CHAPTER

52

Spatial Analysis of Stopover Habitats of Neotropical Migrant Birds

Scott M. Pearson and Theodore R. Simons

Recent declines in populations of Neotropical landbird migrants (Robbins et al. 1989b; Askins et al. 1990; Finch 1991) have prompted a wave of new research into the factors affecting populations of these birds on their breeding and wintering grounds (Hagan and Johnston 1992; Finch and Stangel 1993). Although breeding and wintering activities are essential for population persistence, migration represents a significant event in the yearly life cycle of these birds because it requires a large energetic investment and can represent a period of high mortality. Moreover, areas used by migrating birds for rest and foraging (i.e., stopover areas) are experiencing rapid changes due to increasing urban, residential, and industrial/agricultural development. Increases in the abundance of these habitats may be detrimental to migrants (Yong et al. 1998). Some studies have focused on the factors affecting birds during migration (Moore and Simons 1992; Winker et al. 1992; Watts and Mabey 1993; Morris et al. 1994; Simons et al. 2000; Moore et al. 1995) and are shedding light on how stopover areas can be critical for many migratory species. Designing conservation-oriented studies of the stopover ecology of migrants is complicated by the fact that migration occurs over a broad geographic area, but over a relatively short time period. It is often difficult for field researchers to be in the right place at the right time.

Remote-sensing technology and spatial-modeling techniques are providing new research tools for investigating how the distribution and abundance of habitats may affect wildlife populations. Metrics of landscape pattern provide a means to quantify differences between landscapes. Landscape indices and spatial models (e.g., habitat suitability, individual-based models) are tools that allow biologists to assess how differences in the abundance and spatial arrangement of habitats may affect the suitability of landscapes for selected species. Moreover, these models can be modified to assess the quality of landscapes for species with different habitat needs, physiological requirements, or foraging strategies (Dunning et al. 1995; Turner et al. 1995). Conclusions gleaned from these models, however, need to be interpreted within the context of the model design and assumptions.

We have recently discussed how spatial models can be applied to questions about the stopover ecology of trans-Gulf migrants (Simons et al. 2000). We have shown how models incorporating available data on the arrival condition of migrants, energetic and morphological constraints on movement, and species-specific habitat preferences can provide insights into 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 in this chapter is to explore further how an analysis of landscape composition and spatial models that distinguish between habitat specialists and generalists can improve our understanding of the factors constraining migrants at stopover sites. We hope that the results of this analysis will provide insights that are useful in setting priorities for future research and conservation.

This research will compare five study landscapes located on the northern coast of the Gulf of Mexico using (1) landscape-level metrics of spatial pattern, and (2) output from an individual-based model of stopover habitat use. 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 straightforward measure is the area of suitable habitat types. The spatial arrangement of habitats can also be measured. For example, habitat fragmentation is often quantified using a combination of the number of habitat patches, mean patch size, and area of the largest patch. The juxtaposition of habitat types can be measured with indices of edge density or contagion (Hargis et al. 1997). Landscape-level metrics provide objective measures of habitat patterns; however, interpreting these metrics from the perspective of a species' biology remains challenging.

Field studies have shown that the arrival energetic state of migrants at trans-Gulf stopover sites is highly variable (Moore et al. 1990; Moore and Simons 1992; Morris et al. 1994; Moore et al. 1995; Fransson and Jakobsson 1998). Energy reserves can constrain long- and short-range movements of migrants (Jenni and Jenni-Eiermann 1998). Measurements of fat reserves of birds arriving along the northern Gulf Coast have been used with flight performance models to estimate the potential flight ranges of migrants at coastal stopover sites (Simons et al. 2000). Flight ranges may be as little as a few kilometers in extreme cases and average from tens to several hundred kilometers in most species. Thus, the distribution, abundance, and quality of suitable habitat within the range of migrants at coastal stopover sites can be viewed as an important constraint on the likelihood of a successful migration. Habitat preferences have been demonstrated for migrants during stopover (e.g., Weisbrod et al. 1993; Russell et al. 1994). Along the Gulf Coast, field studies have shown that migrants appear to prefer forests with a well-developed understory and riparian bottomlands over other habitats available at stopover sites (Moore et al. 1990; Simons et al. 2000). These observations suggest habitat specialization may also constrain the suitability of stopover sites for some species.

We have developed an individual-based model that simulates habitat usage and energy gain by birds during migration stopover events. The model is simplistic and makes minimal assumptions about the details of habitat use. It is designed to provide information about the consequences of foraging in landscapes that vary with respect to the abundance, spatial arrangement, and quality of habitats that differ with respect to their foraging returns. Changing the model parameters also allows us to simulate birds that vary in their energy states and habitat specificity (e.g., generalists versus specialists).

The specific objectives of this work were (1) to investigate the relative importance of landscape pattern of habitats, energetic state of arriving birds, and habitat specialization for successful stopover, and (2) to identify the types of landscapes that will provide suitable stopover habitat. This second objective was implemented by ranking a set of real landscapes according to their suitability for stopover habitat use. To achieve these objectives, we analyzed data from remote sensing using modeling and analytical approaches based on an understanding of stopover ecology gained from field studies.

Study Area and Methods

The study landscapes were five 25×25-kilometer regions located along the northern Gulf Coast in the states of Texas, Louisiana, and Mississippi (see Fig. 52.1 in color section). Habitat data for these landscapes were derived from a supervised classification of two 1990 Landsat Thematic Mapper images. The classification was performed by the U.S. Geological Survey's Southern Science Center in Lafayette, Louisiana. The original map consisted of eighteen cover types in raster format having square 28.5×28.5-meter cells. These eighteen habitat types were reclassified into four habitat categories that represent four classes of habitat quality (Table 52.1). Category 1 rep-

TABLE 52.1.

Habitat categories used for landscape suitability analyses.

	Category 1[a]	Category 2	Category 3	Category 4[b]
	Unclassified Water Excavated soil Beach/sand Sand bar Commercial Transportation Industrial	Emergent marsh Residential Pine forest Cropland Orchards	Mixed shrub-scrub Evergreen shrub-scrub Mixed forest	Deciduous forest Bottomland forest
% Total[c]	7.5	53.6	31.4	7.5

[a] Category 1 habitats offer few opportunities for foraging; therefore, this category represents the poorest habitats for migrants.

[b] Category 4 habitats were assumed to be the best habitats for migrants.

[c] The percent representation of each of the categories, summed over all landscapes, is reported.

resented the poorest-quality habitat class. These habitats provide few if any opportunities for foraging by migrating landbirds. Category 4 represents the highest-quality habitats that provide abundant food resources. Assignment of habitats to these classes was based on field studies of habitat usage and habitat-specific weight gain conducted during 1987–1994 (Moore et al. 1990; Kuenzi et al. 1991; Simons et al. 2000).

Landscape Metrics

For each study landscape, the spatial pattern of the four habitat categories was quantified using FRAGSTATS (McGarigal and Marks 1995). For each habitat category, the following metrics were recorded: percentage of total area of map occupied by each habitat category, total number of patches of all habitat types, patch density (number of patches per hectare), mean patch size (hectare), edge density (meters of edge per hectare), Simpson's index, and contagion. Proportion of total area serves a measure of the abundance of the habitat category. Collectively, the number of patches, patch density, and mean patch size provide a means to compare the relative fragmentation or connectivity of a given habitat type among the five study landscapes. Landscapes in which habitats are more fragmented have a greater number of patches, higher patch density, and smaller mean patch size. Edge density and contagion measure the degree of interspersion and contact between habitat types. Edge density will increase in landscapes in which patch sizes are small and patches have complex or elongated shapes (e.g., skinny rectangles or dendritic shapes) rather than compact shapes (e.g., circles or squares). Contagion also measures the degree of habitat fragmentation and contact between habitat types. The contagion value represents the probability that two adjacent cells, chosen at random, will be of the same habitat type. Thus, contagion will be greater for landscapes in which habitats are highly clumped and lower for maps in which habitats are fragmented and highly interspersed. See McGarigal and Marks (1995) for a more complete description of the calculation and interpretation of these landscape metrics.

In addition to the metrics provided by FRAGSTATS, we calculated an index of general landscape quality using the following formula:

$$Quality = P_1 + 2*P_2 + 3*P_3 + 4*P_4$$

where P_x represents the proportion of the total landscape area occupied by habitat category x. Landscapes with a greater proportion of high-quality habitat types will receive a greater-quality score. Although this index will permit the ranking of landscapes with respect to the abundance of habitat categories, it does not indicate anything about the spatial arrangement of habitats within the landscape. This index uses an econometric approach similar to that of a habitat suitability index (HSI). In HSI techniques, each habitat unit (usually an areal unit) is multiplied by an ordinal index of habitat quality.

Individual-based Model

This model uses an energy state index (ESI) to indicate the relative energetic state of birds during migratory stopover. We assume that birds arrive at the stopover site with low energy reserves. During stopover, an individual bird forages to improve its energetic state, rebuilding energy reserves that will fuel its next migratory flight (e.g., Alerstam and Lindstrom 1990; Fransson 1998). The species that inspired this study typically migrate by flying long distances (usually hundreds of kilometers per flight) at night. At the end of one of these long-distance flights, the birds "stop over" and spend one or more days foraging to refuel before the next long-distance flight. The availability of habitats that provide foraging opportunities at the stopover site will determine the rate at which energy reserves can be rebuilt. Birds that land in relatively rich sites will be able to refuel quickly; those that land in poorer sites will take longer to store enough energy to make another long-distance, nocturnal flight (Yong et al. 1998). In a worst case, a migrant in a very poor site may starve because it cannot ingest enough energy to satisfy its immediate energetic needs.

The model incorporates these assumptions about energetic state in the following way. Arriving birds with a given ESI land in a randomly determined cell in the habitat map. By changing the initial ESI value, we simulated birds that have varying levels of energy upon arriving at the stopover site. The bird then foraged by moving from cell to cell. At each cell, ESI is updated using this equation:

$$\mathrm{ESI}_j = (\text{energy gained in cell}_j) - (\text{energy cost of movement and foraging}).$$

Foraging cost was held constant, and foraging gain accrued by the birds as they moved across the landscape depended on the habitat category of each cell encountered. In productive habitats, migrants experienced a net energy gain (i.e., gain is greater than cost). In the poorest habitats, there was a net loss (gain is less than cost).

TABLE 52.2.

Energetic gain values by habitat categories for habitat generalists and specialists. The habitat categories are defined in Table 52.1.

	Habitat category			
	1	2	3	4
Generalist	0.10	0.55	0.75	0.75
Specialist	0.00	0.10	0.45	1.50

The degree of ESI gain or loss depended on whether the bird was classified as a habitat *generalist* or a habitat *specialist* (Table 52.2). For both generalist and specialist, the cost of foraging and moving was fixed at 0.50 ESI units for all habitat types. The habitat-specific gain values were adjusted so that both generalists and specialists would receive the same gain if they encountered equal proportions of the four habitat categories. However, the specialist did better than the generalist on category 4 cells and worse on category 2 and 3 cells.

In the model, the bird continued to forage until its ESI crossed one of two thresholds. If the individual gained enough energy, it left the study landscape on another long-range migratory movement. In contrast, individuals that failed to find productive habitat continually lost energy and died (if the ESI dropped too low). When an individual migrated or died, the number of cells visited was recorded in the model output. For these simulations, the migration threshold was fixed at an ESI of 30.0. The death threshold was set at an ESI of 2.0. Thresholds were the same for both habitat generalists and specialists.

A subroutine that governs movement from cell to cell was used that incorporated knowledge of adjacent cells, ability to choose among cells based on habitat quality, and a northerly bias to movement. When moving from cell to cell, the individual was assumed aware of the habitat types of the adjacent eight cells. The bird would choose cells with higher ESI gain values (i.e., higher habitat-quality category) over cells with lower ESI gain values. Laboratory studies have

TABLE 52.3.

Coefficients used to incorporate a northerly bias to bird movement during stopover.

		North		
	0.90	1.00	0.90	
West	0.75	**Focal Cell**	0.75	**East**
	0.60	0.50	0.60	
		South		

demonstrated a tendency for birds migrating through the northern Gulf in the spring to orient and move northward (Gauthreaux 1971; Emlen 1975). Therefore, we assumed that given two cells of equal habitat quality, a bird is more likely to move to the more northerly cell. This bias was accomplished by discounting the gain value for each cell by its position relative to north. Thus, the bird would calculate an attractiveness value for each cell:

$$Attractiveness = (ESI\ gain)^{*}(nbias)$$

where *nbias* is this discounting coefficient. Table 52.3 shows the *nbias* coefficients used in these simulations. Birds would move to the cell with the greatest attractiveness value. If two cells were equal in greatest attractiveness, choice between them would be made randomly. Birds were not allowed to return to cells that were previously visited. Arriving birds were randomly located in the southern portion of the map to a cell within 1.0 kilometer of the Gulf Coast. Data for birds that wandered to the edge of the map without migrating or dying were discarded, and the simulation was reinitiated for that individual.

Simulation Experiment

A set of simulations was designed to assess the performance of birds using the five study landscapes as potential stopover sites. The goal of this experiment was to determine the relative importance of landscape pattern of habitats, arrival energetic state of arriving birds, and species' habitat specialization to stopover performance. Performance was measured by (1) the proportion of birds that survived and migrated, and (2) the number of cells visited by migrating birds. In highly suitable landscapes, it is expected that a greater proportion of birds will migrate and that fewer cells will be visited during the stopover time because energy gain per cell will be greater on average. However, the actual performance of the birds could be affected by the patchiness and interspersion of habitat types.

A factorial design was used with the following levels: (1) five study landscapes, (2) two levels of habitat specialization, and (3) four levels of arriving ESI. The levels of arrival ESI were set at 5, 10, 15, and 20. For each of forty treatment combinations, five hundred replicate birds were simulated. The relative influence of landscape, arrival ESI, and habitat specialization were compared by examining the magnitude of F scores from the analyses of variance. ANOVAs were conducted using SAS (1985). To improve normality, the proportions of migrants were arcsine–square-root transformed and counts of cells were square-root transformed before conducting the ANOVAs (Sokal and Rohlf 1995).

Results

Differences among the five study landscapes evident in Figure 52.1 were also revealed in the landscape metrics, although variation in the selected metrics was not striking. Comparing the relative abundance of each habitat type is the simplest way to compare the five landscapes. Landscape A had the greatest amount of the highest-quality habitat, category 4 (Fig. 52.2).

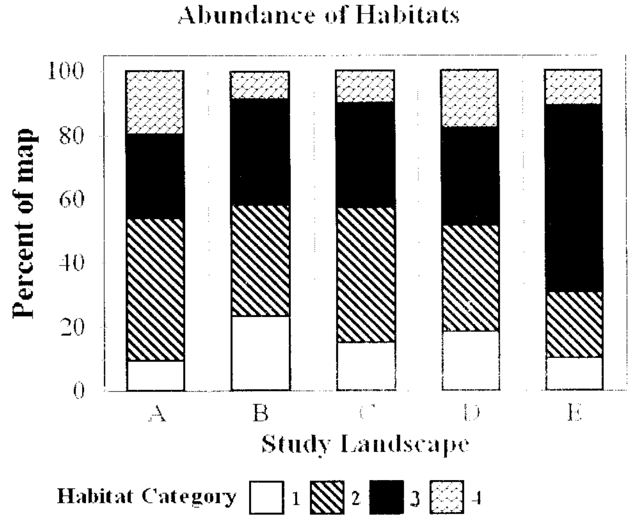

Figure 52.2. The relative abundance of four habitat types in each of the five study landscapes.

TABLE 52.4.

Landscape metrics for five study landscapes.

	Landscape				
Metric[a]	A	B	C	D	E
Number of patches	32,426	31,333	31,059	29,491	31,463
Patch density (no./ha)	51.9	50.2	49.7	47.2	50.4
Mean patch size (ha)	1.93	1.99	2.01	2.12	1.97
Edge density (m/ha)	196.7	194.7	199.3	188.7	192.0
Simpson's index	0.69	0.71	0.68	0.73	0.60
Contagion (%)	34.8	34.0	35.5	31.8	40.9
Quality index[b]	2.57	2.27	2.37	2.47	2.70

[a] See McGarigal and Marks (1995) for a complete description of the first six metrics.

[b] The quality index is described in the methods section of this chapter.

Landscape E had the greatest amount of habitat category 3 and the greatest amount of habitats 3 and 4 combined. There was little difference in the abundance of high-quality habitat among landscapes B, C, and D. Among those three study areas, landscape C had the least amount of poor-quality, category 1 habitat. Landscape D had the greatest value of Simpson's index (Table 52.4) indicating that the habitat categories were most evenly distributed in this map compared to the other five maps. Landscape E had the lowest value of this index due the greater relative abundance of category 3 habitats.

The remaining metrics provide measures of the spatial pattern of the four habitats and their interspersion. The number of patches, patch density, and mean patch size provide a means to compare the relative levels of fragmentation among the five maps. Landscape A had the greatest number of patches, largest patch density, and smallest mean patch size (Table 52.4), which indicates that this map had the greatest degree of habitat fragmentation. In contrast, landscape D had the lowest number of patches, least patch density, and largest mean patch size, indicating that habitats in this landscape tended to be more clumped in larger patches (landscapes A and D, Fig. 52.1).

The interspersion of habitats may be important for birds as they move across the landscapes. Although interspersion is related to measures of habitat fragmentation, the metrics of edge density and contagion provide information on the likelihood that a moving bird will encounter different habitat types during stopover. Landscape C had the greatest edge density (Table 52.4) due to the high interspersion of habitats and the complex shapes of habitat patches evident in northern portion of this map (Fig. 52.1). This landscape had an intermediate level of contagion (Table 52.4) due to the differences between the northern and southern sections of this map. Landscapes B, C, and D show a sharp gradient in the pattern of category 4 habitats. These habitats, which include deciduous and bottomland forests, become more abundant in wetland areas that are farther away from the brackish water influence of the Gulf of Mexico. Landscape E had the highest level of contagion and an intermediate value of edge density (Table 52.4) caused by the increased coverage of category 3 habitats in this map (Fig. 52.2). This habitat dominates much of the middle portions of this landscape (Fig. 52.1).

Probability of Successful Stopover

Highly suitable landscapes would be expected to have a high proportion of birds that acquire enough energy to migrate after stopover. The relative influence of landscape, arrival ESI, and habitat specialization were compared by examining the magnitude of F scores from the analysis of variance. Habitat specialization had the greatest effect on probability of successful migration (Table 52.5). Habitat generalists had consistently higher probabilities of successful stopover than did specialists (Fig. 52.3). The success of specialists varied among landscapes (Fig. 52.3), resulting in a weaker, although significant landscape

TABLE 52.5.

Analysis of variance of the proportion of birds surviving to migrate.

Source	df	Type III SS	F	P
Landscape	4	0.458	34.5	< 0.001
Arrival ESI	1	0.200	60.0	< 0.001
Habitat specialization	1	0.659	198.2	< 0.001
Landscp.xESI	4	0.012	0.9	0.457
Landscp.xSpecialization	4	0.679	51.1	< 0.001
ESIxSpecialization	1	0.001	0.4	0.550
Total	39	6.686		

Note: Proportions were arcsine–square root transformed before analysis.

main effect and landscape × specialization interaction. Among the main effects, arrival ESI had an influence of intermediate magnitude. Higher values of arrival ESI resulted in a greater chance of successful stopover, especially for habitat specialists (Fig. 52.3). There were no significant interactions involving arrival ESI.

Number of Cells Visited by Migrants

Among the main effects, the strongest influences were arrival ESI and landscape pattern (Table 52.6). Increasing arrival ESI tended to reduce the number of cells visited by successful migrants (Fig. 52.4). Landscapes A and E (mean ± SD respectively: 96.0 ± 74.9, 103 ± 778.2) required fewer cells for successful migration than landscapes B, C, and D (136.7 ± 144.4, 136.6 ± 110.1, 159.3 ± 146.0, respectively). The effect of habitat specialization was of intermediate magnitude. However, there were strong interactions between this factor, landscape, and arrival ESI. Arrival ESI had a stronger influence on generalists than on specialists (Fig. 52.4). The number of cells visited was consistently reduced for generalists with higher levels of energy on arrival; the influence of this factor on specialists was less consistent among the landscapes. Specialists visited more cells than generalists did in four of the five landscapes. Specialists visited fewer cells than generalists did in landscape A. The higher efficiency of specialists in this landscape was likely due to the greater abundance and dispersion of category 4 habitats in this map.

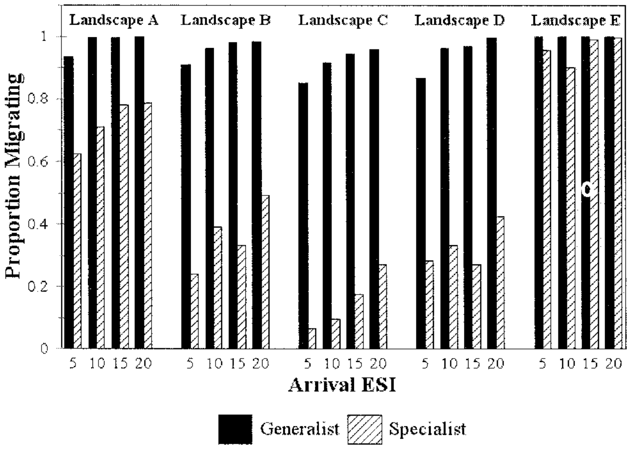

Figure 52.3. The proportion of simulated birds obtaining enough energy to survive and migrate out of the study landscape. Results for the five landscapes are plotted in separate groups of bars. Two types of birds were simulated: habitat specialists and habitat generalists. Each bird began its stopover habitat use with one of four levels of energy reserves. These reserves were tracked in the individual-based model using a energy state index (ESI).

Ranking Study Landscapes

The landscape metrics and output from the individual-based model allowed the ranking of landscapes. The most straightforward means was to use the quality index (Table 52.4) that is similar to HSI approaches. Although this measure is not spatially explicit, it provided an initial intuitive assessment of the relative abundance of high-quality habitats among the alternative landscapes. Based on the quality index, landscapes E and A ranked highest; landscapes C and B

TABLE 52.6.

Analysis of variance of the number of cells visited by successful migrants.[a]

Source	df	Type III SS	F	P
Landscape	4	1,751.2	37.4	< 0.001
Arrival ESI	1	11,544.5	985.6	< 0.001
Habitat specialization	1	1,260.4	107.6	< 0.001
Landscp.xESI	4	885.0	18.9	< 0.001
Landscp. xSpecialization	4	20,044.1	427.8	< 0.001
ESIxSpecialization	1	4,766.2	406.9	< 0.001
Total	14,679	234,342.3		

[a] Cell counts were square root transformed before analysis.

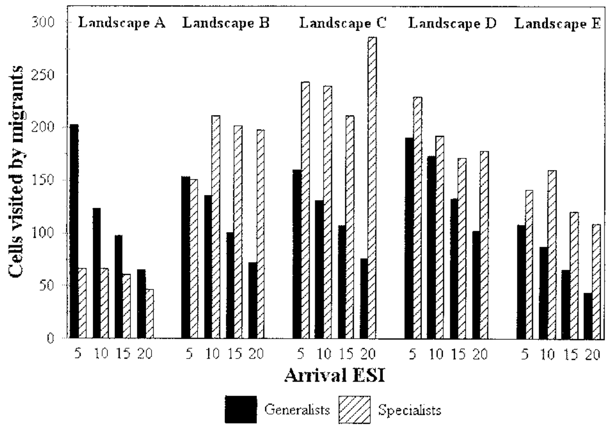

Figure 52.4. The number of cells visited by birds that survived and migrated from study landscape. See Figure 52.3 caption for explanation of format.

ranked the worst (Table 52.7). The high rank of landscape E was produced by its greater relative abundance of category 3 habitats.

Output from the individual-based model provided information on the relative success rates of migrant birds using these landscapes. The proportion of individuals surviving to migrate and the number of cells visited by successful migrants served as measures of success and were used to rank the landscapes. High proportions of successful migrants and low numbers of cells visited were taken to represent the best landscapes. Based on proportion of migrants, landscapes E and A ranked best; landscape C ranked worst (Table 52.7). Landscapes B and D had similar proportions of migrants and were intermediate in rank. Based on the number of cells visited, landscapes A and E again ranked best; landscape D was worst. Landscapes C and B had almost identical numbers of cells visited and had an intermediate rank.

TABLE 52.7.

Ranking of landscapes based on quality index, proportion of successful migrants, and number of cells visited by successful migrants.

	Landscape designation[a]					
Rank		**Quality index[b]**		**Proportion migrants**		**Cells visited**
1 (best)	highest	E	most	E (0.980)	least	A (95.0)
2		A		A (0.854)		E (103.7)
3		D		B (0.662)		C (136.6)
4		C		D (0.638)		B (136.7)
5 (worst)	lowest	B	least	C (0.535)	most	D (159.3)

[a] Mean proportion of successful migrants and mean number of cells visited are reported in parentheses after landscape number in the respective columns.

[b] The quality index is reported in Table 52.4.

In summary, the precise ranking of landscapes depended on the method employed. Although landscapes A and E consistently ranked as the best, the ranking of remaining landscapes varied with method. For example, landscape D ranks as third best with respect to the quality index but fourth or worst according to the individual-based model.

Discussion

Transcontinental migration is a brief period in the annual cycle of a Neotropical migrant bird (i.e., a couple weeks during the spring and autumn). However, successful completion of migration between wintering and breeding grounds is essential to an individual's evolutionary fitness and for the persistence of the population as a whole. Successful migration depends on the existence of suitable stopover habitat along migration routes. The availability and quality of this habitat are as crucial as the quality of wintering and breeding sites. Although stopover sites are used only during a brief period of the year, the existence of high-quality sites is necessary for the continued persistence of these avian species.

Conservation of Stopover Sites: A Challenging Problem

The conservation strategy that led to the present system of waterfowl reserves along the Gulf Coast may not work for migrant songbirds. There are fifteen national wildlife refuges and two national seashores that protect coastal habitat along the northern Gulf Coast. These areas were established primarily for the purposes of waterfowl conservation and recreation. In large part, the remaining coastal cheniers and riparian woodlands that are important to trans-Gulf migrants are unprotected and not in the public trust. The waterfowl refuges were selected because specific locations used by these birds could be identified. Providing habitat for migrating songbirds is not as straightforward.

The geographic extent and stochastic nature of stopover events presents a challenge for the purposes of maintaining populations of migrating songbirds. For example, on the Gulf Coast the exact location of "fall out" events is determined by onshore weather encountered when the birds reach the coast and the weather patterns experienced during their flight over the Gulf of Mexico. Groups of migrant birds may land just about anywhere in a given landscape used for stopover during the course of several seasons. The conservation manager is then faced with the difficulty of devising ways to protect a set of species that are dependent on a particular landscape but whose use of the landscape is geographically random and seasonally ephemeral. Moreover, the manager has little or no control over a vast portion of the landscape that is owned and used by a large number of private landowners. These challenges to protection efforts may seem insurmountable. Nevertheless, we are optimistic that feasible strategies for preserving an essential amount and geographic distribution of stopover habitat can be developed if scientists develop a better understanding of stopover ecology.

The same characteristics of stopover events that discourage managers (i.e., geographically extensive, randomly located, temporally ephemeral) also confound research scientists seeking to conduct field studies. Some of these difficulties may be overcome by the increasing availability and accuracy of remotely sensed data covering large areas. Maps derived from these data allow scientists to examine the relative abundance and spatial pattern of habitats over broad geographic areas. By combining these maps with field studies, researchers should develop a better understanding of the characteristics of landscapes that provide quality stopover sites.

Field Studies at Stopover Sites and Landscape-level Analyses

The analytical and modeling approaches used in this study were developed from the findings of field studies. Although limited in geographic and temporal extent, field studies provide information about the ecology of individual and small groups of birds using stopover habitat. These studies provide information on the important features of habitat use such as coarse-grained and microhabitat preferences, duration of stay at a given site, patterns of movement within a site, energetic condition of arriving birds, and qualitative comparison of relative rates of energy gain among alternative sites. The vegetation types and microhabitats available at a given study site may be quantified, but researchers must rely on accurate maps of surrounding areas to learn about the abundance of habitats in the landscape surrounding the site. Habitat maps permit the study of research questions related to the influence of the surrounding landscape on the use of a given stopover site (e.g., Pearson 1993). For example, does the use of a given 5-hectare study plot of high-quality habitat depend on the abundance of that habitat in the surrounding landscape?

Other questions about landscape-level habitat uses are more difficult (but not impossible) to address with field studies. For example, what is the scale of habitat selection conducted by arriving birds? Once the bird lands, what aspects of the landscape affect its pattern of movement among habitat patches? The geographic extent of migration makes it difficult to design comprehensive field studies. However, we should be able to explore these questions using landscape analyses and spatial models that are based on our understanding of stopover ecology gained from past and present field studies. These explorations should lead to predictions and hypotheses that could be tested in future, carefully designed field studies. The approach taken in our study was to use a model to rank landscapes according to the "success" of migrants during stopover. The measures of success included the duration of stay (i.e., number of cells visited by migrants).

By using the model, we gained insights into how alternative landscape configurations may affect this aspect of stopover ecology, and we generated predictions about the duration of stay that can be tested in future field studies. Analyzing the predictions of a general model can help identify aspects of stopover ecology that need addressing in future field studies. For the conservation manager, a general model could be used to evaluate management alternatives. For example, the performance of migrants could be simulated on alternative landscape patterns produced by different policy options that affect land use on private lands (e.g., conservation easements) or by the creation of new protected areas under public ownership. Given the limited resources for conservation, an approach like this can help managers select strategies to achieve the greatest positive change in the landscape with limited fiscal resources. Thus, landscape analyses and modeling studies provide a powerful tool to complement field studies.

Results from This Study

Habitat specialization emerged as an important influence on the probability of successful stopover and the amount of time needed to rebuild energy reserves (Tables 52.5 and 52.6). Our results indicate that the effects of habitat pattern and abundance on migrants will be amplified for habitat specialists and when birds arrive at stopover sites with their energy reserves depleted. The difference in the relative abundance of habitats in these landscapes is not striking (Fig. 52.2). Although some differences in spatial arrangement of habitats are apparent in Figure 52.1, it is not clear from a cursory inspection of these maps which landscape should be better or worse. A more thorough analysis was needed. While landscape pattern ranked the lowest among main effects in both ANOVAs, these analyses revealed that there were strong interactions among landscape pattern, habitat specialization, and arrival ESI for number of cells visited (Table 52.6). These results suggest that the differences in the abundance and spatial arrangement of habitats matter more for species with specialized habitat needs and less for generalists. Admittedly, this is an intuitive result, but the degree of difference that habitat specialization makes, and the relative ranking of these landscapes, would not have been possible without the use of the model.

Ranking landscapes depends on the method for quantifying habitat suitability. Table 52.7 shows that the exact ranking depends on the schema being used. Landscape C ranks third, fourth, or fifth, depending on which ranking method is employed. The differences in the ranking of this landscape based on proportion of successful migrants versus number of cells visited is due to differences in performance between habitat generalists and specialists. Although the performance of generalists on this landscape was comparable to landscapes B and C, the performance of specialists was much worse. Specialists had the lowest success rates on landscape C (Fig. 52.3) and required a higher number of cells visited (Fig. 52.4) than on any of the other landscapes. Choices about the most desirable criteria for ranking landscapes must be made by knowledgeable managers within the context of specific conservation goals. Spatial models and landscape analyses can provide information useful for comparing alternative criteria.

The results caused us to reevaluate the effects of some landscape features. *A priori*, we expected landscape D to rank high because of the presence of two large river corridors dominated by high-quality deciduous bottomland forest. However, this landscape ranked in the middle or lower half of the rankings (Table 52.7). The presence of large patches of bottomland forest was counteracted by the abundance of large patches of low-quality habitat in the southern portion of the map. The southern region provides none of the category 4 habitats that provide high returns for the habitat specialists. Migrants landing in the southern half had to contend with these relatively poor habitats before encountering the richer sites to the north.

The model output also assisted in interpreting the landscape metrics, such as contagion. While the relative abundance of habitats affects the mean habitat quality, patch size, and interspersion of habitats affect the variance in foraging returns experienced by a bird as it moves across the landscape. Higher levels of interspersion (i.e., low contagion) reduce the variance in foraging returns for a bird visiting a fixed number of cells. Thus, in landscapes with the same levels of interspersion, mean habitat quality (calculated at a scale relevant to a single bird during stopover) is most important. In a landscape with the same mean quality but lower levels of interspersion (i.e., high contagion), the variance among birds will be higher because some will encounter large patches of high-quality habitat while others encounter patches of low-quality habitat.

Changes in interspersion can be good or bad depending on mean habitat quality. If the average habitat quality is great enough for most birds to be successful, then increasing interspersion will require birds to visit a larger area (i.e., more cells), because they will inevitably encounter low-quality sites, although almost all are assured to gather enough energy to migrate. Decreasing interspersion (increasing contagion) would mean that some birds would encounter large patches of rich and poor habitats. More birds would die without migrating because they landed in large patches of low-quality habitat. In contrast, decreasing interspersion could be a good thing for landscapes in which the mean habitat quality is so low that the average foraging return is less than that needed for successful migration. If interspersion is high, practically no birds will be able to obtain enough energy during stopover because they will be receiving the mean return for foraging on this landscape. Alternatively, if rich habitats are more clumped, then at least some birds will land in these areas and become successful, although most will perish because they landed in poor areas. This is a spatially explicit example of issues addressed by the topic of risk-sensitive foraging (e.g., Caraco et al 1980; Stephens and Charnov 1982) investigated in the field of optimal foraging theory. These issues are have been addressed in other systems where prey are cryptic and have heterogeneous spatial distributions by using a combination of field data and simulation modeling (e.g., ungulates; Turner et al. 1994; Pearson et al. 1995).

This understanding helps interpret differences in the performance of migrants on different landscapes. Landscape E consistently ranked high because it has the highest abundance of category 3 and 4 habitats (Table 52.4). Moreover, this map has the highest level of contagion (Table 52.4), driven by the extensive well-connected regions of category 3 habitat. The number of successful migrants is highest on this map (Table 52.7, Fig. 52.3). Habitat generalists do better than specialists do in this landscape because of their higher foraging returns in category 3 habitats (Table 52.2, Fig. 52.4). In contrast, compare landscapes A, B, and C. These three landscapes have a similar level of contagion (Table 52.4). However, the greater abundance of high-quality habitats in landscape A increases the average quality of cells encountered during stopover. This difference results in a greater chance of successful stopover (Fig. 52.3) and fewer cells being visited by successful birds (Fig. 52.4) than in landscapes B and C. Whereas successful habitat generalists visit fewer cells than specialists in landscapes B and C (Fig. 52.4), the greater abundance of category 4 habitats in landscape A (Fig. 52.2) allowed specialists to visited fewer cells than specialists in this landscape. Specialists also had a higher probability of successful migration in landscape A relative to B and C (Fig. 52.3). Thus, this simulation model provided a means to evaluate the relative quality of landscapes from the perspective of birds that have different habitat needs. It also provides a mechanistic understanding of stopover habitat use that enhances our ability to interpret metrics of habitat pattern.

The strengths and weaknesses of a given model should be known by the users. The main value of the simulation model used in this study is to illustrate the complex interactions that shape the process of songbird migration. The factors shaping that process include the pattern, abundance, and quality of stopover habitats, and the mobility and foraging ecology of individual migrants. The individual-based model provides a means to compare landscapes from a less-anthropocentric perspective. The specific weaknesses of this model include the fact that (1) we have little knowledge about how variations in habitat quality at stopover sites translate into different rates of energy gain for migrants even though data on relative abundance of migrants, residency times, and fat condition in different habitats are available; (2) we have little data on movement patterns of migrants during at stopover sites (but see Aborn and Moore 1997); and (3) we know little about the settling patterns of migrants at migratory stopover sites.

Important Considerations in the Use of Metrics and Models

At present, approaches to measuring landscape characteristics include (1) metrics of landscape patterns, and (2) implementation of spatial models. Both of these methods allow the researcher or manager to rank a series of real or hypothetical landscapes based on the abundance and spatial arrangement of habitats. Ranking landscapes with respect to their suitability for a given population or suite of species can be challenging. Obviously, the ranking will depend on the method for quantifying landscape suitability. Researchers and managers should ideally use methods that are both realistic and appropriate for the species of interest. Landscape metrics are useful if they can be readily interpreted—that is, if variation in a metric can be directly related to an important aspect of the species' biology. Some progress has been made in this area, but better links between metrics and specific ecological processes need to be forged. Approaches such as the habitat suitability index move a step beyond the use of landscape metrics because these indices can incorporate the positive and negative influences of diverse habitat measurements from a variety of scales. Spatial models can be more realistic because they can incorporate more-complicated aspects of the species' habitat use, such as the consequences of movement and habitat use on survival and reproduction.

Although spatial models can be realistic, tradeoffs will exist between the general use of a model and the number of assumptions it makes about the species' ecology. The design of any complex model will involve making assumptions about habitat selection or other aspects of habitat use. These assumptions should be testable, or models should be based on our best understanding of species biology. Models involving many precise parameters and detailed mechanisms (e.g., fine-grained habitat selection, movement between cells) are fraught with many more assumptions than models that have fewer details and are more general in design.

Conservation programs often raise questions about the ecology of species, reserve design, or other management issues for which definitive data are not available and/or are difficult to collect. Spatial analyses and modeling are tools that can be useful in making the best of these difficult situations, as long as the model results are viewed within a context of model design, assumptions, parameter values, and spatial (or other) data. Models and analyses based on the current best understanding of a species' ecology can make it possible to pose meaningful "what if" questions about management alternatives or ecological processes. These explorations often generate a better understanding of the system in question, and they can produce hypotheses that can be tested with empirical data from field studies.

Summary

Stopover habitat use presents challenges to research and management due to its broad spatial extent and seasonal, ephemeral time span. A landscape-level approach is essential. Understanding gained from field studies can guide landscape-level analyses that in turn can be used to develop testable hypotheses for future research or to inform difficult management decisions. This study produced findings relevant to management. Landscapes with the greatest amount of high-quality habitat were most suitable, but the spatial arrangement of habitats modified suitability. For example, the fragmentation of habitats as measured by interspersion can be good or bad depending on mean habitat quality experienced by migrants. Decrease interspersion if mean quality is too low. Spatial arrangement becomes more important as landscape-wide average habitat quality declines. Moreover, landscape suitability depends on habitat specialization; the relative performance of generalists and specialists depends on the details of the relative abundance and spatial arrangements of habitats. Given the broad spatial extent of bird migration, policies that favor the protection of high-quality habitats throughout the landscape, including private lands, would be more beneficial than the purchase and management of a few preserves of limited spatial extent.

Acknowledgments

This work received support from a grant from the National Science Foundation DEB 9416803, the U.S. Fish and Wildlife Service, the National Park Service, and the U.S. Geological Survey, Biological Resources Division. The habitat maps were derived from a Landsat image classified by P. O'Neil, U.S. Geological Survey. J. M. Scott and two anonymous reviewers provided valuable comments on the original manuscript.

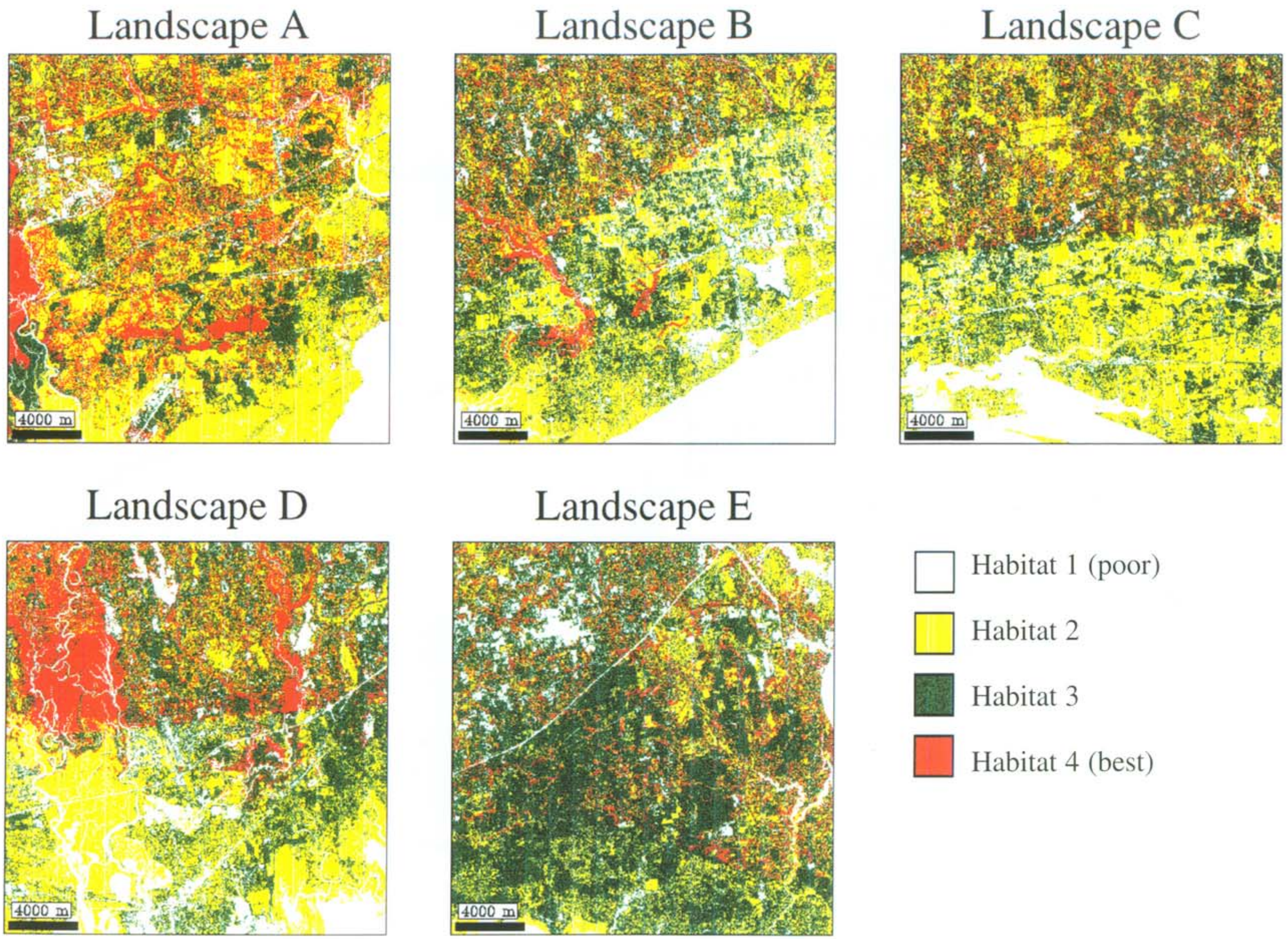

Figure 52.1. The spatial pattern of habitats in five study landscapes of the Gulf Coast. Each study landscape is 25 kilometers by 25 kilometers.