates may be quite different there. Therefore, we did not use mean mass change values (likely

specific to habitat) but we did use red-eyed vireo recapture records (n= 115) to determine the range of reasonable mass change values (see Loria and Moore 1990). We confirmed that the departure masses resulting from the assigned habitat-specific gain values fell within the range observed from the recapture data. While mass change rates at the banding station may not be representative of mean rates at Kisatchie National Forest, we assume the range of variability to be reflective of those experienced by the species in general during spring stopover.

The model generates a movement path for each simulation with cartesian locations for each movement step and body mass in grams at end of each time step. The number and location of cells visited during each step of the simulation are used to calculate the movement rate and linear displacement. FDR is calculated as mass change, the mass at the end of each time period, or at the end of stopover, minus the arrival mass. A status for the simulation is also recorded (normal operation or abnormal run) so that the simulation can be discarded in the rare case of an error (migrant moved off the map or was boxed into a corner).

Model development

Following the initial construction, completion of the model required calibration, verification and validation. During calibration, we iteratively compared the model generated patterns to those observed from the radio-tracking data and reparameterized the movement values until we minimized the difference (Figure 2). The patterns of habitat selection were reflected in the model output and did not need to be adjusted. We compared the model generated displacement distances (linear distance between the first and last point of each hour, n = 500) simulations to the radio-tracking data (n=50 migrants). We adjusted the movement values, which define the number of cells to cross (not the linear distance) until the difference in linear displacement was minimized. We followed the same iterative process to adjust the habitat-specific gain values.

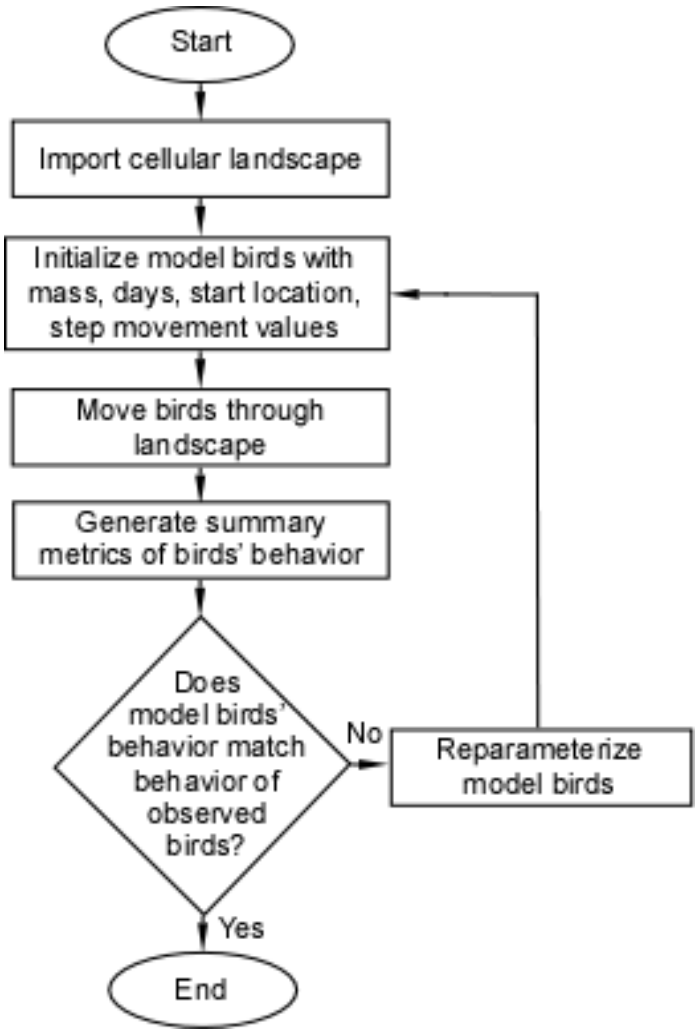

Figure 2. Flow chart depicting the derivation of hourly movement distances from observations of migrant movement behavior.

Once the difference between the model and observed migrant behavior had been minimized, we verified the model using a smaller sample of migrants tracked using the same methods in Kistachie National Forest during the spring of 2009 (n=6). These migrants were not included in the data used for model parameterization and calibration. We simulated migratory movements (n = 60) from the same location where migrants were released. We tested for differences in and that the linear displacement of the migrants tracked and the model generated hourly displacement.

Finally, to be able to apply the model across the Gulf South region, we needed to determine the generality of the behaviors observed in Kisatchie National Forest. To accomplish this objective/goal, we quantitatively compared actual migrant behavior to simulated migrant behavior at a second site in another state. During the spring of 2011, we conducted subsequent translocation experiments and tracking in the Leaf River Wildlife Management Area (LRWMA) of De Soto National Forest, MS (30° 55' N 89° 02' W; Figure 3). De Soto National Forest was selected because the latitude is very similar to Kistachie National Forest and because it contains the hardwood, mixed and pine habitat characteristic of the region. We released migratory red-eyed vireos in a range of energetic conditions (-3.0 to 3.5 condition index) into two

replicates of pine (n = 5) and hardwood (n = 5) habitat (Figure 4). Translocation experiments followed the methods used at Kisatchie National Forest (see above, Derivation of model parameters from field data); migrants were transported from Johnson's Bayou, fitted with radio-transmitters, held overnight, released before first light and followed continuously for ten hours on one day.

We tested for differences between the behavior of migrants stopping over in LRWMA and model generated movement patterns of simulated migrants "released" at the same locations. We tested for similarity in (a) hourly linear displacement patterns, (b) the influence of release habitat, (c) the influence of release condition, and (d) habitat selection.

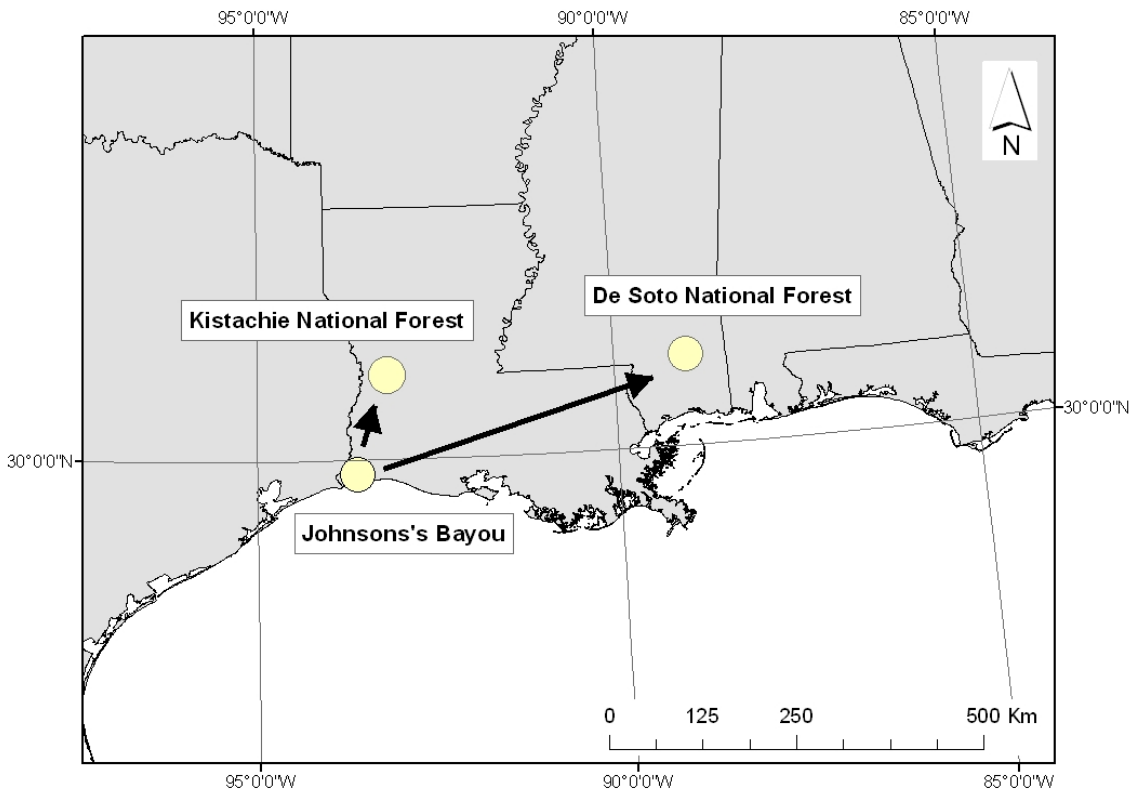

Figure 3. Map of translocation (arrows) from point of capture on the coast at Johnson's Bayou, LA (29° 45' N 93° 30' W) to Kisatchie National Forest, LA (30° 57' N 93° 08' W) for experiments to parameterize the model and to the Leaf River Wildlife Management area in De Soto National Forest, MS (30° 55' N 89° 02' W) to validate the model.

Landscape pattern and stopover performance

We used a factorial experiment to test for effects of the amount of hardwood forest cover and contagion on migrant FDR. We further tested for effects of arrival habitat type and arrival energetic condition on FDR. We altered one raster (gridded) map, a portion of LRWMA, using focal statistics tools in ArcMap (v. 9.3, © ESRI, Redlands, CA) to create nine maps; three levels of hardwood abundance (41 %, 22 %, and 12 %) and three levels of spatial aggregation (high, medium and low) (Figure 5). The LRWMA landscape contained only the three habitat types: pine (30 %), mixed (31 %) and hardwood habitat (40 %) and was naturally low in contagion.

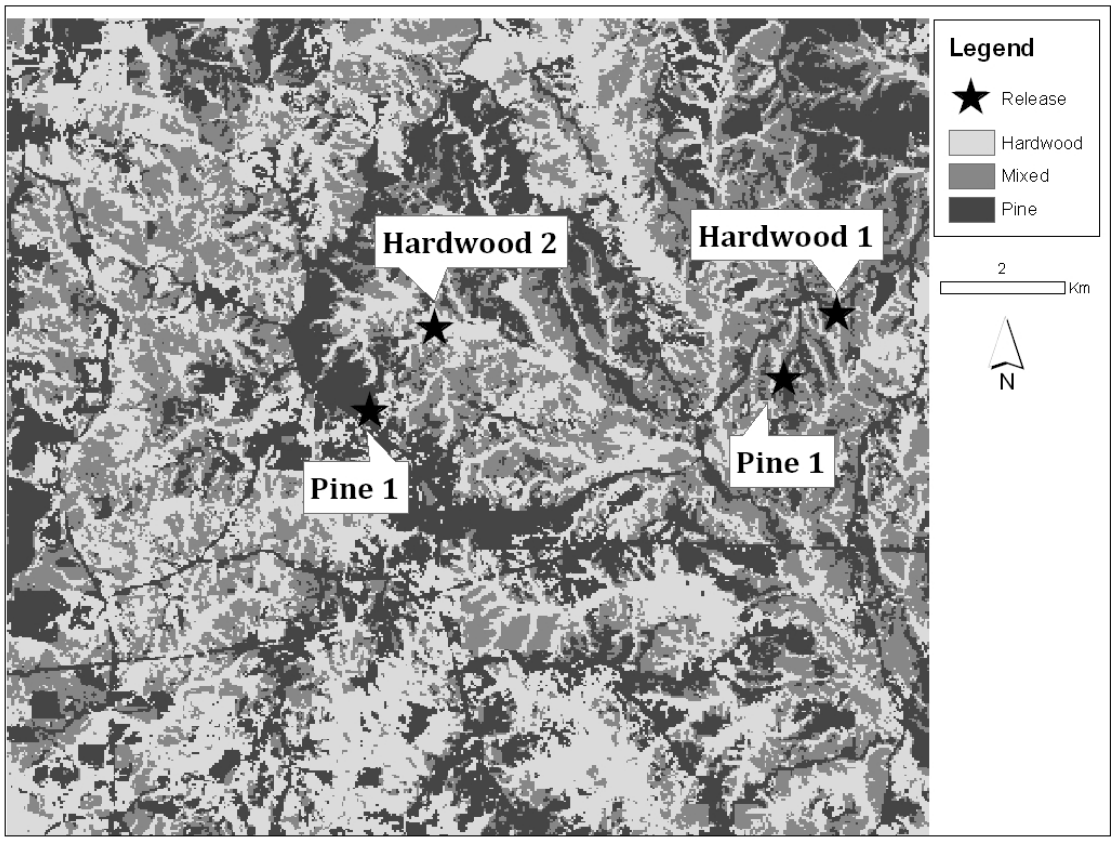

Figure 4. Map of release locations (stars) in hardwood and pine habitat in the Leaf River Wildlife Management Area (grey outline) in De Soto National Forest, MS for model validation of movement behaviors during the spring of 2011.

When altering this landscape, we held the amount of mixed habitat constant (31 %) and increased the amount of pine habitat while decreasing hardwood habitat. We simulated 60 migrants landing in each of the nine landscapes and stopping over for one 12 hr day. The simulated birds arrived in each landscape at random locations with the range of masses observed for the species (12 to 23 g). We calculated FDR by subtracting each individual's arrival mass from the end of day mass. We used ANOVA and post-hoc Tukey's HSD to test for differences in mass change for each variable (level of contagion, amount of hardwood, arrival habitat type and arrival condition) and an interaction between contagion and amount of hardwood.

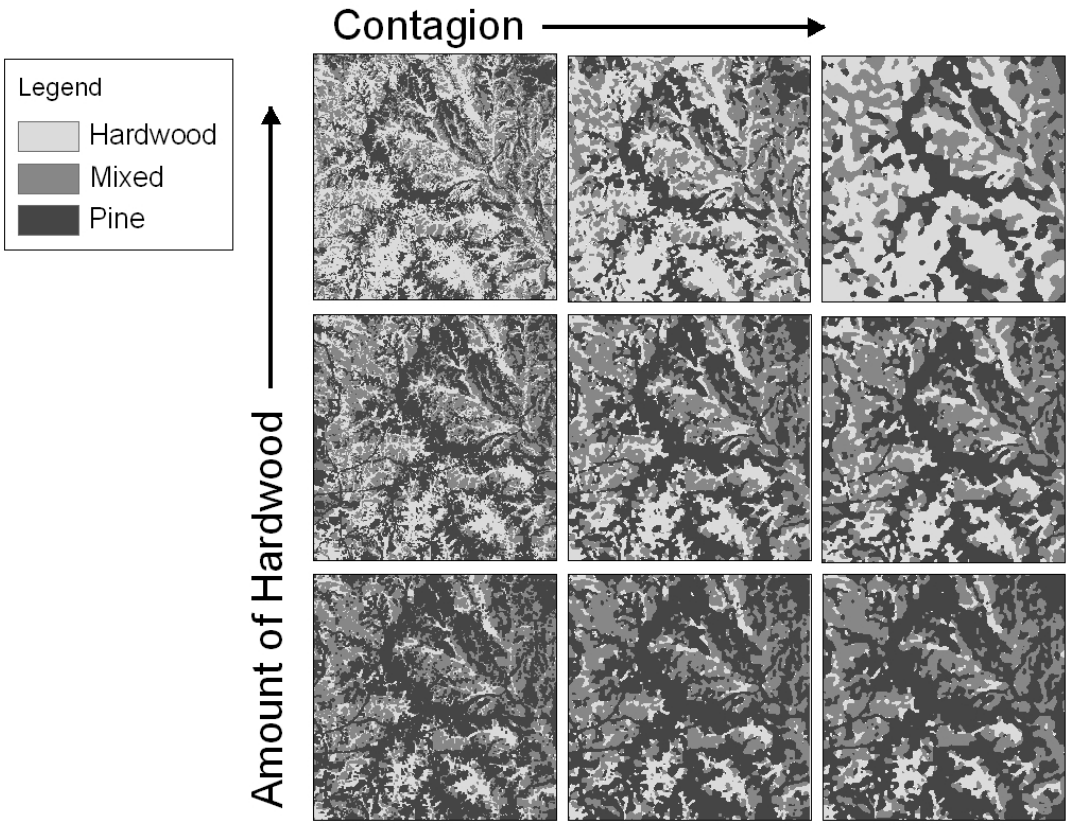

Figure 5. Design of the factorial experiment using nine maps with low, medium and high contagion (level of spatial aggregation of habitat; left to right column) and high (41%), medium (22%) and low (12%) amount of hardwood forest cover (top to bottom row). The map in the top left corner (low contagion, high hardwood forest cover) is a portion of the Leaf River Wildlife Management area in De Soto National Forest.

Results

Model development

We verified that the linear displacement distances of six migrants released in hardwood habitat did not differ from the linear displacement of simulations from the same release location ($F = 0.005$, $df = 1$, $P = 0.94$). The validation showed a high level of agreement between the simulated behavior and the behavior of the birds that we released and tracked (see example in Figure 6). The hourly movement pattern of actual migrants was similar to the hourly movement pattern of simulated migrants. In fact, there was no difference in hourly linear displacement (all $P > 0.05$) except during the first 2 hrs when the tracked migrants moved further than simulated ($P = 0.02$). The release habitat type influenced initial linear displacement distances in similar ways; migrants released in pine moved further than those released in hardwood during the first hour ($P < 0.01$) but not during second hour ($P = 0.38$). Arrival energetic condition influenced linear displacement in similar ways; migrants in poorer energetic condition moved further from their release sites than migrants in better condition ($P=0.01$). Finally, migrants showed the same patterns of habitat selection; by the end of the day all migrants tracked in LRWMA had moved into either mixed or hardwood habitat but predominately into hardwood.

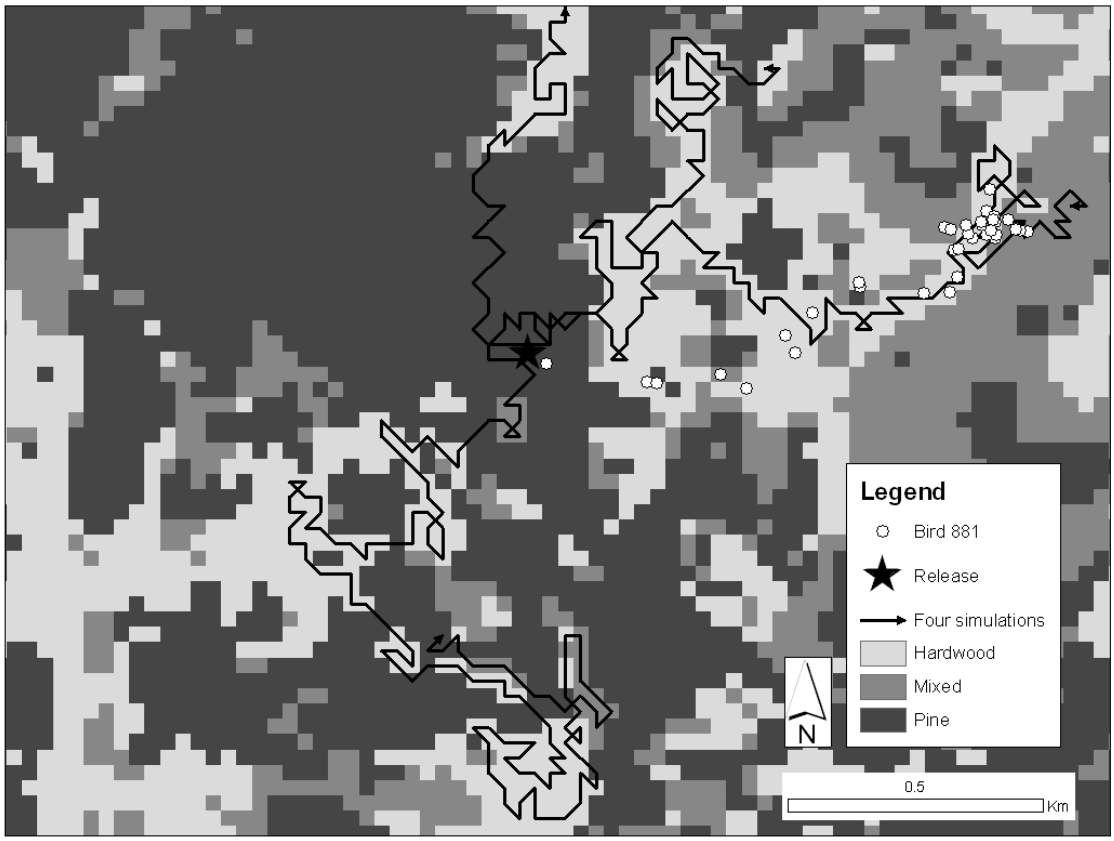

Figure 6. Example of four model simulated movements (black lines, each ending in an arrow) and bird tracking points (circles) from the same release location (star) which were compared during the model validation process.

Landscape pattern and stopover performance

FDR (mass change/ day) increased with the amount of hardwood forest cover ($F= 30.03$, $df= 2$, $P< 0.01$; all comparisons $P < 0.05$; Figure 7a) but decreased as habitat became more aggregated ($F= 13.65$, $df= 2$, $P< 0.01$, Figure 7b). FDR was higher in the landscape with low contagion, or little spatial aggregation of habitat, than in the landscape with high contagion, high spatial aggregation of habitat ($P< 0.01$) but was not different between landscapes with medium versus low or high contagion ($P > 0.10$). There was no interaction between the amount of hardwood and level of contagion ($F= 0.73$, $df= 4$, $P= 0.57$). FDR was also influenced by the arrival habitat type ($F= 54.26$, $df= 2$, $P< 0.01$). Migrants arriving in pine habitat had lower FDR during the first day of stopover than those arriving in mixed or hardwood (all comparisons $P< 0.01$; Figure 7c). Finally, leaner migrants gained more mass on the first day of stopover than fatter migrants ($F= 4.35$, $df= 1$, $P< 0.05$).

Discussion

Despite its central importance to our understanding of migration, there is surprisingly little information about the influence of environmental factors on fuel deposition rates during stopover (Jenni and Schaub 2003, Schaub et al. 2008). We found the amount of hardwood forest at a stopover site positively influenced refueling rate. Buler et al. (2007) found the

strongest predictor of migrant density in southern Mississippi and Louisiana was the abundance of hardwood habitat in a landscape which was positively correlated with arthropod abundance. Ktitorov et al. (2008) found fuel deposition rates of two songbird species (Willow Warbler, *Phylloscopus trochilus* and Eurasian Redstart, *Phoenicurus phoenicurus*) captured at netting stations across Europe were highest at sites with more forest cover. Our work supports the suggestion that migrants may use hardwood as a cue to select high quality landscapes (Buler at al. 2007) because we found fuel deposition rates to be higher in landscapes with more hardwood cover.

Fragmentation of habitat may only affect birds and mammals when the amount of suitable habitat covers < 30% of the landscape (Andrén 1994). We reduced the amount of high quality habitat from approximately 40 to 20 and 10% and, counter to our expectations, we found increasing fragmentation was beneficial for refueling migrants. Actually, an intermediate amount of fragmentation did not impact FDR but migrants had higher FDR in the landscape with low, versus high, contagion. Quickly locating habitat with sufficient food resources may be the most important factor determining a successful migration and migrants that arrived in higher quality habitat types gained more mass. Therefore, differences in FDR may be most influenced by whether or not an individual experiences an initial searching cost. Migrants arriving at random in a landscape where hardwood habitat is less spatially aggregated are more likely to find hardwood habitat and quickly benefit from increased foraging success in that habitat type (Simons et al. 2000). Evidence of searching costs, in the form of an observed mass loss after initial capture, from banding data is mixed (reviewed in Schwilch & Jenni 2001). We found no evidence for an acclimation period prior to foraging; migrants began foraging almost immediately upon release in habitat with abundant food. Delingat et al. (2006) also observed foraging from one minute to half an hour after moving and releasing Northern wheatears (*Oenanthe oenanthe*), presumably into habitat with abundant food. There are expected to be energetic costs associated with an increased searching period prior to foraging upon arrival at stopover sites. If necessary at each stop along a migrants' journey, these initial periods would affect the refueling rate or duration of stay at each stopover (Alerstam and Lindstrom 1990, Alerstam and Hedenstrom 1998) and would cumulatively result in a significant energetic or time cost to migration (Lindstrom 1991).

Migrants arriving in poorer condition are the most likely to be negatively impacted by reduced habitat availability at stopover sites because of their increased energetic demands and reduced margin of safety. We found migrants that arrived in poorer energetic condition gained more mass during stopover than migrants that arrived with greater fuel reserves. A migrant's behavior during stopover is expected to be strongly influenced by its energetic condition because they are often under pressure to replenish up to 50% of their mass as fuel reserves during stopover (Blem 1980). For example, leaner migrants move further and faster during stopover (Moore and Aborn 2000, Chernetsov 2006, Matthews and Rodewald 2010) likely because they are under more pressure to quickly replenish depleted fuel stores. Further, the conditions of long-distance spring migrants arriving at stopover sites are likely to be influenced by the environment they experienced in their over-wintering areas in the Neotropics (Wolfe and Ralph 2009, K. Paxton unpublished data) many of which are rapidly being converted to landscapes dominated by agricultural land uses (Houghton 1994, Foley et al. 2005) thereby increasing the likelihood that migrants will arrive in increasingly poorer condition.

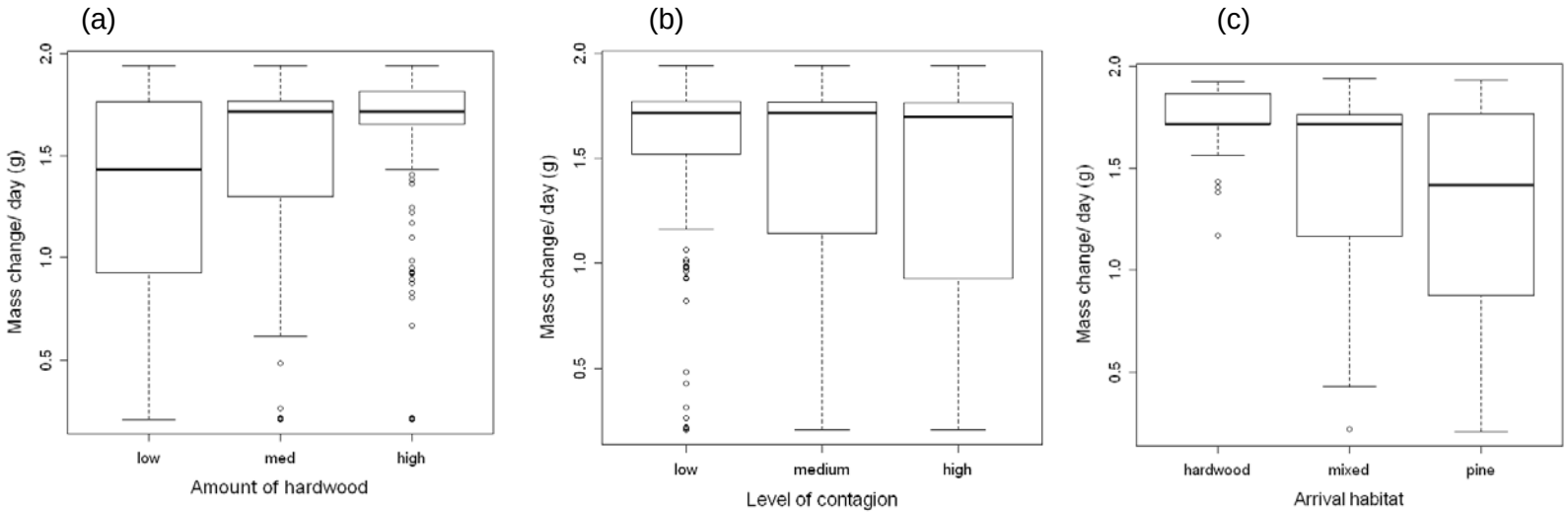

Figure 7. Boxplots of fuel deposition rate (mass change/day in g) after stopping over for one day in landscapes with (a) a low, medium or high proportion of hardwood habitat, (b) three levels of the degree of spatial aggregation of habitat: low, medium or high, (c) after landing in hardwood, mixed or pine habitat and stopping over for one day (n = 180 simulations/ factor). Circles represent outliers (less than 3/2 times of lower quartile), box is bound by 25 and 95% quartiles with median values in center. Whiskers represent maximum and minimum values (excluding outliers).

Conservation Implications

The experimental and individual-based modeling approach adopted in this study provides much needed information about how migrants make decisions in unfamiliar landscapes during stopover as well as the fitness consequences of those decisions. This information is necessary to evaluate the contribution of the migratory period to long-term population change or to forecast how demography of migrants relates to changes in the composition and configuration of human actions. There is every reason to believe that events during migration influence fitness (Sandberg and Moore 1996, Sillet and Holmes 2002, Smith and Moore 2003), but we have difficulty quantifying impacts of the landscape through which migrants must pass. This model is a tool for assessing the effects of the factors influencing migratory refueling during stopover. For example, the model can be used to derive the difference in FDR between (a) alternative landscapes, (b) in one landscape before and after the addition of suitable habitat (c) through time, or (d) as a consequence of habitat loss. Most intercontinental songbirds migrate at night and stop only briefly during the day to rest and refuel and for this reason much of migratory natural history remains poorly understood. Nevertheless, a clear understanding of the contribution of the migratory period for long-term population change is needed if we are to conserve these populations (Moore et al. 1990) in a rapidly changing world where many migratory species are currently in decline (Wilcove and Wikelski 2008).

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