APPLICATION OF SPATIAL MODELS TO THE STOPOVER ECOLOGY OF TRANS-GULF MIGRANTS

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Abstract. Studies at migratory stopover sites along the northern coast of the Gulf of Mexico are providing an understanding of how weather, habitat, and energetic factors combine to shape the stopover ecology of trans-Gulf migrants. We are coupling this understanding with analyses of landscape-level patterns of habitat availability by using spatially explicit models to simulate avian movements through stopover habitats. The probability that an individual migrant will complete a migration successfully is determined by the bird's energetic status and flight morphology, and the quality, quantity, and spatial pattern of habitats encountered during migration. The models evaluate habitat patches according to their distance from the coast, isolation from other patches of suitable habitat, and habitat quality. Evaluation procedures have been developed from available data on the arrival condition of migrants, energetic and morphological constraints on movement, and species-specific habitat preferences. Window analysis and individual-based modeling are used to demonstrate how the abundance, quality, and spatial pattern of habitats interact with the arrival energetic state of migrants to determine the suitability of migratory stopover habitats along the northern Gulf coast. Our goal is to understand how landscape-scale patterns of habitat conversion may be affecting populations of trans-Gulf migrants.

Key Words: birds, landscape pattern, migration, spatial models, stopover ecology.

Ecologists are beginning to appreciate how the spatial and temporal scale of the data they collect influence their understanding of natural patterns and processes (Wiens 1981, 1989; Edwards et al. 1994, Pearson et al. 1996). As May (1994) has recently pointed out "the answers to ecological questions-and ultimately the understanding of ecological systems-depend on whether or not the system is studied at an appropriate scale," noting an "increasing need for ecologists in general, and conservation biologists in particular, to deal with larger spatial scales than most of us are used to, or happy with."

Recent declines in populations of nearctic-neotropical [4] landbird migrants (Robbins et al. 1989b, Askins 1990) have prompted a wave of new research into the factors affecting populations of these birds on their breeding and wintering grounds (Hagan and Johnson 1992, Finch and Stangel 1993) and a smaller number of studies on the factors affecting birds during migration (Moore and Simons 1992a, Watts and Mabey 1993, Moore et al. 1995). Designing conservation-oriented studies of the stopover ecology of migrants is complicated by the fact that migration occurs over a broad geographic scale, but over a relatively short temporal scale.

Remote sensing technology and spatial modeling techniques are providing new research tools for investigating how the distribution and abundance of habitats may be affecting wildlife populations. Our objective is to use these tools to understand how variation in the landscape-level pattern of habitats affects migrant birds. We will use spatially explicit models to explore the effects of changing landscape patterns on the probability of a successful migration. These models, while simplistic, incorporate some basic bird biology and analyze landscape-level variation in habitats from the perspective of migrants with different energetic states. We hope that the results of this analysis will be useful in setting priorities for future research and conservation.

The conceptual framework for developing our spatial models is straightforward (Fig. 1). Spring migrants make landfall in landscapes containing habitats that vary in suitability for foraging. The abundance and spatial pattern of high-quality habitat in these landscapes will likely affect the probability of a successful migration. We know that arriving migrants vary in their energetic condition-some are lean, while some have considerable fat stores remaining. As long as favorable habitat is readily available, both fat and lean birds eventually find suitable habitat. But as suitable habitat is lost and accessibility declines, a fat-depleted migrant's ability to find good habitat may be limited because the benefits of rejecting suboptimal habitat may be outweighed by the cost of finding better sites. Ultimately, the interplay of a migrant's energetic state and the abundance and spatial configuration of stopover habitats, will determine the likelihood of a successful migration.

METHODS

Landscape-level metrics provide a means to quantify the abundance and spatial pattern of habitat types in study landscapes (Turner and Gardner 1991). The most straight-forward measure is the area of suitable habitat types. Habitat connectivity or fragmentation can also be measured using indices of spatial pattern. Examples of such indices include contagion (the probability that
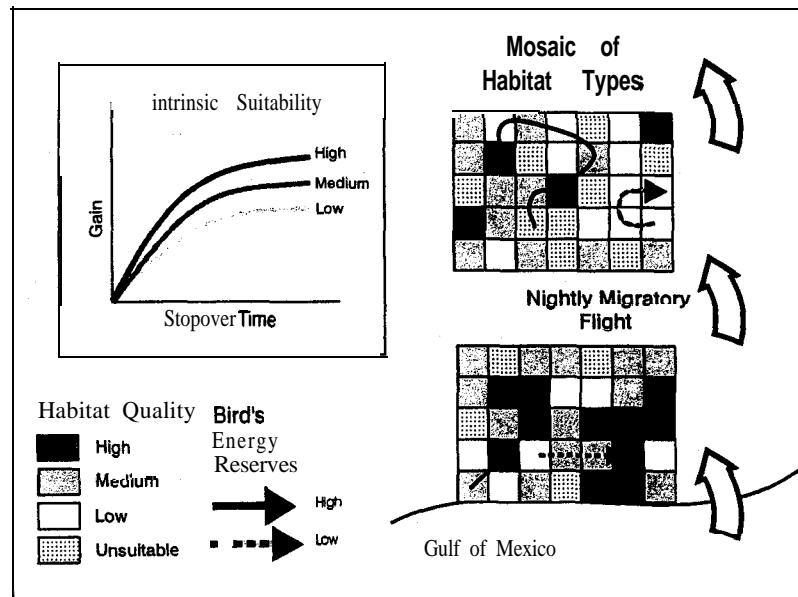
FIGURE 1. Conceptual spatial model. Migrants arrive along the northern Gulf coast with different amounts of stored fat, and they encounter habitats of varying intrinsic suitability. When high quality stopover habitat is available (lower matrix) birds with both high and low energy reserves find suitable stopover habitat. As suitable habitat is lost (upper matrix) birds begin to use sub-optimal stopover sites, which may reduce the probability of a successful migration, especially for birds with low energy reserves.

two adjacent cells are of the same habitat type), the number and size of patches of each habitat type, and the area of the largest patch divided by the total area of all patches of that habitat type. This final index provides a measure of fragmentation that varies over the interval [0,1] where 0 = highly fragmented and 1 = a homogeneous landscape. These metrics provide a means to quantitatively compare landscapes. The models described below provide measures of landscape conditións from the perspective of migrant birds. These models include (1) a window analysis that assesses the landscape in the vicinity of a bird making landfall, and (2) an individual-based model that simulates the energetic state of birds foraging in habitats of varying quality.

MODEL INPUT PARAMETERS

The parameters in our models included energetic, flight performance, and habitat variables. The energetic status of spring migrants was measured between 1987-1994 using mist nets to sample birds at stopover sites along the northern Gulf coast (Moore et al. 1990, Kuenzi et al. 1991, Moore and Simons 1992a). Birds were weighed on electroñic scales to the nearest 0.05 gram, banded, and released. Fat reserves were estimated by visual inspection of all birds, which were ranked on an ordinal scale from zero to five according to the method described by Helms and Drury (1960).

Measurements of birds' energy reserves and win8 spans were used to calculate flight range estimates, using the flight performance equations developed by Pennycuick (1989).

Habitat data were derived from a supervised classification of two 1990 Landsat Thematic Mapper scenes of the northern Gulf coast produced by the National Biological Service Southern Science Center in Lafayette, LA. This map was comprised of 18 original cover types in raster format, with a cell size of 28.5 m X 28.5 m. The 18 original cover types were aggregated to produce four habitat types that were then used in all spatial analyses (see RESULTS).

The habitat associations of birds were determined through a combination of IO-min point counts (N = 500 points) at barrier island sites (Moore et al. 1990) and l-km strip transects (Emlen 1977) at mainland sites (N = 117 transects from 9 paired sites, see Table 2 for sampling design; Moore and Simons 1992b). Census results were then used to assign each of the original 18 habitat types to one of four habitat categories that ranged from low (category 1) to high (category 4) suitability as migratory bird stopover habitat. These four habitat categories were used in all subsequent analyses. This ranking of habitat quality assumes that the relative abundance of migrants in stopover habitats reflects relative habitat quality although this assumption was not tested empirically.

SPATIAL ANALYSES

We used spatial analyses to examine how the abundance and spatial configuration of habitats might affect the suitability of stopover habitat for spring migrants. We did this using a window analysis technique and through the application of an individual-based model to our field data and habitat map.

Window analysis

In the window analysis, a hypothetical individual bird was randomly located in a block of arrival habitat.

A window was then projected from the arrival location, with the size of the window reflecting the individual bird's energetic state. This window represented the area that could be searched and sampled by a bird, given its energetic condition on arrival (i.e., the greater the bird's energy stores, the larger the window). Habitat measures, such as mean habitat rank, were calculated from all of the cells within a window. The window's pie-piece-like shape reflected a migrant's tendency to move northward during spring migration (Gauthreaux 1991). The window analysis allowed us to quantify the range of foraging conditions experienced by arriving birds, and the probability that a single bird would land in an area of specified quality (e.g., very rich, moderate, or poor quality).

Individual-based model

A second approach involved the development of an individual-based model. This method allowed us to begin to examine the relative importance of and the interaction between the energetic state of arriving birds and the spatial pattern of habitat within a landscape. It is impossible to precisely model the details of the behavior and energy dynamics of birds during stopover because of our lack of data and knowledge about these organisms. However, this model incorporates the most basic components of the biology of a migrant: (a) variation in habitat quality, and (b) changes in its energetic state due to foraging.

Our model used an Energy State Index (ESI) to indicate the relative energetic state of birds during migratory stopover. After landing in a random location within 10 km of the Gulf of Mexico, the "virtual" birds moved from cell to cell across the habitat map selecting the adjacent cell with the highest habitat value at each iteration of the model. After visiting each cell, the ESI of a bird was incremented to account for the amount of energy gained (due to foraging) and lost (due to energetic costs of foraging and movement) while occupying that cell.

Foraging costs were held constant for all habitat types, but the foraging gain accrued by birds as they moved across the landscape was determined by the habitat type of the cells the birds encountered. A bird's ESI was updated as it moved from habitat cell to habitat cell in the simulations. In productive habitats, migrants experienced a net energy gain (ESI gain > ESI cost). In poor habitats, migrants experienced a net energy loss (ESI gain < ESI cost). Foraging gains reflected our estimate of habitat quality based on field observations of the relative abundance of birds in these habitats. Four habitat categories were created from the original habitat types. Foraging gains equaled 0.1 in category 1 (poor) habitats, 0.25 in category 2 habitats, 0.8 in category 3 habitats, and 1.0 in category 4 (rich) habitats. Foraging costs were fixed at 0.5. The pattern of movement from cell to cell was determined by variation in habitat quality in adjacent cells. The model also incorporated a northward bias in movement to reflect the tendency for birds to orient northward during spring migration (Gauthreaux 1991). Birds moved from the current cell to one of the adjacent cell by choosing the cell with the highest value of the following expression: NBIAS*GAIN. NBIAS is a coefficient (range o-1.00) representing the northward bias.

NBIAS has the following values: 1.00 for the cell directly north (N) of the current cell, 0.75 for cells to the NW and NE, 0.50 for cells to W and E, 0.25 for cells to SW and SE, and 0.10 for the cell directly south (S). GAIN is the habitat-dependent foraging gain listed in the previous paragraph. Birds were not allowed to return to previously visited cells. In the individual-based model, a virtual bird began with an ESI of 10.0 and continued moving until it crossed one of two energy thresholds. If it gained enough energy (ESI ≥ 30.0). it left the study landscape on another long-range migratory movement. If its ESI dropped low enough (ESI < 2.0) because it failed to find productive habitats and lost energy, it ran out of energy and died. When an individual either migrated or died, the number of cells visited was recorded. In this way, the relative suitability of different landscapes could be examined by simulating a large number of individuals and keeping track of mortality and the number of cells visited before migration. Higher quality landscapes were characterized by low mortality and a lower numbers of cells visited by successful migrants.

RESULTS

ENERGETIC PARAMETERS

Table 1 summarizes spring data on arrival weight and condition collected from 1987-1992 on Horn Island and East Ship Island, Mississippi, for 14 common trans-Gulf migrants. The mean mass of "0" fat-class birds is close to the fat-free weights obtained in the laboratory (Dunning 1993). The span of annual mean weights measured in the field ranged from approximately fat-free levels, to weights indicating fat stores of about 10% body weight. These data provide reasonable estimates of the variability of energy stores to be expected among spring migrants arriving along the northern coast of the Gulf of Mexico following trans-Gulf migration.

FLIGHT PERFORMANCE PARAMETERS

Applying these fat store estimates to the flight performance models developed by Pennycuick (1989) provides an estimate of the potential flight ranges of migrants after their arrival at coastal stopover sites (Table 1). Minimum range estimates, based on the range of mean annual arrival weights, indicate that in some years many birds are incapable of further migratory movement (flight ranges of tens of kilometers). Average arrival weights for the period 1987-1992 suggest ranges of tens to several hundred km for most species, while under the best of conditions ranges can exceeded 500 km. While observational evidence indicates that migration is concentrated during periods of favorable weather (Buskirk 1980, Gauthreaux 1991), prevailing winds will. scale potential flight ranges up or down. For example, a 4 m/sec (14.4 km/hr) head wind reduced these range estimates by approximately SO%, while a 4 m/sec tail wind increased

TABLE 1. ARRIVAL WEIGHTS AND POTENTIAL FLIGHT RANGES OF COMMON TRANS-GULF MIGRANTS

Species[a]	N (1987–1992)	Wing span[b] (m)	Wet weight[c] (g)	Fat free mass[c] (g)	Mean mass "0" fat-class birds (g)	Mean arrival mass all birds (g)	Range of mean annual arrival weights[d] (g)	Potential range[e] still air (km)			Potential range (mean fat levels) with wind (km)	
								Minimum	Mean	Maximum	4 m/sec head wind	4 m/sec tail wind
RTHU	31	0.1100	3.64	2.62	2.88	2.9	2.87-2.96	0	21	83	10	32
COYE	285	0.1725	10.78	8.36	8.86	9.14	7.93-9.61	0	114	298	63	165
BGGN	44	0.1830	6.00	4.67	5.69	6.16	5.45-8.13	0	310	1390	165	431
NOPA	82	0.1885	7.60	5.93	6.69	6.97	6.20-7.46	0	161	429	88	234
WEVI	1554	0.1940	10.04	8.29	10.04	10.65	10.27-10.99	89	231	353	124	338
SWWA	42	0.1960	18.90	14.70	13.28	13.59	12.77-16.88	0	88	915	52	121
PROW	176	0.1990	13.94	11.01	11.37	11.94	10.72-13.18	0	192	579	104	270
HOWA	680	0.2035	10.29	8.20	9.11	9.42	8.86-10.43	0	135	547	75	195
ACFL	110	0.2050	12.90	10.03	11.38	11.75	11.43-11.93	18	128	188	70	181
INBU	825	0.2100	15.45	12.34	12.08	13.16	12.07-14.16	0	346	641	157	406
REVI	2462	0.2400	18.88	14.59	14.34	15.6	14.38-17.56	12	363	874	194	534
SUTA	370	0.2860	36.50	24.73	25.95	26.94	24.45-29.04	0	169	508	99	232
GCFL	56	0.2870	33.50	26.06	32.11	32.6	29.79-33.49	0	67	185	42	90
WOTH	416	0.3270	56.92	42.21	39.03	40.6	39.15-44.98	14	122	664	76	168

[a] Species Codes: RTHU Ruby-throated Hummingbird. *Archilochus colubris*, COYE Common Yellowthroat, *Geothlypis trichas*, BGGN Black-throated Green Warbler. *Dendroica virens*, NOPA Northern Parula, *Parula americana*, WEVI White-eyed Vireo. *Vireo griseus*. SWWA Swainson's Warbler, *Limnothlypis swainsonii*. PROW Prothonotary Warbler, *Protonotaria citrea*, HOWA Hooded Warbler. *Wilsonia citrina*, ACFL Acadian Flycatcher, *Empidnonax virescens*, INBU Indigo Bunting. *Passerina cyanea*, REVI Red-eyed Vireo. *Vireo olivaceus*, SUTA Summer Tanager. *Piranga rubra*, GCFL Great-crested Flycatcher. *Myiarchus crinitus*, WOTH Wood Thrush. *Hylocichla mustelina*.
[b] Source: HOWA, NOPA, COYE, REVI, WOTH. RTHU from R. Mulvihill, Powder Mill Nature Reserve; WEVI from M. Woodrey, MS Nat. Hist. Mus.: BGGN. GCFL. PROW, ACFL, SWWA from D. Evered, FL State Univ.; INBU from Horn Island 1994 (F. Moore. unpubl. data).
[c] Source: HOWA, REVI, WEVI, INBU, COYE, NOPA, PROW, SUTA, WOTH. RTHLJ from E.P Odum in Dunning (1993): BGGN. GCFL. YTVI, ACFL. SWWA estimated as % wet weight (77.79%) reported in Dunning (1993).
[d] Source: Spring 19x7-1992. East Ship Island and Horn Island. MS (E Moore, unpubl. data).
[e] Source: Pennycuick 1989, Prog_1 .bas for analysis of powered flight. Estimates assume air at altitude of 350 m above sea level and "0" fat mass for empty body mass.

TABLE 2. Habitat Associations[a] of Common Trans-Gulf Migrants in the Coastal Zone of Mississippi

Species[b]	1992 Bottom-land	1992 Pine	1993 Bottom-land	1993 Pine with under-story	1993 Pine without under-story
HOWA	249	18	161	126	0
REVI	230	16	211	13	0
WEVI	203	70	77	52	0
BGGN	82	2	117	21	1
GCFL	47	6	66	22	6
INBU	15	63	11	4	24
COYE	16	31	6	32	69
NOPA	47	8	39	0	0
YTVI	42	9	31	4	4
PROW	62	8	16	0	0
ACFL	45	0	26	1	0
SUTA	21	15	18	28	7
WOTH	32	1	15	3	0
RTHU	17	2	15	6	2
SWWA	14	1	3	0	0
Total individuals	1122	250	812	312	113
%	82	18	66	25	9
Total species	43	26	40	30	16

[a] 1992 = 9 sites X 7 replicates = 63 l-km strip transect censuses/habitat (2 habitat types/site) (F = 7.09, P < 0.01); 1993 = 9 sites X 6 replicates = 54 l-km strip transect censuses/habitat (3 habitat types/site) (F = 4.87, P < 0.01). Numbers represent total number of individuals recorded in each habitat type.
[b] See Table 1 for species codes.

them by a similar amount (Table 1). The effects of head and tail winds can be used in this model to simulate the variability in weather conditions encountered by migrants.

HABITAT PARAMETERS

Censuses at mainland and barrier island stopover sites indicate that birds select habitats nonrandomly during'migration. We have found that, although scrub/shrub and forest habitats accounted for 20% of the available habitat, they were associated with over 70% of the migrants observed in censuses on Horn Island, Mississippi (Moore et al. 1990). Censuses conducted during the spring of 1992 and 1993 at adjacent mainland sites showed that the number of individuals and total number of species detected was considerably greaten within riparian bottomlands and pine forests with a well developed shrub understory than in other habitats. Approximately 80% of all detections were in these two habitat types (Table 2).

We assume that the differences in habitat preference that we have observed in the field reflect real differences in habitat quality. However, our understanding of the quantitative differences between habitats is still very limited. Some evidence is available from measurements of migrant turnover rates and estimates of prey availability made at stopover sites.

We have found that birds without fat stores are more likely to be recaptured at stopover sites (Kuenzi et al. 1991, Moore and Simons 1992a), suggesting that birds with sufficient energy stores resume migration sooner or select better habitats. We have also documented differences in recapture rates at different stopover habitats. For example, 20.7% ($N = $ 8,392 total captures, 1988-1991) of the birds stopping at Peveto Beach in southwest Louisiana stay one or more days and are recaptured versus 8.9% ($N = $ 12,080 total captures, 1987-1991) at East Ship Island, Mississippi ($P < 0.001$). Again, we interpret this difference to be a reflection of habitat quality. Rates of mass gain during stopover are generally higher at the Louisiana site (Fig. 2a), which is consistent with measurements of higher insect prey densities at that site (Fig. 2b). Until we understand more fully the factors that determine the quality of migratory bird stopover habitats, we will be limited to grouping habitats into fairly coarse categories of habitat quality. Nevertheless, habitat groupings that rank habitats according to their suitability for passage migrants are useful for exploring the effect of landscape-level patterns of habitat availability.

ANALYSIS OF SPATIAL PATTERN AND STOPOVER HABITAT SUITABILITY

In an initial attempt to explore how variability in habitat quality might affect migrants that depend on coastal stopover habitats, we reduced the 18 cover types of our original landcover map to four habitat categories. These categories reflected the relative abundance of migrants in coastal habitats based on our experience and the results of our field censuses (Table 3). These ranged from category 1 habitats (urban, industrial, open water, and beach habitats), which were classified as unsuitable, to category 4 habitats (wetland-forested and deciduous. bottomland forest), which we believed to represent the richest stopover habitat types. We then subdivided the coastline into five study areas of approximately 1200 km² each and ranked the areas according to their average habitat rank. Ranks reflected the average habitat score calculated from the reclassified cells within each study area (Fig. 3). Area 2 had the lowest habitat rank followed by areas 3, 4, 1 and area 5 with the highest habitat rank.

Several spatial indices were calculated for areas 1 and 2 as an example of how measures such as contagion can be applied to stopover habitats (Table 4). In this comparison, the contagion indices are similar. That is, the probability that two adjacent 28.5 m x 28.5 m cells will be of the same habitat type is similar in both areas. On the other hand, the juxtaposition of cells of dif-
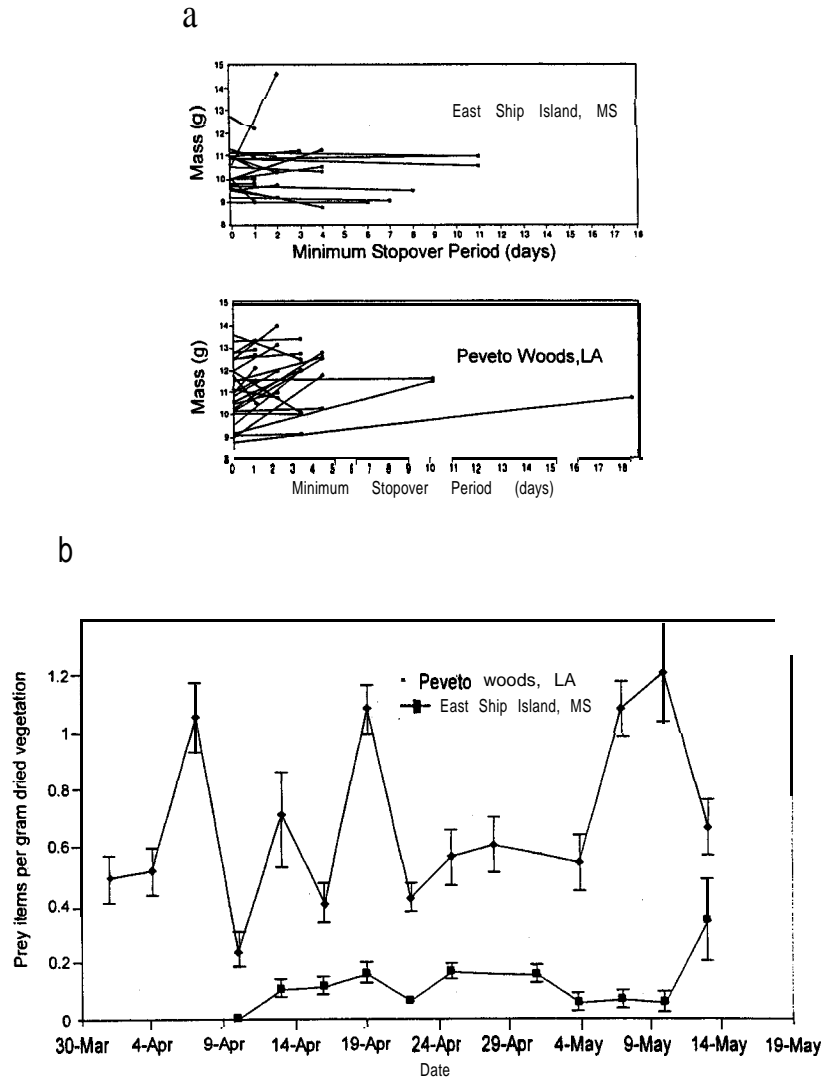
a

b

FIGURE 2. Evidence of variability in stopover habitat quality. (a) Weight trajectories (first and last capture) of individual White-eyed Vireos at stopover sites in southwest Louisiana (N = 33) are consistently higher than those on the Mississippi barrier islands (N = 30). (b) Abundance of prey for foliage gleaning birds is consistently higher (P < 0.05, Student's t-test) at the Louisiana stopover site. See Kuenzi et al. (1991) for sampling methods.

ferent habitat types, an edge index, suggests an important difference between the two areas. The probability that cells of low quality (category 1 or 2) habitat will be adjacent to cells of high quality habitat (category 4) is significantly greater in area 1 than in area 2. These transition probabilities may not be important to migrants that arrive along the coast with significant energy stores (i.e., potential ranges of hundreds of km), but they may be very significant to birds with depleted stores and limited ability to search for suitable stopover habitats.

The window analysis allowed us to quantify the variation in landscape-level foraging opportunities experienced by arriving migrants. With-

in the same landscape, there are likely to be rich as well as poor areas, but an individual bird can only use a small portion of the available habitat due to ecological, morphological, and energetic constraints. Figure 4a illustrates two windows randomly placed in Study Area 5. In the analysis, the size of the window was allowed to vary to simulate the variability in the energetic state of birds arriving in stopover habitats following trans-Gulf flights. For the purpose of this analysis, the window radius simulated birds arriving with effective ranges of from 1-30 lan, the lower range of mobility estimated from field and flight performance data.

The technique allowed us to analyze how the

TABLE 3. HABITAT CATEGORIES USED IN SPATIAL MODELS

Category 1	Category 2	Category 3	Category 4
unclassified	wetland/emergent marsh	wetland/mixed scrub-shrub	wetland/forested/deciduous
water	residential	upland/woody/evergreen/scrub-shrub	wetland/forested/deciduous/bottom-land forest
excavated soil	upland/woody/pine forest	upland/woody/mixed/shrub-scrub	
beach/sand	upland/herbaceous cropland	upland/woody/mixed forest	
wetland/sand bar	upland/orchards		
commercial			
transportation			
industrial			
% Total landscape 7.5	53.6	31.4	7.5

Note: Category 1 habitats were assumed to represent the poorest habitats for migrants, category 4 habitats were assumed to represent the best habitats for migrants.

energetic state of arriving birds affected their ability to use available habitats. Figure **5a** depicts how increasing the window radius (simulating arriving birds with improving energetic states) affects the mean habitat rank (quality) of the habitats available to migrants. While the lack of a trend may reflect the relatively homogeneous nature of the habitats at this scale, habitat variability appears to decline as the window radius increases, suggesting that habitat suitability thresholds may exist for birds during stopover. This specific result could simply be a sampling artifact, but a similar analysis across a range of landscapes may reveal patterns that improve our understanding of how energetic status and the degree of habitat specialization interact to shape. the stopover ecology of migrants. Certainly, the variability in habitat quality in a landscape might be just as important to some migrants as average habitat conditions.

We also examined variability in habitat quality among our study landscapes. Figure **5b** -shows the mean habitat rank of 50 IO-km radius windows randomly placed in each of the five study areas. The richest study area (area 5) showed less variability than the poorer habitats (areas 2, 3, and 4). Again, the biological significance of these patterns is probably a function of the scale at which birds are sampling stopover habitats. For example, in spite of the fact that area 4 (Fig. 3) contains a corridor of rich deciduous bottomland forest, birds arriving in the area with an effective range of 10 km will on average encounter habitats that are of lower quality than the area as a whole (Fig. 5b). **Rescaling** the analysis, by increasing the effective range to simulate birds arriving with more fat, or reducing the effective range to simulate the effects of headwinds, would undoubtedly alter the rankings of the sites.

Individual-based models provide another tool to evaluate how the spatial pattern and quality of stopover habitats may affect **trans-**Gulf migrants. Several examples will illustrate how we have applied individual-based models to these questions. The basic premise of the model is that on rich landscapes few individuals should die, and the number of cells visited should be low, while on poor landscapes more individuals will die, and the number of cells visited by successful migrants is expected to increase. Figure 4b illustrates the movement of two "virtual" birds placed randomly within a study landscape. Note that the birds tend to track the richer (darker) habitat types. We might predict that the effects of landscape quality and arrival condition on the movement and survival of birds will not be strictly additive. For example the model can be used to examine
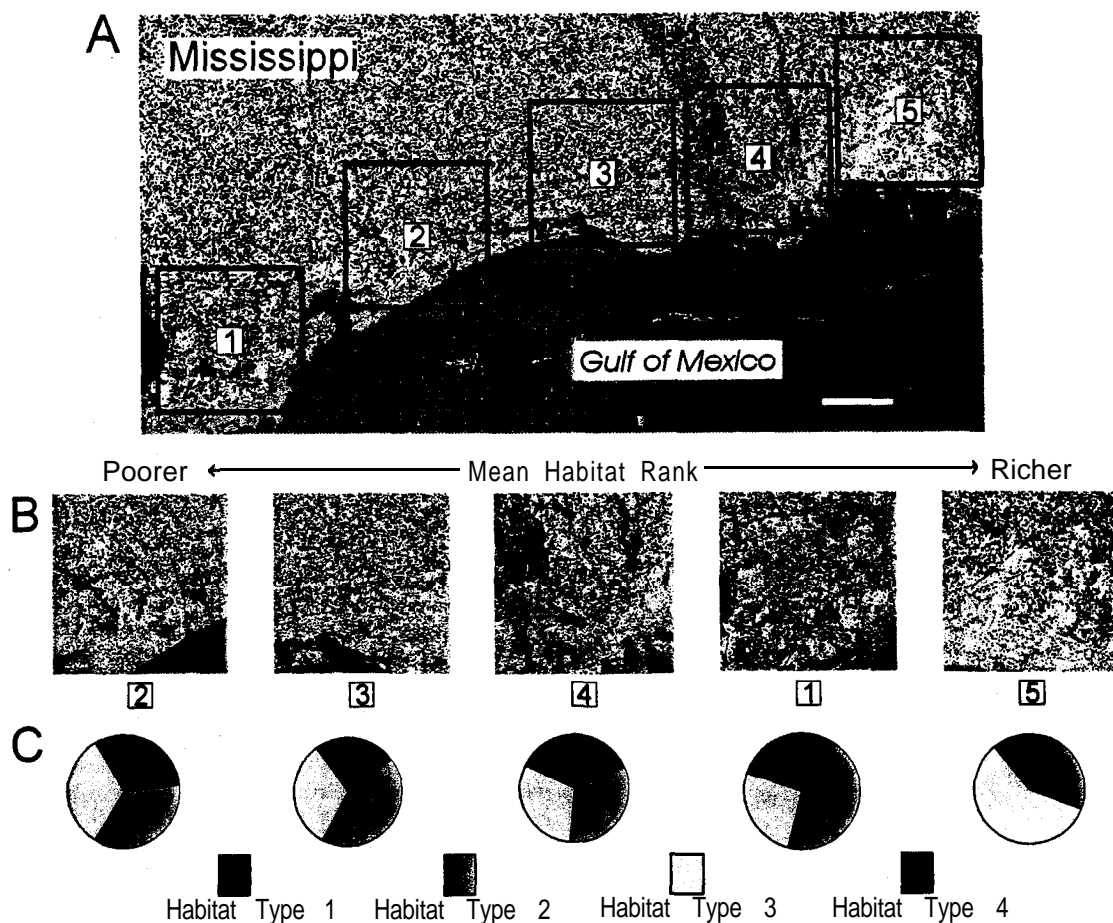
FIGURE 3. Composition of coastal habitats. Five study areas were selected and classified according to the categories described in Table 3. Mean habitat ranks were calculated for each study area based on the abundance of habitats in each of the four categories. Mean habitat ranks for the individual study areas were: Area 2 (2.27), Area 3 (2.38), Area 4 (2.47), Area 1 (2.56). Area 5 (2.69).

TABLE 4. SPATIAL INDICES FOR AREAS 1 AND 2

Index	Area 1	Area 2
Contagion[a]	0.389	0.388
Edge Index[b]		
1 and 2	27484	49007
1 and 3	26518	65183
1 and 4	10717	6211
2 and 3	147589	19488 1
2 and 4	137474	47672
3 and 4	81223	61347

[a] The probability that two adjacent cells will be of the same habitat type.
[b] A measure of the contrast between adjacent cells. e.g., the probability that a high quality habitat cell will be adjacent to a low quality cell.

whether birds that arrive with very low energy reserves experience disproportionately greater rates of mortality and slower rates of energy gain and if so, how those rates vary with changes in average habitat quality.

Simulations of 200 hypothetical individuals showed that both habitat quality and the arrival energy state index (ESI) affected the percentage of birds that survived to continue migrating (Fig. 6). It appeared that a bird's energetic state upon arrival was most significant in landscapes of intermediate habitat quality. In very rich (high habitat rank) or very poor (low habitat rank) landscapes, arrival ESI was not well correlated with survival. Landscape suitability, as measured by habitat rank, affected both the mean and variance of the number of cells visited by simulated migrants (Fig. 7). These trends suggest that the relationship between these factors
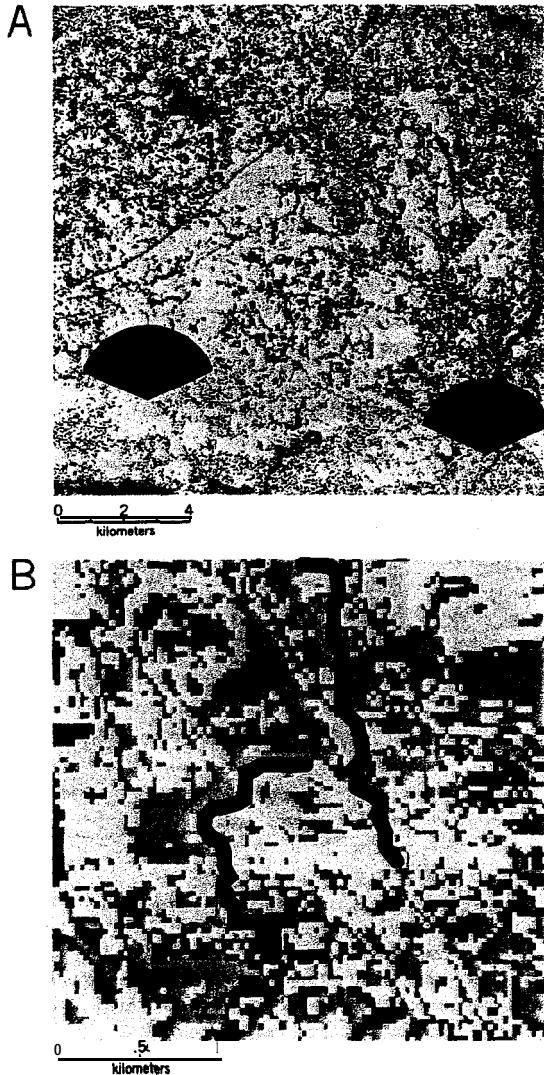
A

B

FIGURE 4. Window analysis. (a) Random projection of two windows over study area 5. Shape of window reflects migrant's tendency to move northward during spring migration. Size. of window represents energetic state upon arrival. Cell size 90m x 90m. (b) Individual-based model. Movement of two "virtual" migrants placed randomly in a study landscape. Birds tend to track richer (darker) habitat types.

*

is probably not linear, and that the variance in the number of cells visited decreases in richer habitats. As we might expect, the arrival ESI is inversely related to the mean number of cells visited by migrants that survive to continue migration (Fig. 8).

An analysis of variance tested for the effects of mean habitat rank (MAP) and the arrival energetic state (ESI) on the number of cells visited by individuals that survived to migrate. The

a

b
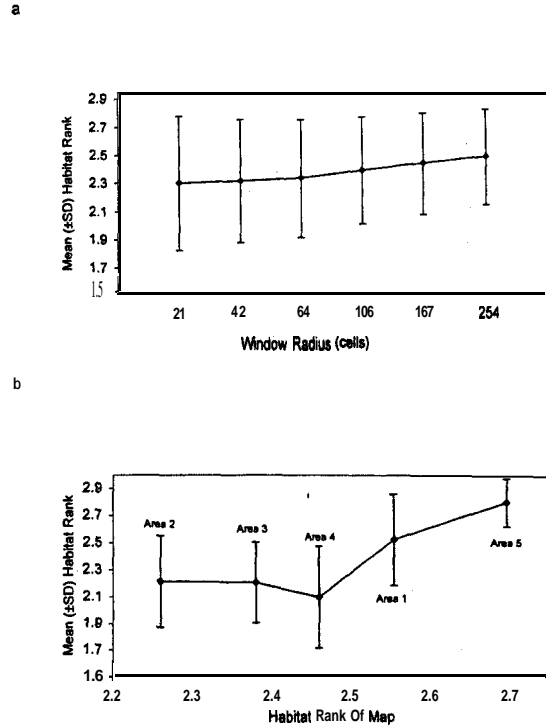
FIGURE 5. Window analysis. (a) Relationship of window size (radius from l-30 km) to mean habitat rank (N = 50 windows at each radius). (b) Mean habitat rank of 50 IO-km windows versus the habitat rank of the entire study area map.

model used was: Cells visited = MAP + ESI + MAP x ESI. This analysis showed that both the study landscape (Fig. 7; F = 226.71, df = 4, P < 0.001) and the energetic state of arriving birds (Fig. 8; F = 35.69, df = 3, P < 0.001) significantly affected the number of cells that migrant birds visited. Moreover, because the interaction term is significant (F = 6.04, df = 12, P < 0.001) we know that the effects of landscape and ESI are not strictly additive. Figure 9 provides
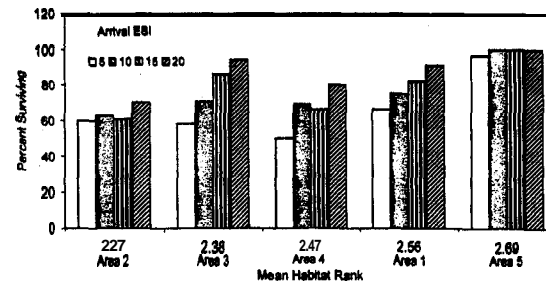

FIGURE 6. Effect of arrival energetic state (ESI) and habitat rank on the percentage of individuals surviving in the individual-based model.
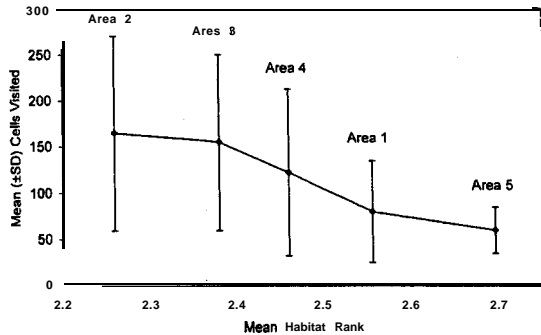
FIGURE 7. Relationship between mean habitat rank of the study area and the mean number of cells visited by 200 "virtual" migrants in the individual-based model.

FIGURE 8. Influence of arrival energetic state (ESI) on the mean number of cells visited by "virtual" migrants that survived to migrate.

evidence that the effect of arrival ESI was greater in the richer landscapes (especially areas 1 and 5). ESI was not a good predictor of the number of cells visited on the poorer landscapes (areas 2 and 3).

DISCUSSION

Spatial models allow us to explore the interplay of organisms and the landscapes they occupy, in particular the relationship between the ecology and behavior of individual species and the spatial variability of the habitats they occupy. We believe that the quality and spatial pattern of habitats, and the energetic status of birds when they arrive at stopover sites impose important constraints on the likelihood that individual birds will migrate successfully.

Techniques such as window analysis allow us to examine how variations in the energetic state of arriving birds and local weather conditions determine the scale at which birds experience stopover landscapes. Individual-based models, while having more assumptions, allow us to conduct a sensitivity analysis of the relative importance of physiological and ecological constraints, and they suggest new hypotheses to test with field data. For example, by projecting current trends in, habitat conversion into the future, we can explore the potential impact on species with differing habitat requirements and flight ranges, or how the interplay of habitat patchiness and arrival energetic state affect the likelihood of a successful migration. Behavioral characteristics of migrants, such as territoriality (Rappole and Warner 1976) and ecological plasticity (Greenberg 1990) can also be incorporated into these models. Such refinements will require better information on the behavioral ecology and habitat requirements of individual species, and the status and trends of the habitats they occupy.
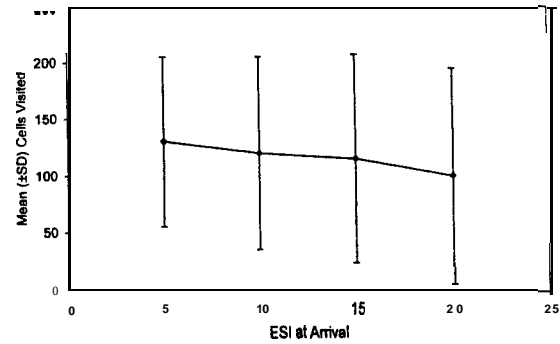
As Moore and Abom *(this volume)* have shown, radio telemetry holds tremendous promise for improving our knowledge of the ecology of migrants at stopover sites. Larger scale studies, while logistically challenging, would also seem well warranted.

Information of this type will be particularly important as landscapes become increasingly modified by human activity. Recent projections indicate that coastal communities surrounding the Gulf of Mexico are likely to experience significant population growth over the next 15–20 years (Fig. 10). If patterns of habitat loss elsewhere are a guide, we can predict that the coastal deciduous and riparian bottomland habitats that are clearly important to migrants will be lost at a disproportionately high rate. We feel that spatial models integrating information about the ecological requirements of migrants and the spatial patterns of stopover habitat will be essential in helping to set research and conservation priorities in the future.
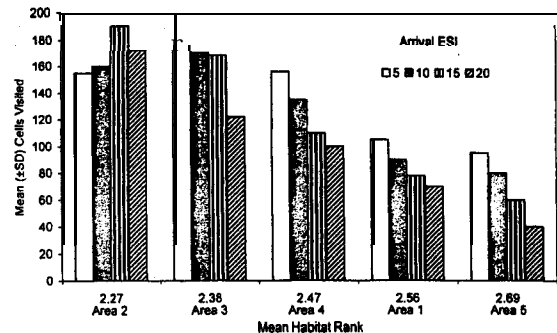

FIGURE 9. Interaction of arrival energetic state (ESI) and habitat rank of the study area on the mean number of cells visited by "virtual" migrants that survived to migrate.
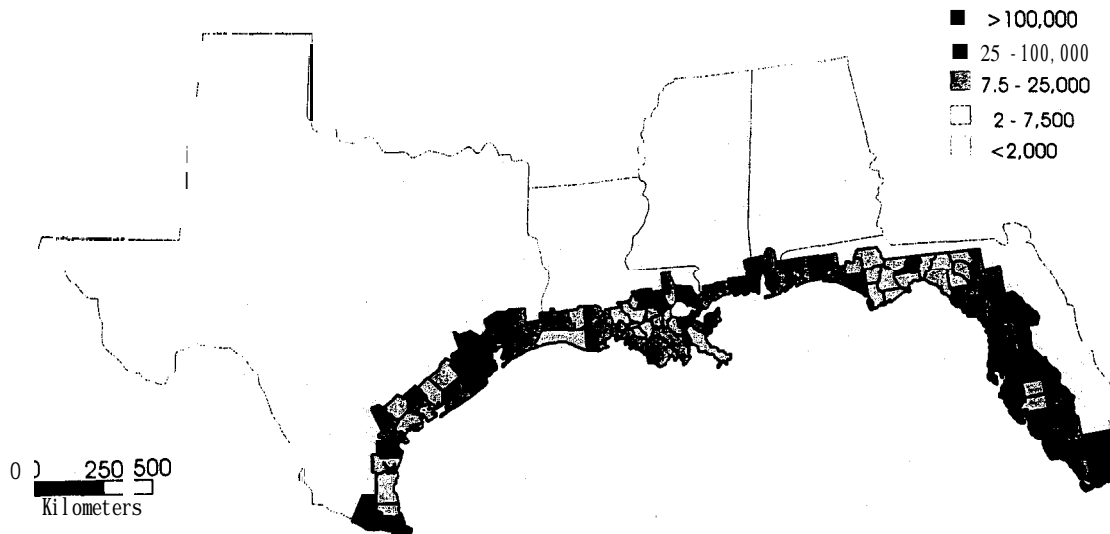
FIGURE 10.   Projected population growth by county along the northern Gulf coast 1988-2010 (Culliton et al. 1990).