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Effects of landscape composition and configuration on migrating songbirds: inference from an individual-based model

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Abstract. The behavior of long-distance migrants during stopover is constrained by the need to quickly and safely replenish energetic reserves. Replenishing fuel stores at stopover sites requires adjusting to unfamiliar landscapes with little to no information about the distribution of resources. Despite their critical importance to the success of songbird migration, the effects of landscape composition and configuration on fuel deposition rates (FDR [g/d]), the currency of migration, has not been tested empirically. Our objectives were to understand the effects of heterogeneous landscapes on FDR of forest-dwelling songbirds during spring migration. The results of field experiments were used to parameterize a spatially explicit, individual-based model of forest songbird movement and resulting FDR. Further field experiments were used to validate the results from the individual-based model. In simulation experiments, we altered a Gulf South landscape in a factorial design to predict the effects of future patterns under different scenarios of land use change in which the abundance of high-quality hardwood habitat and the spatial aggregation of habitat varied. Simulated FDR decreased as the amount of hardwood in the landscape decreased from 41% to 22% to 12%. Further, migrants that arrived in higher-quality habitat types gained more mass. Counter to our expectations, FDR was higher with lower spatial aggregation of habitat. Differences in refueling rates may be most influenced by whether or not an individual experiences an initial searching cost after landing in poor-quality habitat. Therefore, quickly locating habitat with sufficient food resources at each stopover may be the most important factor determining a successful migration. Our findings provide empirical evidence for the argument that hardwood forest cover is a primary determinant of the quality of a stopover site in this region. This study represents the first effort to empirically quantify FDRs based on the configuration of landscapes.

Key words: individual-based model; landscape ecology; Nearctic–Neotropical migrant; Red-eyed Vireo; stopover ecology; translocation experiment; Vireo olivaceus.

Introduction

How quickly and safely spring migrating songbirds access food resources when they stopover in unfamiliar landscapes along their journey are thought to determine not only their survival, but also their time of arrival on the breeding grounds, which influences reproductive success (e.g., Smith and Moore 2003, 2005). A successful long-distance migrant most often needs to replenish energetic reserves at multiple stopover sites. In fact, the cumulative duration of stopover periods far exceeds time spent in flight and largely determines the duration of the migratory period (Alerstam 2003, Hedenström and Alerstam 1997). Forested areas across the eastern United States are declining largely due to urban growth, timber harvesting, and other development (Drummond and Loveland 2010). The consequences of these changes in landscape composition and configuration have been well studied for breeding birds (e.g., Andrén 1994, Trzcinski et al. 1999, Smith et al. 2011), yet we have surprisingly little information about how migrants respond to and are affected by landscapes during stopover periods (Freemark et al. 1995, Chernetsov 2006).

Habitat characteristics and availability at a stopover site may be the greatest determinants of refueling rates (Schaub and Jenni 2001, Dunn 2002). The amount of hardwood forest cover positively influenced the abundance of spring migrants detected in Gulf South landscapes (Buler et al. 2007, Buler and Moore 2011). Further, fuel deposition rates (FDR) of two songbird species captured multiple times in nets were higher at sites in Europe with more forest cover (Ktitorov et al. 2008). Moreover, it is conceivable that, 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 Lindström 1990, Alerstam and Hedenström 1998).

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Over half of the bird species breeding in the forests of eastern North America engage in annual migrations of hundreds to thousands of kilometers, and the Gulf South region (i.e., United States along the north coast of the Gulf of Mexico) harbors critical stopover areas for migrants prior to, and after, crossing the Gulf of Mexico, the largest obstacle that eastern migratory birds face. Our objective was to produce a realistic and accurate model of stopover ecology for a common and representative forest-dwelling migrant songbird and to use this model to quantify the impacts of landscape pattern on migrating songbirds during stopover. Successful refueling during migration is influenced by a variety of factors (reviewed in Jenni and Schaub 2003) and spatially explicit, individual-based models are a powerful tool for evaluating behavioral responses to a changing environment (McLane et al. 2011). We build on previous work demonstrating the predictive ability of models for this critical period when migrants are thought to be most at risk (Simons et al. 2000, Pearson and Simons 2002). We incorporated the results of field experiments (see Cohen et al. 2012) designed to parameterize a spatially explicit individual-based model of migrant behavior during stopover (Simons et al. 2000, Pearson and Simons 2002) and validated the applicability of the model for the region with further field experiments. We assessed the influence of landscape patterns on FDR (g/d), the currency of migration, by applying the model to an existing landscape in the Gulf South United States, which we altered to reflect likely land use changes. We examined how the abundance and configuration of suitable habitat in a landscape affect FDR and movement patterns of nocturnal migrants during stopover. We tested the expectations that FDR of forest songbirds during stopover is positively related to the amount of hardwood forest cover and the level o f habitat contagion, a measure of spatial aggregation. 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 higher-quality hardwood habitat, as opposed to lower-quality pine or mixed wood habitats.

METHODS

Field experiments during spring migration over a four-year period provided the empirical foundation for the model. The experiments quantified and validated the influence of exogenous and endogenous factors on migrant movement and refueling. The model incorporates multiple factors to simulate the movement of virtual migrants on a raster map of forested habitats. As migrants move, they gain and lose energy, quantified by body mass, according to the foraging opportunities presented by different habitat types.

Derivation of model parameters from field experiments

Research relevant to this modeling effort is described briefly herein and details of these field studies are available in Cohen et al. (2012). The Red-eyed Vireo (*Vireo olivaceus*) was chosen as a model species because it is one of the most common long-distance migrants breeding in the deciduous forests of eastern North America (Cimprich et al. 2000). During 2007 and 2008, migrating Red-eyed Vireos that varied in energetic condition were captured, translocated to a new landscape, and released in one of three habitat types common throughout the region: upland longleaf pine (*Pinus palustris*) savanna (pine), bottomland hardwood forest (hardwood), and mixed forest composed of both pines and hardwoods (mixed; Fig. 1). This approach replicated the situation of limited information that migrants face upon arrival at each stopover site while controlling for arrival habitat type and energetic condition. The movements of migrants were followed continuously from the initiation of stopover using radiotelemetry. Movement was measured in relation to habitat type, energetic condition, and time of day, and habitat selection was also measured. Migrants could not be recaptured to measure mass change, but the distribution of food and foraging success rates in the available forested habitat types were measured. Migratory Red-eyed Vireos moved to select habitat types characterized by greater food resources and where foraging success was greater (hardwood > mixed > pine). Movement of Red-eyed Vireos was influenced by habitat and energetic condition. Migrants with lower body masses (i.e., without fat reserves), moved faster and farther than heavier vireos with fat reserves. Also, the farthest and fastest movements were on the morning of earlier stopover days. These movement and habitat selection patterns were then used to parameterize the individual-based model. The experiment was then repeated in 2009 at the same site and in 2011 at another site (see *Methods: Model validation*) to validate the movement and habitat selection components of the individual-based model.

Model description

The model simulates the movement and energy status of songbirds during stopover. Virtual migrants move and forage on a landscape represented by a grid map of square cells representing one of four habitat types (hardwood, pine, mixed forest, non-forest). A simulation follows one virtual migrant and records habitat associations, movement patterns, and changes in body mass, a measure of energetic status and fuel deposition rate (FDR [g/d]), for a 12-h stopover day. At the start of the simulation, the position of the virtual migrant is determined by randomly selecting a forested cell in the middle 50% of the habitat map. Migrants did not land in non-forested habitat types, which were either roads or open pasture in these landscapes, where forest-dwelling migrants are not known to land (reviewed in Chernetsov 2006). There are three parameters in the model, movement distance (specified dependent upon four factors), movement direction (stochastic but dependent

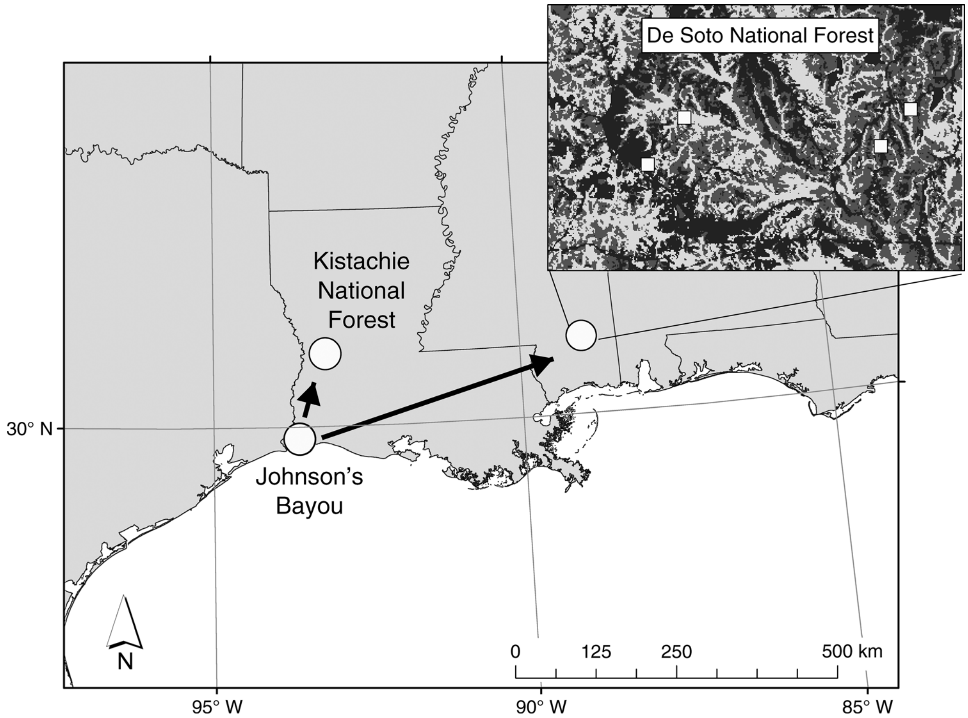

FIG. 1. Map of translocation (arrows) from point of capture of Red-eyed Vireo (*Vireo olivaceus*) on the coast at Johnson's Bayou (29°45′ N 93°30′ W) to release locations (circles) in Kisatchie National Forest, Louisiana, USA (30°57′ N 93°08′ W) for experiments to parameterize and validate the model and in De Soto National Forest, Mississippi, USA (30°55′ N 89°02′ W), to validate the model at another stopover site. The inset is a map of release locations (squares) in hardwood and pine habitat in De Soto National Forest.

on surrounding habitat types), and mass gain (specified dependent upon habitat type and distance moved).

The hourly movement distance of the virtual migrant is determined by the hour of the day, the day of stopover, the virtual migrant's updated body mass (energetic condition), and the habitat type occupied at the end of the previous hour. The number of cells virtual migrants cross each hour, dependent on these four factors, is specified in Table 1 (Cohen et al. 2012). The movement direction of the virtual migrants is determined by habitat preference of observed migrants (order of preference: hardwood > mixed > pine > non-forested; Cohen et al. 2012). In the field experiments, observed migrants moved directly toward high-quality habitats (with greater food abundance; see Cohen et al. 2012) within 50 m of their locations; a distance greater than a single cell (each cell is 28.5 m^2). Therefore, movement direction is determined by identifying the cells of highest habitat quality within the 24-cell window. This permits virtual migrants to assess the habitat quality of the eight adjacent cells and the next "ring" of 16 cells and cross adjacent cells of low quality in order to move toward high-quality cells just beyond. If the highest-quality cells are found among eight adjacent cells, then the virtual migrant moves into one of those cells. Otherwise, if the highest-quality cells are found in the 16 distal cells, then direction is determined by those cells. When two or more cells of equal quality are present, one of them is selected randomly. Virtual migrants cannot revisit cells, except when all surrounding cells had been visited. However, migrants are allowed to pass through an adjacent, previously visited cell to reach a distal cell that had not been previously visited. If the virtual migrant reached the edge of the habitat map or if movement was blocked by previously visited cells, the data from that individual was discarded.

Body mass is updated each hour based on the number of cells crossed and the habitat type of the last cell. Energetic condition is represented by body mass change due to foraging. We assumed a virtual migrant was either actively foraging or moving during the hours of the stopover simulation. The energetic costs of both foraging and flight between patches during stopover are likely negligible and both represent lost foraging time (Lindström 1991), so the "cost of movement" was implemented as a loss of foraging time. The mean time for observed migrants to move across cells when not foraging (E. B. Cohen, *unpublished data*) was subtracted from one hour to calculate a fraction of that hour available for foraging (crossing cells diagonally was adjusted for distance). Observed migrants show short periods of directed movement followed by a prolonged periods of foraging (E. B. Cohen, *unpublished data*). Therefore, we assumed that foraging occurred in the last

TABLE 1. Hourly movement distance (cells/h) of virtual Red-eyed Vireo (*Vireo olivaceus*) migrants as determined by the day of stopover, hours after sunrise, mass (g) class, and habitat type used in the simulations.

Day and hours after sunrise†	Hardwood 1	Hardwood 2	Hardwood 3	Mixed 1	Mixed 2	Mixed 3	Pine 1	Pine 2	Pine 3
Day 1									
0–2	6	4	5	8	5	5	12	6	5
2–6	2	2	2	3	3	3	4	4	4
6–8	1	1	1	1	1	1	2	2	2
8–12	1	1	1	1	1	1	1	1	1
Day 2									
0–12	3	3	3	2	2	2	3	3	3

Habitat type and mass class‡

† Sunrise occurs at 06:00 hours at the study site.
‡ Body mass classes are: 1 (<15 g), 2 (15–16.4 g), 3 (>16.4 g).

cell of the movement at each hour time step. Energetic gain is based on the habitat type of that cell and the fraction of the hour available for foraging. At the end of each hour, the virtual migrant's body mass was updated by adding body mass gained from foraging as follows:

$$\text{Body mass} = \text{current mass} + (\text{foraging time} \times \text{habitat-specific foraging gain}).$$

Body mass gain depended on habitat types. The field study revealed that food availability varied by habitat type as measured by the overall abundance of arthropods and foraging success rates of observed migrants (Cohen et al. 2012). Therefore, foraging gain rates (Table 2) were estimated from arthropod abundance by habitat type (from Cohen et al. 2012) and mass gain values from prior field studies of Red-eyed Vireos (Loria and Moore 1990; F. R. Moore, *unpublished data*). We set the maximum mass change (g/h) value for hardwood habitat from previously unpublished data of spring recaptures of migrating Red-eyed Vireos in this region ($n = 95$ from 1996 to 2008; F. R. Moore, *unpublished data*), used the mean arthropod abundance in each habitat type (from Cohen et al. 2012) as a scaling factor to determine the relative refueling benefit (g/h) of the mixed and pine habitat types, and verified that the mixed and pine values fell within the range observed in recapture data (Loria and Moore 1990; F. R. Moore, *unpublished data*). The foraging benefit of non-forest habitat was assumed to be zero. To verify the habitat-specific foraging gain values, we simulated virtual migrants, arriving with variable masses, for one 12-h stopover day and confirmed that the end of day mass was within the range observed for the species captured in the region during migration ($n = 1775$ from 1998 to 2006; F. R. Moore, *unpublished data*). Relative foraging success between habitat types (number of successful attacks per unit time spent foraging) supported these estimates (Cohen et al. 2012).

At the end of each simulation, the following data were recorded for virtual migrants: initial body mass, habitat type of starting location, movement rate, linear displacement from starting location, and FDR. Linear displacement was calculated as the linear distance between the centroids of the starting and ending map cells. FDR was calculated as change in body mass between the start and end of the simulation.

Model validation

Following the initial construction, the model was subjected to parameter calibration and validation. During calibration, the hourly linear displacement distances moved during simulations were iteratively compared to patterns of movements observed from the radio-tracking data. Simulations used maps of the landscape where the observed migrants were released. We adjusted the number of cells crossed at each hourly step to minimize differences between observed (from 2007 and 2008, $n = 50$ migrants) and simulated movement values for each stopover day, time of day, mass category, and land cover class. The observed patterns of habitat selection followed Cohen et al. (2012).

Once the differences between the model and observed migrant behavior had been minimized, we validated the model with field data not used in model construction. During the spring of 2009, we tracked six migrants released at one of the hardwood locations in Kisatchie National Forest. We tested for differences in the hourly linear displacement distances (during the first five hours of the first stopover day) between the observed and simulated stopover movements ($n = 60$) initiated from the same release location in hardwood habitat with a mixed-effects model including the hour of the day and the release mass as covariates.

Finally, we assessed the applicability of the constructed model to the broader region by validating it at a distant site in the same region with another year of field experiments. During the spring of 2011, we validated the

TABLE 2. Habitat-specific mass change values (g/h) of virtual migrants used in the simulations.

	Habitat type			
Parameter set†	Hardwood	Mixed	Pine	Non-forest
Estimated	0.18	0.09	0.02	0.00
Doubled	0.36	0.20	0.04	0.00
Halved	0.09	0.05	0.01	0.00
Half difference	0.14	0.10	0.06	0.00
No difference	0.10	0.10	0.10	0.00

† Estimated parameter set was used for most simulations. Remaining parameter sets were used for the sensitivity analysis.

model in De Soto National Forest, Mississippi, USA (30°55′ N, 89°02′ W; Fig. 1), which is over 400 km from Kisatchie National Forest, Louisiana, but is similar in latitude and contains the same habitat types characteristic of the region. We released migrating Red-eyed Vireos with a range of body masses into two replicates of pine ($n = 5$) and hardwood ($n = 5$) habitat (Fig. 1) and followed them continuously for one day from dawn to dusk following the same methodology as in Cohen et al. (2012). We used a mixed-effects model to validate that migrants tracked in De Soto National forest were influenced by the hour of the day, release habitat type (pine vs. hardwood), and release mass as were the migrants observed in Kisatchie National Forest. We then compared model simulations, initiated from the same four map locations as the release locations ($n = 89$), to the movements of migrants ($n = 10$) during the first 10 hours of the first day of stopover. We tested for differences in hourly linear displacement between tracked and simulated migrants with a mixed-effects model including the hour of the day, the release habitat type, the release body mass, and the interaction between the release type (observed, simulated) and the release habitat type as covariates. It is a limitation of this study that we could not validate our results with respect to FDR. We attempted to recapture migrants in the field but were not successful. Also, we did not validate movement for migrants arriving in mixed habitat.

Analyses were conducted in R 2.12.2 (R Development Core Team 2010). Means ± SD are reported unless stated otherwise. For all mixed-effects models, we included the individual as a random effect to account for repeated hourly measures for individuals and used lmer function in R package lme4 (Zuur et al. 2009, R Development Core Team 2010, Bates 2012). We used a Markov chain Monte Carlo (MCMC) approach to compute P values and 95% highest posterior density credible intervals (HPD) for fixed effects on the basis of a MCMC sample with 10 000 simulations (pvals.fnc function in R package languageR; Baayen 2011). The degree of freedom used for the t distribution by the MCMC simulations is an upper bound: the number of observations minus the number of mixed-effects parameters (Baayen 2011).

Sensitivity analysis

We conducted a sensitivity analysis to better understand the relative influence of the habitat-specific foraging and movement parameters. Stopover performance was measured by FDR (body mass change per day), and we measured the relative change in FDR when foraging gain values and movement parameters were altered. Four sets of foraging gain values were used (Table 2). Two sets of values were created by doubling and halving foraging gains relative to original values for all habitat types as estimated from the field data. Two additional sets were altered to explore the effect of habitat-specific differences in foraging gain. The first set (half difference) reduced the variation in gain rates among the forested habitat types while keeping the average across habitats similar to the original values. The last set (no difference) eliminated habitat specific differences by using the same gain rate for all habitats. Three sets of movement parameters were used in the sensitivity analysis. In addition to the original movement rates based on body mass, day, time, and habitat (Table 1), two other parameter sets were created. In the first set, all values were set to the minimum (1 cell/h). In the second set, all values were set to the mean of the original (3 cells/h). Simulations in the sensitivity analysis were conducted using the habitat map for the De Soto National Forest study area using a full array of arrival body masses (12.5–23 g, intervals of 0.5 g), random arrival locations, the gain parameter sets in Table 2, and the movement parameter sets described in the preceding sentences. Twenty-five replicate migrants were simulated for each combination of body masses (22), gain values (6), and movement parameter sets (3). Therefore, 1650 simulations were compared for each of the three sets. Mean and variance of FDR for each combination were calculated and compared graphically.

Using the model to predict FDR under different scenarios of land cover

We applied the model to explore the effects on FDR of changing patterns of stopover habitat. A series of maps were created to alter the abundance of hardwood forest and spatial aggregation of habitat types (contagion). Contagion is a measure of the extent to which cells of similar class are aggregated, so a landscape with

TABLE 3. Spatial metrics for maps used in the factorial experiment.

Hardwood (%)†	Contagion	LPI‡	Edge density (m/ha)	Patch area (ha)§		
				Mean	SD	CV
41	low	17	157	3	56	1619
41	medium	23	68	11	126	1198
41	high	23	35	31	230	751
22	low	16	119	6	69	1239
22	medium	35	62	12	181	1546
22	high	36	48	19	235	1252
12	low	47	85	9	206	2333
12	medium	53	51	15	303	2015
12	high	54	41	22	376	1709

Notes: Maps consisted of three forested cover types: hardwood, mixed, and pine. The maps varied in the amount of hardwood forest and level of contagion (spatial aggregation of habitat types).

† Percentage of area covering map.

‡ Largest patch index (LPI) = (area of largest patch)/(area of total landscape).

§ Area of all patches regardless of forest cover type.

high contagion contains large "contagious" distributions of forest types (McGarigal et al. 2012). We did so by altering one raster map, a portion of De Soto National Forest, to create nine maps (Table 3, Fig. 2). That landscape contained only the three habitat types: pine (30%), mixed (31%), and hardwood habitat (41%) and was naturally low in contagion. Starting with the De Soto map, we reduced the amount of hardwood to

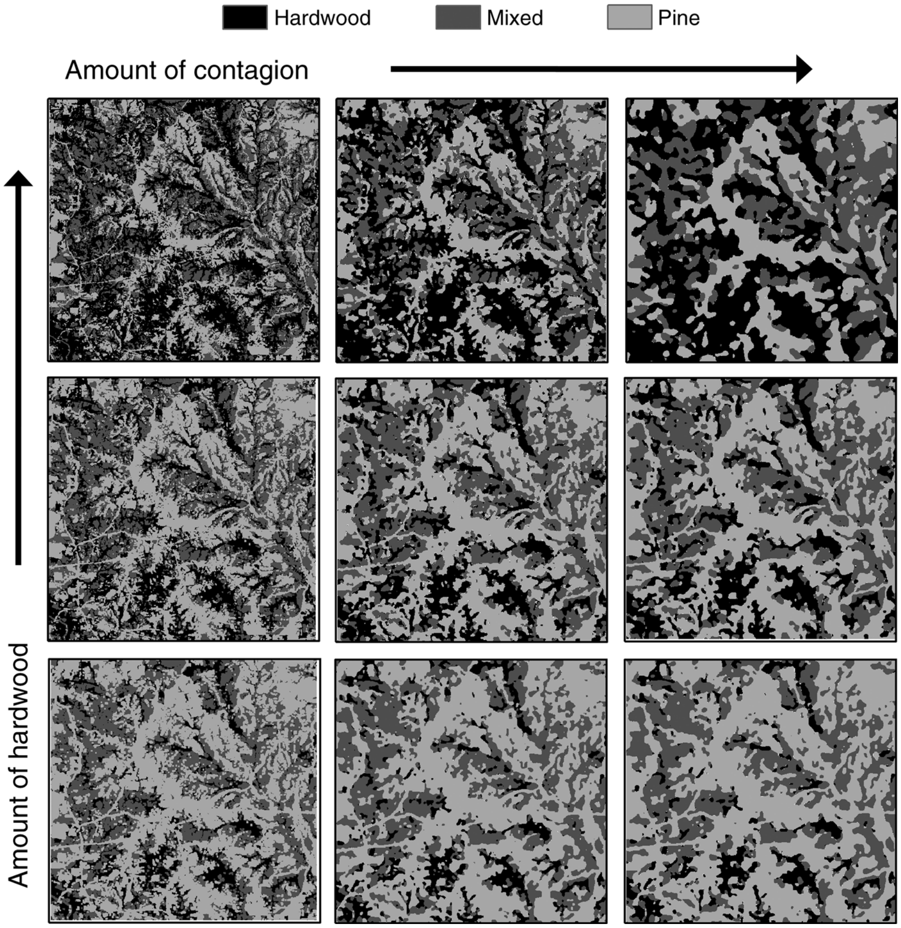

FIG. 2. Maps with low, medium, and high contagion (level of spatial aggregation of habitat; left to right column) and high (41%), medium (22%), and low (12%) amount of hardwood forest cover (top to bottom row). The map in the top left corner (low contagion, high hardwood forest cover) depicts a portion of De Soto National Forest. Further explanation of how these were generated is given in *Methods: Using the model to predict FDR under different scenarios of land cover*.

create three levels of hardwood abundance (41%, 22%, and 12%). While decreasing hardwood habitat, we attempted to hold the amount of mixed habitat constant across the three maps and increase the amount of the poorest-quality habitat, pine. The three hardwood abundance maps were each altered to create two additional maps with increasing spatial aggregation of habitat, as measured by contagion (low, medium, and high; Fig. 2). We altered the original landscape using focal statistics tools in ArcMap (v. 9.3; ESRI 2009) and calculated landscape metrics in Fragstats (version 4.1; McGarigal et al. 2012). For each map, we measured the percentage of the map area that is hardwood, the contagion (a measure of spatial aggregation based on the probabilities of finding a cell of each type next to a cell of each other type), the largest patch index (area of largest patch/area of total landscape), the edge density (the sum of the lengths of all edge segments in the landscape, divided by the total landscape area), and the mean patch area of all patches regardless of forest cover type.

We used a factorial experiment to test for effects of the amount of hardwood forest cover and contagion on FDR of virtual migrants. We also tested for the effects of arrival habitat type and arrival energetic condition on migrant FDR. We simulated 60 migrants landing in each of the nine maps and stopping over for one 12-h day. The simulated migrants arrived in each landscape at random locations with the range of masses observed for the species (12–23 g). ANOVA and post hoc Tukey's HSD were used to test for differences in mass change for each variable (amount of hardwood, level of contagion, and arrival habitat type) and an interaction between contagion and amount of hardwood. We tested the influence of the same set of variables on movement patterns (linear displacement distance [m/h]) with an ANOVA and post hoc Tukey's HSD.

RESULTS

Model validation

The movement distances were not different between the simulated and observed migrants. The hourly linear displacement distances of migrants tracked and released in Kisatchie National Forest (not used in model construction) did not differ from the displacement distances of simulations from the same location (estimate = –1.35, SE = 9.94, t = –0.14, P = 0.89; n = 6 observed and 60 simulated migrants; 103 ± 117, 102 ± 51 m/h linear displacement during the first five hours of stopover for observed and simulated migrants, respectively). As observed in Cohen et al. (2012), the majority of migrants released in hardwood (5/6) remained in hardwood habitat.

The hour of the day, release habitat type (pine vs. hardwood), and release mass influenced the movement of observed migrants in De Soto National Forest, replicating the pattern of behaviors observed in Kisatchie National Forest (see Cohen et al. 2012). Hourly linear displacement was greater initially, and then declined throughout the day (estimate = –22.32, SE = 4.65, t = –4.80, $P < 0.0001$, n = 10 observed migrants; 264 ± 157, 294 ± 310, 128 ± 105, 97 ± 86, 46 ± 27 m/h during the first, second, third, fourth, and fifth hour of the day, respectively), and migrants released in pine habitat initially moved farther than those released in hardwood (390 ± 79, 389 ± 412, 173 ± 132, 117 ± 112, 46 ± 25 m/h during the first, second, third, fourth, and fifth hour of the day for those released in pine, respectively, and 138 ± 96, 200 ± 157, 83 ± 45, 76 ± 55, 47 ± 31 m/h during the first, second, third, fourth, and fifth hour of the day for those released in hardwood, respectively) but did not move significantly differently throughout the full stopover day (estimate = –78.66, SE = 40.93, t = –1.92, P = 0.05, n = 5 migrants observed in pine and 5 observed in hardwood; 161 ± 201 and 86 ± 87 m/h throughout the day for migrants released in pine and hardwood, respectively). Arrival energetic condition influenced linear displacement in similar ways; migrants in poorer energetic condition initially moved farther from their release sites than migrants in better condition (206 ± 236 and 132 ± 123 m/h during the first five hours of the day for migrants $\leq$15 g and migrants >15 g, respectively), but did not move significantly differently for the duration of the stopover day (estimate = –31.48, SE = 16.57, t = –1.90, P = 0.06, n = 10 observed migrants; 157 ± 190 and 87 ± 103 m/h throughout the day for migrants $\leq$15 g and migrants >15 g, respectively). Further, the majority of observed migrants released in pine habitat in De Soto National Forest also moved into hardwood habitat by the end of the day (4/5).

We found correspondence in behavior between simulations from the model and migrants translocated and tracked in De Soto National Forest (see example in Fig. 3). The linear displacement distance of simulated migrants was not different from the movement pattern of observed migrants released at the same locations in De Soto National Forest (estimate = 22.31, SE = 13.27, t = 1.68, P = 0.09, n = 10 observed and 89 simulated migrants; 109 ± 113 m/h, 82 ± 46 m/h linear displacement on the first day of stopover for observed and simulated migrants, respectively). However, there was also a significant interaction between the release type (simulated vs. observed) and release habitat type (pine vs. hardwood) (estimate = –26.23, SE = 6.08, t = –4.31, $P < 0.0001$, n = 10 observed and 89 simulated migrants). There was no difference in movement between simulated and observed migrants released in pine (estimate = –9.09, SE = 17.58, t = –0.52, P = 0.61, n = 5 observed and 39 simulated migrants). There was a difference between simulated and observed migrants released in hardwood (estimate = –283.13, SE = 18.24, t = –15.52, $P < 0.001$, n = 5 observed and 44 simulated migrants) in that the observed moved farther than the simulated migrants. However, overall we found strong

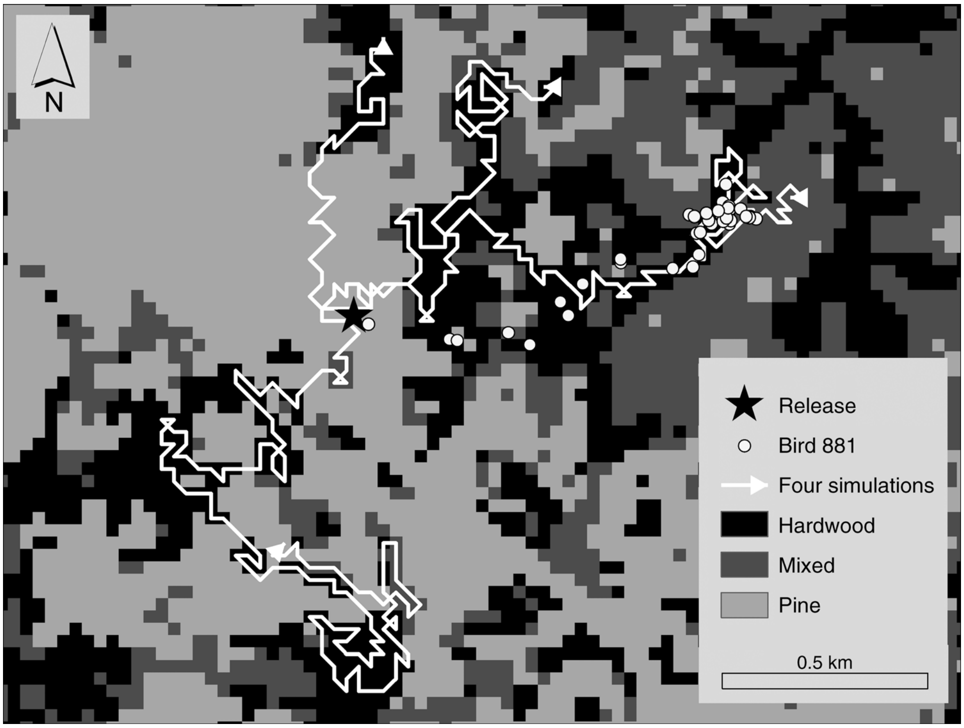

FIG. 3. Example of four simulated movements (white lines, each ending in an arrow) and bird tracking points (circles) from the same release location (star) that were compared during the model validation process by a specific single bird (number 881).

concordance between the observed and simulated migrants in the pattern of movement in relation to the time of day, release habitat, and release condition, as well as the actual hourly distances moved, suggesting that the constructed model reflects the behavior of migrants across the region.

Sensitivity analysis

The sensitivity analysis revealed the relative importance of the habitat specific foraging gain and movement rates employed in this model. Doubling and halving gain values resulted in a roughly proportional change in the mass gain (Gain set A in Fig. 4). Reducing the habitat-

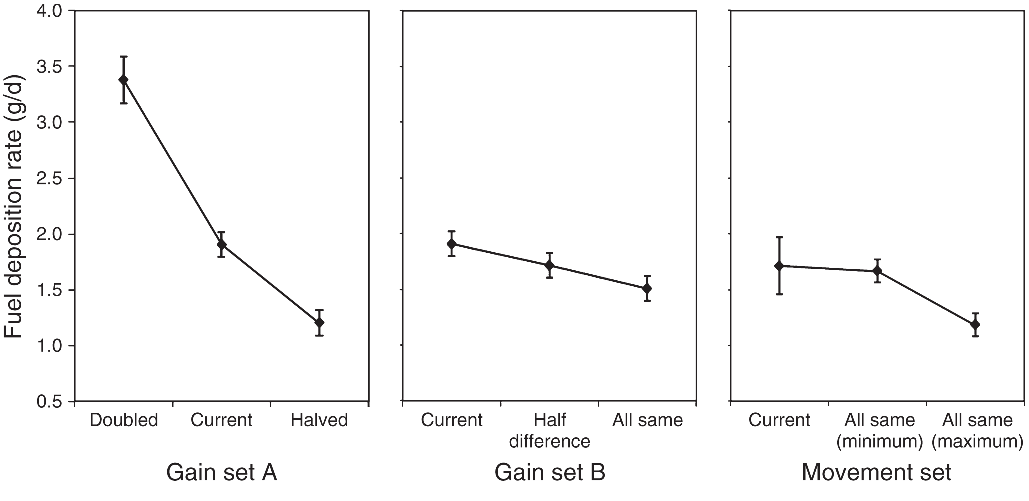

FIG. 4. Sensitivity of fuel deposition rates (FDR) to variation in foraging and movement parameters. Graphs show change in FDR (FDR = body mass gain [g/d]) when habitat-specific gain and movement rates are altered. Error bars show 95% confidence intervals. In Gain set A, FDR values for each habitat were doubled (2×) and halved (0.5×) with respect to values used in simulations. In Gain set B, habitat-specific variability in FDR was reduced. In this set, the difference between the habitat-specific FDR values was reduced by half, and all habitats were set to be equal. In the movement set, variation in time and habitat-specific movement distances were altered by setting all distances to the minimum value and alternatively the maximum movement distance.

specific variability in gain value reduced the mass change of simulated migrants, but the effects of this reduction were relatively minor (Gain set B in Fig. 4). With respect to movement, setting movement values to the minimum values resulted in a similar biomass gain rate as for the original values except that variation among simulations was somewhat reduced. Setting movement values to the maximum significantly reduced the daily gain rate (Movement set in Fig. 4). Overall, the sensitivity analysis revealed that the magnitude of the gain values was more important in determining FDRs than habitat- and time-specific variation in foraging gain rates and movement rates.

Simulation experiment: landscape pattern and migrant refueling rates

FDR was positively influenced by the amount of hardwood forest cover ($F = 34.76$, df = 2, 529, $P < 0.001$; high 1.61 ± 0.38 g/h, medium 1.51 ± 0.46 g/h, low 1.25 ± 0.57 g/h; Fig. 5a). The amount of habitat contagion also influenced FDR ($F = 13.55$, df = 2, 529, $P < 0.001$; Fig. 5b), but not in the direction that we expected. FDR was higher in the landscape with low contagion, or little spatial aggregation of habitat (1.57 ± 0.40 g/h), than in the landscape with high contagion (1.34 ± 0.55 g/h, $P < 0.01$), but was not different between landscapes with medium contagion (1.47 ± 0.51 g/h, $P = 0.34$). There was no significant interaction between the amount of hardwood and level of contagion ($F = 0.90$, df = 4, 529, $P = 0.46$). Not unexpectedly, FDR was also influenced by the arrival habitat type ($F = 43.45$, df = 2, 529, $P < 0.001$). Migrants initially landing in pine habitat had lower FDR (1.77 ± 0.12 g/h) than those arriving in the higher-quality hardwood habitat (1.22 ± 0.59 g/h, $P = 0.02$), but not than those arriving in the mixed (1.53 ± 0.38 g/h, $P = 0.93$). Movement was not influenced by the amount of hardwood forest cover ($F = 0.76$, df = 2, 529, $P = 0.47$; Fig. 5c) or the level of contagion ($F = 0.94$, df = 2, 529, $P = 0.39$; Fig. 5d), and there was no significant interaction between them ($F = 1.19$, df = 2, 529, $P = 0.31$). Migrants that landed in poorer-quality pine habitat also moved farther than migrants that landed in the other two habitat types ($F = 5.53$, df = 2, 529, $P < 0.01$: hardwood, 272.64 ± 143.87 m; mixed, 273.10 ± 135.30 m; pine, 315.19 ± 137.88 m).

DISCUSSION

The composition and configuration of landscapes influenced the fuel deposition rates of a migrant songbird species across the Gulf South region, a critical gateway for long-distance songbird migrants in eastern North America. Our findings provide empirical evidence for the argument that hardwood forest cover is a primary determinant of the quality of a stopover site in this region (Mehlman et al. 2005, Buler and Moore 2011). In our simulations, the amount of hardwood forest at a stopover site positively influenced FDRs. While density may not always reflect quality (Van Horne 1983), Buler at al. (2007) found the strongest predictor of migrant density across southern Mississippi and Louisiana to be abundance of hardwood habitat in a landscape, which was also positively correlated with arthropod abundance. Further, fuel deposition rates of two Palearctic-African songbird migrants, Willow Warbler (*Phylloscopus trochilus*) and Eurasian Redstart (*Phoenicurus phoenicurus*) recaptured at netting stations were correlated with the amount of forest cover (Ktitorov et al. 2008). Our results represent the first support for the importance of the amount of hardwood on FDR when considering movement and foraging, which incorporate the possibility of locating and exploiting hardwood patches.

The negative effects of habitat fragmentation (reduced contagion) have been well studied for birds on breeding grounds (see reviews in Andrén 1994, Stephens et al. 2004), and fragmentation effects are greatest when the amount of suitable habitat covers <30% of the landscape (Andrén 1994). In contrast, we found fine-scale fragmentation (i.e., low contagion) may be beneficial during stopover in landscapes with low levels of high-quality habitat. Considering all levels of hardwood abundance in our simulations, FDR was higher in the landscape that was more fragmented (i.e., lower contagion; Fig. 5b). In landscapes with little high-quality hardwood habitat, quickly locating habitat with sufficient food resources may be the most important factor determining a successful migration because migrants arriving in landscapes where hardwood habitat is interspersed with other habitat types are more likely to encounter hardwood habitat quickly and benefit from the increased foraging success in that habitat type (Simons et al. 2000). Therefore, FDR may be strongly influenced by the initial cost of searching for high-quality habitat after arrival.

Evidence of searching costs is mixed (reviewed in Schwilch and Jenni 2001). It comes primarily from banding data, where an observed mass loss after initial capture may be due either to a searching cost or to handling effects (Schwilch and Jenni 2001, Chernetsov 2006). In our field studies (Cohen et al. 2012), we found no evidence for an acclimation period between release and initiation of foraging; migrants began foraging almost immediately upon release in the hardwood habitat with abundant food. Delingat et al. (2006) also observed foraging soon after moving and releasing Northern Wheatears (*Oenanthe oenanthe*). If prey is scarce, energetic costs associated with an increased searching period prior to foraging would be expected. If extensive searching for profitable habitats is necessary at each stop along a migrants' journey, these costs would affect the refueling rate or duration of stay at each stopover (Alerstam and Lindström 1990, Alerstam and Hedenström 1998) and would cumulatively result in a significant energetic or time cost to migration (Lindström 1991).

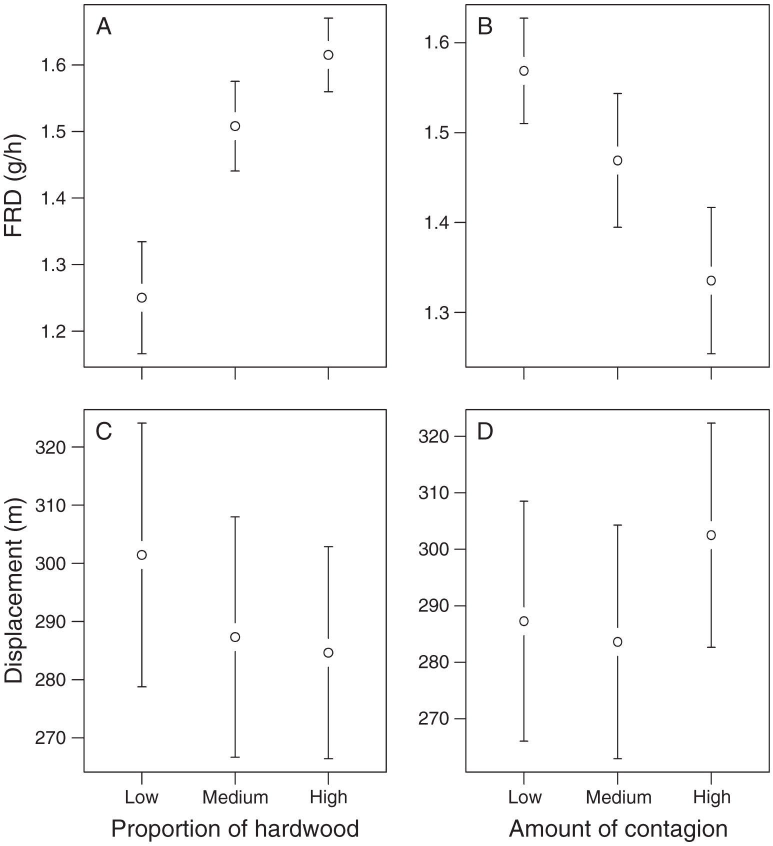

Fig. 5. FDR (body mass gain [g/h]) and linear movement distance (m/h) after one day in landscapes with a low, medium, or high proportion of hardwood habitat and three levels of the degree of spatial aggregation of habitat: low, medium, or high ($n = 180$ simulations/factor). Error bars show 95% confidence intervals.

Landscape change has the potential to interfere with successful migration. Landscapes across eastern North America are undergoing rapid changes, and these changes are only likely to increase, especially near coastlines (Crossett et al. 2004, Drummond and Loveland 2010; see Buler and Moore 2011). Our sensitivity analysis suggests that the foraging gain value of habitat types has the greatest influence on FDR. In highly deforested landscapes, high densities of migrants might deplete food resources with small forest patches (Moore and Wang 1991, Kelly et al. 2002), but our model did not incorporate such an effect. The behavioral rules in this model may have concentrated migrants in hardwood cells because movement distance and foraging gain were not affected by cells visited during the hour. Therefore, virtual migrants were less likely to forage in lower-quality patches, which may explain why FDRs were not directly proportional to the scaling of foraging gains in the sensitivity analysis. While this movement rule resulted in simulated paths similar to those observed, it may have effectively increased patch separation in the highly aggregated landscapes. These results illustrate the need for further work on density effects during stopover in increasingly smaller habitat patches of forest types (e.g., declining food and/or increasing predation).

There is every reason to expect that the behaviors observed in the Red-eyed Vireo may be generalized to other migratory songbird species breeding in the forests of Eastern North America, but the extent to which this model is generalizable to other species also requires more work. The Red-eyed Vireo is similar in many fundamental ways to other intercontinental migratory songbirds. For example, Red-eyed Vireos are similar to other nocturnal migrants in that they adjust their foraging behavior in response to energetic state (Loria and Moore 1990, Wang and Moore 2005) and continue migration when they have sufficient fuel stores (Sandberg and Moore 1996). Future work applying this model to other species and to estimate FDR as a continuous function over a broader range of landscape scenarios would allow assessments of the relative impacts of specific landscape changes undergoing in this region.

Migration is a critical phase in the life cycle of migratory passerine birds, but much of the research on how these populations are regulated continues to focus primarily on events associated with the stationary phases of the migrant's annual cycle (e.g., Terborgh 1989, Sherry and Holmes 1995, Newton 2006). Arriving on time and in good condition to breeding areas requires successfully refueling at spring stopover sites. Therefore, how well a migrant quickly and safely refuels at stopovers will likely influence their subsequent reproductive success (e.g., Smith and Moore 2003, Moore et al. 2005, Newton 2006). Even infrequent encounters with high-quality sites could be crucial to enhancing fuel deposition, and thereby, migration speed (McLaren et al. 2013). Meanwhile, rapid changes to landscapes and climate due to unprecedented human activity may be inflating the risks associated with migration (Wilcove and Wikelski 2008). En route, migrants may encounter wind turbines, tall structures, light pollution, and nonnative predators. Furthermore, the conditions of long-distance spring migrants arriving at stopover sites are likely to be influenced by conditions in their overwintering areas in the neotropics (Wolfe and Ralph 2009). Many of these landscapes are rapidly being converted to agricultural land uses (Houghton 1994, Foley et al. 2005), thereby increasing the likelihood that migrants will arrive at stopover sites in increasingly poorer condition.

Incorporating the migratory period into comprehensive conservation strategies requires identifying and protecting important stopover sites (Moore et al. 1995, 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 composition and configuration, translate into the refueling value of stopping over at a site. Predicting the effects of changes in land use requires understanding how migrants move through landscapes, how they select and use habitats, and the energetic consequences of those behaviors (Knowlton and Graham 2010). 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 and the fitness consequences of those decisions. 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. 1995) in a rapidly changing world where many migratory species are currently in decline (Wilcove and Wikelski 2008).

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