

PART 2

**Remote sensing of Cape Sable Seaside Sparrow breeding
habitat and determinants of territory density**

Abstract

Satellite data and demographic surveys of Cape Sable Seaside Sparrow breeding activity were used to construct a model to identify potential breeding habitat. A number of habitat rules were resolved to define the spatial extent of potential breeding habitat. The territory density of sparrows was found to be an increasing function of the percent cover of a particular habitat supertype (aggregation of structurally similar habitat classes). This habitat class includes floral alliances similar to those previously found to be associated with known breeding areas. Furthermore, sparrow territories were found only in areas where a minimum critical threshold coverage of that habitat supertype was exceeded. Analyses of seven years of population survey data for this area reveal recent declines in breeding territory density. These declines show a spatial pattern. Territory densities are declining in the drier habitat near the center of the largest sub-population, but are stable or slightly increasing in the peripheral marshy areas (with low breeding habitat cover in 1993). We suspect these declines are due to microhabitat changes, shrub invasion or anthropogenic disturbance. We compare habitat selection characteristics of the Cape Sable Seaside Sparrow with those of other Seaside Sparrow races at the scale of their "ecological neighborhood". Finally, we highlight the advantages of combining this model with a spatially explicit population model for conservation management of this species.

dissimilar to the effect of hydrology on other Seaside Sparrows. Salt marsh races breed in habitat located above tidal extremes, but even this habitat can be flattened by storm surges, heavy snows, and even ice flows at more northern latitudes (Post 1974).

Fire is another major factor shaping habitat availability for the Cape Sable Seaside Sparrow. The temporal and spatial patterns of hydrologic disturbances, in association with topography and the effects of fire, result in a patchy landscape. In the prairies of the southern Everglades moderate flood levels may isolate islands of higher elevation from the spread of flames. Also, fire cannot directly affect any flooded habitat, although nutrients released by fire may subsequently be transported by wind or water to affect unburned habitat. Fire also maintains the grassland prairies by removing young hardwood trees and invasive shrubs (Craighead 1971). Fluctuating hydrologic patterns cause the distinct habitat types of the Everglades to be organized along isoclines, ranging from wet marsh to drier prairie. These processes of fire and hydrology result in a mosaic of seres, some of which provide optimal breeding habitat, whereas others lack the structural or biotic characteristics typical of breeding habitat (Lockwood et al. in prep., Mayer et al. in prep.).

Various studies suggest that higher patch heterogeneity is associated with Seaside Sparrow breeding areas (Post 1974, Post et al. 1983, Werner 1975, Werner and Woolfenden 1983, Greenlaw 1983, Curnutt et al. 1998). In this paper we examine the characteristics of local heterogeneity that define suitable Cape Sable Seaside Sparrow breeding habitat.

Remote sensing and GAP analysis

GAP analysis is a mapping process whereby image processors and botanists analyze remotely sensed spectral data from satellites. They use field and aerial photograph/videograph groundtruthing data to classify the type of vegetation/habitat that dominates a particular location. This type is correlated with the spectral signature produced by seven wavelength bands in the LANDSAT image, for that location. Any other pixel (~28.5m resolution) in the image with the same spectral signature is classified as that type of habitat.

Our analysis utilized The Nature Conservancy's (TNC) GAP-analyzed vegetation map (from NASA LANDSAT satellite data) of the southern Florida Everglades (The Nature Conservancy 1993/1994). We determined the broad-scale vegetational characteristics and the local heterogeneity associated with locations of breeding sparrows in the southern Everglades. We mapped the known locations of breeding Cape Sable Seaside Sparrows over the TNC vegetation map and analyzed the habitat characteristics in the vicinity of those locations. This process resulted in a set of rules that define potential sparrow breeding habitat, which we then applied to the entire habitat map. This resulted in a map of potential Cape Sable Seaside Sparrow breeding habitat. We applied this technique to two sub-regions, each of which defines the extent of distinct sparrow sub-populations, and asked whether the same habitat rules apply to both. Furthermore, we explored the relationship between breeding territory density and the percentage coverage of breeding habitat as defined by this model.

Seaside Sparrows and landscape heterogeneity

It is clear that Seaside Sparrows respond to patch heterogeneity within the ecosystems they inhabit and that they are opportunistic and can quickly adapt to changing conditions. Post (1974) reported space related behavioral differences within a population of the Northern Seaside Sparrow (*A. m. maritimus*) after winter storms altered the habitat. In one year, pairs of Seaside Sparrows defended large distinct territories (in which they both nested and foraged) within extensive patches of salt marsh habitat. By the next breeding season winter storms had flattened much of the area leaving only smaller islands of suitable breeding habitat. Returning sparrows established smaller territories in these patches but foraged farther afield in local ecotones.

A comparative ecological study by Post et al. (1983) showed that a Florida population of *A. m. maritimus* preferred to nest in less tall and dense vegetation than their New York counterparts, and that their foraging behavior corresponded to the geographically different invertebrate distributions. Although the percentage coverage and plant diversity of the southern salt marsh habitat was higher than that of the northern salt marsh, resulting in a different appearance, various structural measurements classified them as similar. This phenomenon is also true for the Cape Sable race in that at least two sub-populations inhabit areas with differing relative dominance of prairie vegetation alliances but with similar structural variables (Mayer in prep.).

Patch heterogeneity of marshes in which Seaside Sparrows breed may differ at a local scale. Greenlaw (1983) studied two neighboring marshes, Oak Beach and West Gilgo marshes on Long Island, New York, inhabited by Seaside Sparrows. The spatial heterogeneity of vegetation patch type differed between these marshes and "involves only a comparatively few species of plant, [and] is conspicuous to an observer on the ground observations and in high-resolution aerial photographs". Greenlaw mapped the extent of vegetation patches, superimposed individual sparrow territories and concluded that habitat use (and behavior) differed across a gradient between low elevation marsh and high elevation marsh. In low elevation marsh, territories were contiguous or slightly overlapping. They incorporated a mixture of brackish pools and mud pannes within a matrix of tall and short forms of cordgrass. In higher marshes, territories were more discrete and centered upon patches of a low shrub (*Iva frutescens*) surrounded by mixed salt-meadow grasses (*Spartina patens*, *Distichlis spicata*).

These observations reveal that Seaside Sparrows are able to exploit different habitats and their breeding behavior may vary within and between geographically isolated sub-populations.

Distribution of the Cape Sable Seaside Sparrow

The Cape Sable Seaside Sparrow was originally described as inhabiting the cordgrass (*Spartina*) dominated coastal prairies of Cape Sable (Howell 1919). Since then the vegetation patterns in that area have changed drastically and the area is now dominated by halophytic shrub species (Taylor 1983). This change is attributed to the effects of the

1937 hurricane, which deposited a 4-meter high storm surge across Cape Sable. The modern distribution of the sparrow includes habitat dominated by muhly grass (*Muhlenbergia capillaris*) in drier locations, and sparse sawgrass (*Cladium jamaicense*) in wetter locations and now more rarely cordgrass (Curnutt et al. 1998, Werner 1975, Werner and Woolfenden 1983, Bass and Kushlan 1982). A number of other grass and sedge genera are found associated with Cape Sable Seaside Sparrow habitat, including *Rynchospora*, *Eragrostis*, *Panicum*, *Eleocharis*, and *Andropogon*.

Since 1975 the sparrow has disappeared from Werner's study area, which was located on both sides of the main road through the Everglades National Park, east of the bridge crossing Taylor Slough. The area was then dominated by muhly grass and is now dominated by dense sawgrass; this community shift is attributed to the effects of long term flooding (Nott et al. 1998). There is no exact record of how long *Muhlenbergia* dominated prairie has existed in the southern Everglades. Porter (1967) describes prairie with the current Big Cypress National Preserve, in which *M. capillaris* was the dominant species in 1965. Although Porter claims that Davis (1943) did not find muhly grass in Big Cypress at that time, this is untrue. Davis clearly describes *M. capillaris* as a tall grass frequently found in this area (p.164). With regard to the southern Everglades (p.268), Davis may have confused *M. capillaris* with one of the bunchgrasses he ascribed to the genus *Aristida*, some species of which are very similar in appearance if no inflorescence is present. Therefore, it is possible that the Cape Sable Seaside Sparrow inhabited the southern prairies, outside of Cape Sable, many years before they were described in this area. (Otherwise, *M. capillaris* is commonly

found associated with dune succession (Johnson 1997) in northeast Florida, and was used for basket weaving by several North American Indian tribes (Anonymous 1994).)

Appropriate scale of investigation

Satellite imagery allowed us to determine spatial heterogeneity at multiple scales but the choice of scale requires careful consideration. The spatial resolution of the analysis should be determined by the home range or activity space of the organism in question (Addicott et al. 1983). We adopted the term "ecological neighborhood" to describe this scale. At too coarse or fine a resolution the ecological response of a species may not be detectable (Pearson 1993). Wiens et al. (1987) studied patterns of habitat association among shrub-steppe birds at a variety of scales. They concluded that variations in population densities correlated with different variables at each scale. They state that the patterns of habitat association were dependent upon the scale of the investigation. For the purposes of this investigation we consider the scale of the Cape Sable Seaside Sparrow's breeding activity.

Firstly, the size of an individual territory is approximately 100m across (Pimm et al. 1995). This represents the minimum resolution applicable. Secondly, Cape Sable Seaside Sparrows are gregarious during the breeding season and occupy discrete but nearly touching, or slightly overlapping, territories (Post 1974, Werner 1975, Greenlaw 1983). Thirdly, recent studies (unpubl.) show that in the non-breeding season sparrows remain in the region containing their nesting areas,

moving a maximum of only a few kilometers from their natal or breeding site. For these reasons a cell resolution of 500m is the logical choice to represent the activity space of a group of breeding sparrows. Conveniently, the effective resolution of the demographic survey matches the ecological scale; observers can detect birds several hundred meters distant in any direction.

Identifying sub-regions

A false color satellite image (Figure B-1) depicts The Nature Conservancy's (TNC) vegetation map (The Nature Conservancy 1993/1994) for the southern tip of Florida. Superimposed upon this map are the locations of singing male sparrows (blue triangles) surveyed during the 1993 breeding season. We chose this year because the satellite image used for the TNC vegetation map was obtained during the drier periods of December 1993 and April 1994 and ground-truthed shortly afterwards. In that year, three trained observers conducted a helicopter-based survey of breeding sparrows, in accordance with established protocols (Kushlan and Bass 1983).

The geographic range of the sparrow shown in Figure B-1 is easily split into three sub-regions. The three rectangles (bordered in red) encapsulate the "western", "eastern" and "Ingraham" sparrow sub-populations that we considered separately. Table 1 provides the Universal Transverse Mercator (UTM) coordinates which describe the spatial extent and also the size of the resultant 500m resolution landscape associated with each area modeled. This study considers the western and Ingraham sub-regions in detail.

Table 1. Corner coordinates (Universal Transverse Mercator projection) of the extent of sub-regions within the geographic range of the Cape Sable Seaside Sparrow and row-column sizes of resultant landscapes (500m resolution cells). The total number of sites surveyed, and the number of sites occupied by singing males, were extracted from the 1993 demographic survey data.

	Sub-region		
	Western	Ingraham	Eastern
North Row UTM's	2 851 069	2 812 569	2 830 069
South Row UTM's	2 821 569	2 795 569	2 808 569
West Column UTM's	499 665	516 165	522 165
East Column UTM's	517 665	540 165	544 165
Rows	59	34	43
Columns	36	48	44
No. Survey sites	363	204	
No. Occupied sites	17	62	

These areas are shown in more detail (28.5-meter pixels) with a 500m grid superimposed on each habitat map in Figure B-2(a,b,c). The cells containing singing male sparrows, as surveyed in 1993, are shown as red squares. Table B-1 provides a color-coded key to the TNC vegetation type classifications, which are also assigned a number and brief description.

Methods

Habitat associations

Cape Sable Seaside Sparrows breed in grassland habitats and are not associated with habitats dominated by pine forest or cypress domes. Although individual breeding territories do not contain shrubs or trees of any kind, small tree islands that typically dot the prairie landscape may separate them. It is thought that such features are avoided because they provide cover for predators. Both hawks and snakes are known predators of the Cape Sable Seaside Sparrow.

To determine the sparrow's tolerance to each of ~40 individual habitat types for each sub-region, we counted the number of 28.5m-cells of each habitat type within each 500m resolution cell (maximum of 308 equals 100%). We expressed each count for each cell as percentage cover. For each sub-region we extracted a number of 500m cells (Table 1) associated with the known locations of breeding sparrows observed in the 1993 extensive sparrow survey. Comparing these cells we determined the number of breeding sites associated with an increasing percentage cover of each habitat type. Then for each habitat type we recorded the maximum percentage cover (MPC), associated with cells where singing males were detected (Table 2). An MPC level of 41 indicates that no breeding site is covered by greater than 41% of that type. We also expressed the number of sites containing each individual habitat type as a percentage of the total number of sites (OCC). What we are interested in is the presence (or absence) of breeding activity as a function of the amount of each type of habitat cover in the 500m cells.

Table 2. Tolerance and vegetation type coverage measurements (by habitat supertype category) for the Western and Ingraham sub-populations of Cape Sable Seaside Sparrow. Estimated from The Nature Conservancy vegetation map of South Florida. Only habitat types present in one or the other region are shown. See text for detailed descriptions of variables.

Western					Ingraham				
TNC habitat					TNC habitat				
Type number	MPC	OCC	MPC	OCC	Type number	MPC	OCC	MPC	OCC
Dry					Tree				
29	85	100	79	84	1	12	47	10	16
33	81	94	100	98	9	3	29	14	19
30	27	65	76	81	8	6	24	1	3
39	6	41	1	2	19	2	12	11	3
					3	1	0	1	0
					21	1	0	1	2
Marsh					6	1	0	1	0
25	52	94	14	50	13	1	0	1	0
34	47	76	10	53	15	1	0	6	10
24	15	35	1	5	2	1	0	1	3
23	24	41	6	11	7	1	0	5	5
32	27	29	10	65					
40	1	6	1	0	Other				
38	1	0	1	0	26	16	29	8	6
41	1	0	2	2	36	1	0	1	0
0	1	0	1	2	35	1	0	1	0
31	1	0	1	0	37	1	0	1	0

First we ranked the habitat types by MPC for each sub-region and tested whether they were significantly different from one another using Kendall's rank correlation.

Habitat supertypes

Our primary objective is to identify those 500m cells that contain potential breeding habitat. If territorial males have a preference for a particular habitat type(s), we would expect to find a high percentage cover of that type associated with most of the cells they occupy. Below

a given percentage cover of this habitat type we would expect to find fewer or no territorial males. Conversely, if territorial males have an aversion for a particular habitat type(s), we would expect to find a small or no percentage cover of that type associated with most of the cells occupied by territorial males. Although these habitat types may be utilized for other purposes (foraging or non-breeding season habitat), they do not provide suitable nesting habitat. For instance sawgrass sways are a common feature of the prairie in which sparrows are known to forage but not nest. Likewise, small tree islands and cypress stands exist in the prairie breeding grounds but are not utilized for nesting or foraging. For these reasons we classified the range of TNC habitat types to represent breeding and non-breeding habitat.

We know that the Cape Sable Seaside Sparrow nests in both muhly grass and sparse sawgrass dominated areas. We selected a set of TNC habitat types corresponding to the "sparse *Cladium* prairie" and "Muhlenbergia prairie" breeding habitats described by Werner and Woolfenden (1983). They represent drier habitat types in which nesting may occur and this set is henceforth referred to as "dry" habitat supertype (TNC habitat classes 29, 30, 33, and 39 in Table 2). We expected most occupied cells to contain a higher percentage cover of this supertype. Accordingly, we plotted the number of breeding sites against the combined percentage cover of this supertype and recorded the minimum percentage coverage associated with cells in which singing males were detected (a few outlying points were discarded if they were isolated from the continuous distribution). This value is termed the minimum threshold of dry prairie habitat supertype (MINDRY).

We also know that Seaside Sparrows do not breed in wetter locations, where a longer hydroperiod does not allow completion of the 33-45 day breeding cycle (Lockwood et al. 1997). We chose a set representing the "marsh" habitat supertype (TNC habitat classes 0, 23, 24, 25, 31, 32, 34, 38, 40, and 41) containing individual types associated with long-hydroperiods (shorter dry period). We would not expect high percentage cover of this habitat supertype to be associated with high territory densities, so we determined the maximum percentage cover recorded in cells containing singing males. This value is the maximum threshold of the marsh habitat supertype (MAXWET).

As we mentioned earlier, Cape Sable Seaside Sparrows are known to avoid trees when establishing breeding territories. We chose the TNC habitat types 1 through 22 as the "tree" supertype. This includes pine, hardwood, cypress, willow, mangrove and a number of different shrubland alliances. Although larger patches of trees are apparent throughout the Everglades landscape in the TNC habitat map, patches that are sub-28.5m resolution may remain undetected. We complemented the TNC map by including the locations of tree infested survey sites from the 1992 survey data when O.L.Bass, Jr. of the Everglades National Park recorded the main tree types occurring within the sparrow's range.

We plotted the number of breeding sites against the percentage cover of the tree supertype and recorded the maximum percentage cover associated with a cell where territorial males were detected (a few outlying points were discarded if they were isolated from the continuous distribution). This value is termed the maximum tree habitat threshold

(MAXTREE). We determined the frequency distributions of each supertype (for occupied sites only). Finally, because we know the sparrow utilizes both dry and wet prairie types, as shown above, we combined the "marsh" and "dry" habitat types and determined the minimum percentage coverage for inhabited cells (MINCOV).

We summarized the results of this analysis in Table 3, created a map of breeding and non-breeding habitat and superimposed the 1993 distribution of territorial males.

Sparrow survey protocol

An important assumption of the survey technique (Bass and Kushlan 1983) is that the number of singing males detected at any survey site reflects the density of territories in the vicinity of that site. This survey is conducted annually during the sparrow breeding season, in the months of April and May. Each day an observer(s) visits a number of

Table 3. Estimates of the minimum dry supertype cover threshold (MINDRY), maximum marsh supertype cover threshold (MAXWET), minimum dry + marsh supertype cover threshold (MAXCOV) and maximum tree supertype cover threshold (MAXTREE) of Cape Sable Seaside Sparrow breeding habitat for each sub-region.

Habitat supertype threshold variable	Model sub-region	
	Western	Ingraham
MINDRY	56	54
MAXWET	46	35
MINCOV	94	91
MAXTREE	5	9

sites (20-30) arranged at the vertices of a fixed 1-kilometer grid. Over a ten-minute period the observer records the number of singing males, water levels, vegetation coverage, and dominance. The daily transects are chosen in accordance with a stratified random sampling method. In this way it is unlikely that a site is ever visited on the same day in subsequent years.

Predicting territory densities

We expected the potential territory density to increase with the percentage of dry habitat supertype present. To explore this hypothesis we regressed the maximum number of males, observed during the 1993 survey, against the percent cover of dry habitat supertype for each area. However, adverse weather conditions or standing water may reduce the number of actively singing males detected at a site in any single year, and 1993 was a wetter than average year. For this reason we recorded the highest number of singing males observed in any year between 1993 and 1998 at each survey site. Because a stratified random survey technique is used, it is likely that a site that was visited on a "bad" day in one year was visited on a "good" day in at least one other year. Therefore, using the maximum recorded number of singing males should give us a better idea of the maximum number of territories a cell can support.

A potential problem with this approach lies in the fact that the habitat rules refer to the state of the landscape in 1993. It is inevitable that habitat dominance within some portions of it will have since changed. If the habitat within a cell degraded between 1993 and

1998 (and potential territory density decreased) we would expect a high number to have been recorded earlier in the period. Conversely, if the percentage of suitable breeding habitat within a cell improved we would get a higher maximum density than was possible in 1993. Despite this possible bias we felt this was the best method to use because, as we shall see, the population is in general decline.

We also obtained an estimate of the upper limit (maximum territory packing) to this relationship for each sub-population. We used a quartile regression technique (Scharf et al. 1998), which is useful when examining potential ecological relationships at the boundaries of the polygonal shaped scatterplots so common to ecology. Lanza et al. (1986) used a similar method to establish the relationship between habitat suitability and point counts for three avian species; pine warbler, prairie warbler, and pileated woodpecker. In this case we used 4 categories of percent cover (each with an equal number of data points). For each of these four sets of data points we discarded all but the top 25% of values (singing males). We then performed an ANOVA on this 75th quartile of singing males by cover category. This method is particularly applicable to the results of the survey because our interest lies in establishing a relationship that describes the maximum number of territories that a given percentage of habitat type can support. It removes the lower counts that resulted from visiting sites on days when the conditions were unfavorable for singing. The quartile categories for dry cover habitat are 25th=88.4, 50th=97.1 and 75th=99.55.

Inspection of the maps of survey data for this area revealed a possible decline in the center portion of the Ingraham breeding range. To test

this we obtained an estimate of the trend in the number of singing males recorded over seven years (1992-98 inclusive) for each survey site in the Ingraham area. To account for "bad" survey years, we took the maximum level recorded in the period 1995-1998 and subtracted the maximum level recorded in the period 1992-1994. We only chose those sites occupied for five years or more (occupation levels were too low in recent years across the Western area to apply this technique to those data). We calculated the number of territories lost between these two periods, identified the geographic center point of the Ingraham breeding range and looked at the relationship between the distance from the geographic center of the area and the loss or gain of territories using linear regression.

Results

Regional habitat patterns

Figure B-1 shows that Cape Sable Seaside Sparrows appear to occupy similarly colored areas west and east of Shark Slough. In the west they predominantly occupy the sparse *Cladium*-alliance (TNC type 29) that dominates the areas on the flanks of East Slough but are also found in the drier *Muhlenbergia*-alliance (TNC type 33) dominated areas. Of a total of 29 habitat types present in all survey sites, 17 are represented (by more than 1% total coverage) in the Ingraham sites and 20 in the western sites, with 14 types in common. In the Ingraham sub-population the situation is reversed, with most sites occupied by sparrows being found in the dry prairie areas. This visual interpretation is supported by the results shown in Table 2. The

magnitude and rank order of individual MPCs are not significantly different between the western and Ingraham sub-populations (Kendall's $\tau_b = 0.538$, $p=0.01$). We excluded cases with joint absence of habitat types from the calculations of Kendall's τ (Bullock 1971). Clearly, there is a difference between the sub-regions in the heterogeneity of habitat types found within cells where singing males were detected. The western sub-region contains higher values of OCC for most of the marsh types than the Ingraham sub-region. This means that relatively more cells contain at least some marsh in the western sub-region. Interestingly, Nott et al. (1998) showed a significant shift towards marsh species in this area since 1992.

In general all sparrow sites have less than 40% marsh supertype coverage and greater than 50% dry supertype coverage (Figure B-3). Clearly, territorial males show a preference for dry habitat and an aversion to marsh habitat. These superotypes are commonly spatially correlated with each other across the landscape and represent the gradient from high elevation dry prairie to low elevation marshland. Not surprisingly, then the combined coverage of these types exceeds 90% in all but a few sparrow occupied cells. We regarded those cases outside the continuous distribution as outliers (possibly due to habitat misclassification or spatial inaccuracy in the survey location) and discarded them. The coverage thresholds of each supertype are comparable between sub-regions (Table 3). These supertype thresholds provide the rules by which breeding habitat and non-breeding habitat are defined.

Regional maps of breeding habitat

A map summarizing these results for the western sub-region is shown in Figure B-4 (see Figure B-7 for Ingraham sub-region). For the western area suitable breeding habitat (light colored background) lies mainly within a north-south oriented strip representing East Slough (Figure B-2b). From this strip, narrow corridors follow small tributaries draining southwesterly from the higher ground of Rattlesnake Ridge. Much of the area is unavailable for breeding due to the presence of trees (vertical crosses), insufficient dry habitat coverage (MINDRY), or less than the combined coverage of the marsh and dry supertypes (diamonds). Cells marked with diagonal crosses represent those dominated by marsh habitat types. The yellow dots represent cells in which territorial males were detected in 1993.

The sparrow breeding grounds of the Ingraham area are less fragmented than those of the western area. They are bounded by pinelands to the northeast, marshier habitat of to the southeast (Taylor Slough) and northwest (Shark River Slough), and semi-permanently flooded shrubland (also depicted as vertical crosses) to the southwest.

Sparrow territories and habitat type cover

The results of the regression of singing males against dry habitat coverage in Figure B-5a reveals a significant positive relationship between the number of males detected in the 1993 survey year and the percentage coverage of the dry (breeding) habitat supertype. Not

surprisingly, relationship is negative but less significant for the marsh supertype and not significant against percent coverage of the combined supertypes (not shown). This supports the hypothesis that sparrow territory density increases with the percent cover of dry habitat supertype.

The upper quartile ANOVA of the maximum number of singing males (observed in any year between 1992 and 1998) by dry habitat cover class reveals a clear and positive relationship ($p=0.001$) between the maximum territory density and the dry habitat supertype cover (Figure B-5b). This ranges from a mean of 3.8 territories for the lowest category (50-88.4%) to over 5 for the highest category (>99.55%).

Since 1992 there has been a general decline (-13%) in the number of male territories detected in the Ingraham area. Inspection of Figure B-6 reveals a spatial pattern to these declines. The sites close to the center of the range (shown in Figure B-6) lost territories (downward pointing triangles), whereas sites at the southern periphery made slight gains (upward pointing triangles). This is supported by Figure B-7, which shows a significant negative relationship between the decline in territory density and the distance from the center of their range. Generally, dry habitat coverage declines towards the peripheral areas.

Discussion

Of the many questions that remain to be answered about Cape Sable Seaside Sparrow (and all avian species) population dynamics, at least three of them concern their choice of breeding habitat. Firstly, what kind of habitats do they breed in and how can we recognize them? Secondly, once an area has been chosen what are the biotic and structural characteristics that define a territory? Lastly, what fine scale characteristics determine the choice of nesting site within a territory? This study only addresses the first of these questions.

Habitat rules

The methods we used here appear to successfully answer this first question. We can now delineate the extent of potential breeding habitat from satellite imagery, at least at the scale of the sparrow's ecological neighborhood. Clearly, combinations of individual TNC habitat types are important for the sparrow and it appears that the higher the percentage of the drier prairie types the higher the territory density. Our results indicate that it is possible to predict territory density based on the local percent cover of this type, which is resolved from satellite imagery. Within a 500m cell sparrows require that at least 50% of the area is covered with the dry supertype. Furthermore, the total coverage of this and the marsh supertype must exceed 90%. This is consequence of the spatial patterns of elevation (topography) and seasonal flooding levels, which determine the relevant proportions and proximity of the supertypes. Only small fractions (<10%) of other types (mainly trees) are present. This is in accordance with field observations within the long-term study plots whereby small tree islands and the occasional cypress dome are scattered throughout

the prairie matrix in which sparrows successfully breed. It appears that such features are more common within the western region where 8 of the 17 occupied sites contained small patches of trees.

The values of the minimum levels of dry habitat coverage (MINDRY) for both sub-regions correspond to the generally accepted threshold of 59% coverage, below which landscape connectivity drops to very low levels (With et al. 1997). This phenomenon of percolation theory relates to an organism's ability to move through a landscape from cells of one type to cells of the same type. Just below this threshold the probability of moving to suitable habitat cells without crossing cells of another type drop precipitously to very low levels. This may be critical if the cells it has to cross contain habitat that represents a psychological barrier to movement. Along with this sudden drop in connectivity, there is also a shift in the distribution of patch size, from few large patches to many small patches of contiguous habitat. Below the critical level it is unlikely that a patch large enough for a single territory exists. The level of fragmentation is an important issue for a species such as the Cape Sable Seaside Sparrow. It is not only secretive and requires large areas of dense grassland within which to establish breeding territories, but it also appears to have an aversion to treelines (Dean pers. comm.). Our results show that above the critical level of coverage the number of territories a 500m cell can support rises.

Habitat use

The predictive maps of potential breeding habitat (Figures B-4, B-7) reveal the presence of small areas in which breeding sparrows have never been observed. There are many possible explanations for this and the real reason may involve a combination of several. Assuming these areas are in fact dominated by prairie (and not misclassified by the GAP-analysis technique), it is possible that the finer scale structural characteristics of the vegetation make it unsuitable for sparrows to breed in. Sparrows choose nest sites based on the presence of a few discrete perches (normally *Cladium* inflorescences) adjacent to thick graminoid ground cover (Lockwood pers. comm.). In the Ingraham area this cover is dominated by muhly grass, which provides a raised mat of dead material upon which the nest can be built (Lockwood et al. 1997). Typically, live muhly grass provides a "roof" over the nest site.

Such characteristics develop over a number of years after fire and local territory density increases accordingly (Werner 1975, Werner and Woolfenden 1983). Suitable characteristics may then persist for a number of years before shrub and tree invasions occur, Curnutt et al. (1998) suggest that high densities may still be found 13 years after fire. A fire burned much of the Ingraham area in 1989 but high numbers of breeding sparrows have been observed there since 1992. Taylor (1983) implicates soil depth in the speed of the recovery process whereby deeper soils allow faster recovery.

Declining territory densities

It appears that there is general decline in the number of territories in the Ingraham area and that they are selectively being lost from the

center of the distribution. However, territory density has slightly increased in the peripheral areas closer to the marsh dominated areas. This is opposite to the situation in the western breeding area. The Ingraham area is a gently sloping plain across which water flows from northeast to southwest. The highest cover of dry habitat is in the center; however, the higher ground of Old Ingraham Highway, which supports trees and shrubs (and potential predators) bisects this area.

It is reasonable to assume that, in the Ingraham area, territory density is declining due to habitat degradation. There are two possible explanations, both of which pertain to succession and the effects of fire. Firstly, shrub invasion invariably happens in areas adjacent to tree dominated areas, where the tree seed bank is richest. The old highway is also associated with abandoned agricultural areas abandoned in the 1930's. The road is constructed of rock "borrowed" from a canal which runs parallel to it and the "ridge and furrow" farming techniques are visible in satellite images of the area. The ridges of these features represent higher ground and encourage the spread of shrubs and trees by providing woody plants a refuge from seasonal flooding.

Despite the proximity of many sparrow territories to these areas and the threat of gradually spreading shrub habitat, the fine-scale structure of the prairie may also have changed since the fire of 1989. Lockwood (pers. comm.) and Taylor (1983) suggest that sparrows prefer to choose territories in areas that are not too choked with dead vegetation. After a fire the amount of dead material accumulates over time. In the first year the vegetation appears too sparse to support nesting sites. Taylor (1983) reported that territory density increases

as the ratio of live to dead material decreases, but begins to decline after four years. It is possible that the birds abandon their territories because they can not successfully forage in tangles of dead material. Either they have difficulty moving freely, or invertebrate prey items can escape more easily. If this is true, these areas should be the immediate concern of fire management. If ground surveys detect high frequencies of shrub invasion and increased proportions of dead material (detailed plant surveys have been conducted since 1994) then managed burning may help these areas recover.

Unoccupied habitat

Obviously, this GAP-analysis technique is not able to differentiate between suitable and unsuitable habitat based on fine-scale (<28.5m) structural and floristic characteristics. It is also possible that some unoccupied areas we define as potential habitat may be misclassified and do not contain the vegetation alliances attributed to them. It is entirely possible that extensive shrub invasion may not be detected by satellite imagery (i.e. they represent sub-28.5m features). Analysis of aerial photography (Digital Orthographic Quadrats) may support this hypothesis or reveal other fine-scale characteristics and features that inhibit breeding behavior.

Another reason these areas are unoccupied is that sparrows may not have found them. Barriers to dispersal can isolate habitat; in the Everglades small patches of muhly prairie exist within the cypress-dominated areas west of Shark River slough, and within pine forests adjacent to the Ingraham breeding areas. To date sparrows have not been

detected in these patches (O.L. Bass Jr., J.L. Curnutt pers. comm.). Sparrows tend to avoid expansive areas of trees and it would be unlikely that they would penetrate far into a forest. They also fly very low and therefore would be unlikely to be found flying over a forest.

Alternatively, individuals of low-abundance populations may not have encountered available breeding habitat. Sparrows are highly philopatric, returning to within 300m of their nest site between years (Lockwood in prep.). If sparrow productivity is low in such populations there is little chance of dispersal and recruitment into unoccupied areas. In addition, as in many passerines, con-specific attraction is clearly part of their behavior. They are not found in single isolated territories. Typically a 500x500m patch of breeding habitat will contain upwards of eight discrete or slightly overlapping territories. This is not unusual for grassland passerines but it means that many low abundance populations are found in small isolated clusters.

Usefulness as a management model

From the above considerations, it is clear that predicting the demographic patterns of the Cape Sable Seaside Sparrow is not a simple matter of just detecting suitable habitat. For dispersing individuals, chance may determine whether a sparrow finds suitable habitat or not. If an isolated patch is inhabited by an older group of individuals, it may become unoccupied if their breeding effort fails, and they all die out within a short period. A patch of suitable habitat may be inaccessible due to the type of vegetation surrounding it. The recent

high water levels have fragmented the western prairies into small breeding areas isolated from one another, and the population has declined. Only small aggregates of breeding individuals remain that will take some time to produce enough recruits to fill the breeding habitat that may become available if future years are drier. It is for these reasons that merely defining the extent of potential habitat is of limited use to the conservation management of this (and other) species.

We can now model breeding habitat availability (this paper), and historical hydrologic patterns relative to topography (Nott et al. 1998, previous chapter). It is therefore, possible to construct a spatially explicit population model and attempt to describe the historical demography of the Cape Sable Seaside Sparrow sub-populations. This effort will be based on our knowledge of the sparrows' ecology and breeding behavior; and is the subject of the next paper in this series.

This study successfully manages to identify the coarser scale vegetational requirements for Cape Sable Seaside Sparrows to establish territories. As pointed out earlier in this discussion, the ability to identify the required characteristics of a single territory, or at an even finer scale, the characteristics of a suitable nesting site, require further investigation.

Acknowledgements

We would like to acknowledge the various agencies and individuals whose data, ideas, support and encouragement made this research possible. We thank the Biological Resources Division of the United States Geological Survey for their financial support under cooperative agreement 1445-CA09-95-0094 Subagreement #3 and the National Park Service for their financial support of ongoing field research. We thank Leonard Pearlstine of the Florida Cooperative Fish and Wildlife Research Unit, University of Florida for providing support regarding the TNC habitat map. We especially thank Oron L. Bass Jr. for his long term dedication to the plight of the Cape Sable Seaside Sparrow, along with Thomas Brooks, John Curnutt, Julie Lockwood, and Lisa Manne for their involvement in the demographic survey. We acknowledge Mathworks Inc. for providing the MatLab software and subsequent technical support that allowed these analyses to be conducted. We thank Don DeAngelis for his comments on earlier manuscripts.

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Table B-1. Color coded key to habitat types of southern Florida as depicted in Figures B-1, and B2(a to c). The associated descriptions refer to the vegetational alliances defined in The Nature Conservancy's Southeastern Region classification scheme 1993/1994 (The Nature Conservancy 1993/1994).

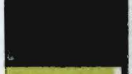
	0 Open Water
	1 <i>Magnolia virginiana</i> - <i>Chrysobalanus icaco</i>
	2 Tropical or subtropical seasonal lowland evergreen forest
	5 <i>Rhizophora mangle</i> (w/ hurricane damage)
	7 <i>Pinus elliottii</i> (w/ <i>Sabal palmetto</i> , <i>Serenoa repens</i>)
	8 <i>Taxodium ascendens</i>
	9 <i>Roystonea elata</i> - <i>Taxodium distichum</i>
	15 <i>Pinus elliottii</i>
	19 <i>Schinus terebinthifolius</i> seasonally flooded (includes upland)
	21 <i>Rhizophora mangle</i> sparse, semipermanently flooded
	23 Flooded tropical or subtropical broad-leaved evergreen shrubland
	24 <i>Cephalanthus occidentalis</i> - <i>Cladium mariscus</i>
	25 <i>Cephalanthus occidentalis</i> - <i>Typha domingensis</i>
	26 <i>Schinus terebinthifolius</i>
	29 <i>Cladium mariscus</i> ssp. <i>jamaicense</i>
	30 <i>Cladium mariscus</i> ssp. <i>jamaicense</i> (sparse)
	32 <i>Eleocharis cellulosa</i> (sparse) (w/ <i>Typha domingensis</i>)
	33 <i>Muhlenbergia filipes</i> (w/scattered Pine, Dwarf Cypress)
	34 <i>Typha domingensis</i>
	38 Wetland Grassland
	39 <i>Muhlenbergia filipes</i>
	40 Semipermanently flooded tropical or subtropical vegetation
	41 <i>Bacopa caroliniana</i> - <i>Utricularia</i> spp.

Figure B-1. A false color satellite image depicting the entire geographic range of the Cape Sable Seaside Sparrow at the southern tip of Florida. Different colors represent different vegetation types (see Table A-2) as classified by The Nature Conservancy from thematic mapping satellite images (30-meter resolution LANDSAT TM) taken in December 1993 and April 1994. The white area to the central right hand side of the figure represents the city of Homestead, Florida and its associated minor road system (gray lines). Thick black lines represent major trunk roads and the thinner jagged black lines represent the boundaries of the Everglades National Park (central portion bordering Homestead) and Big Cypress National Preserve (top left portion). Boxes bordered in red divide the geographic range of the Cape Sable Seaside Sparrow into three main sub-regions. The locations of singing males found during the 1992 extensive survey are shown as blue triangles. These sub-regions are named: "Western" (top left), "Ingraham" (bottom right) and "Eastern" (top right) and are shown individually in Figure B-2.

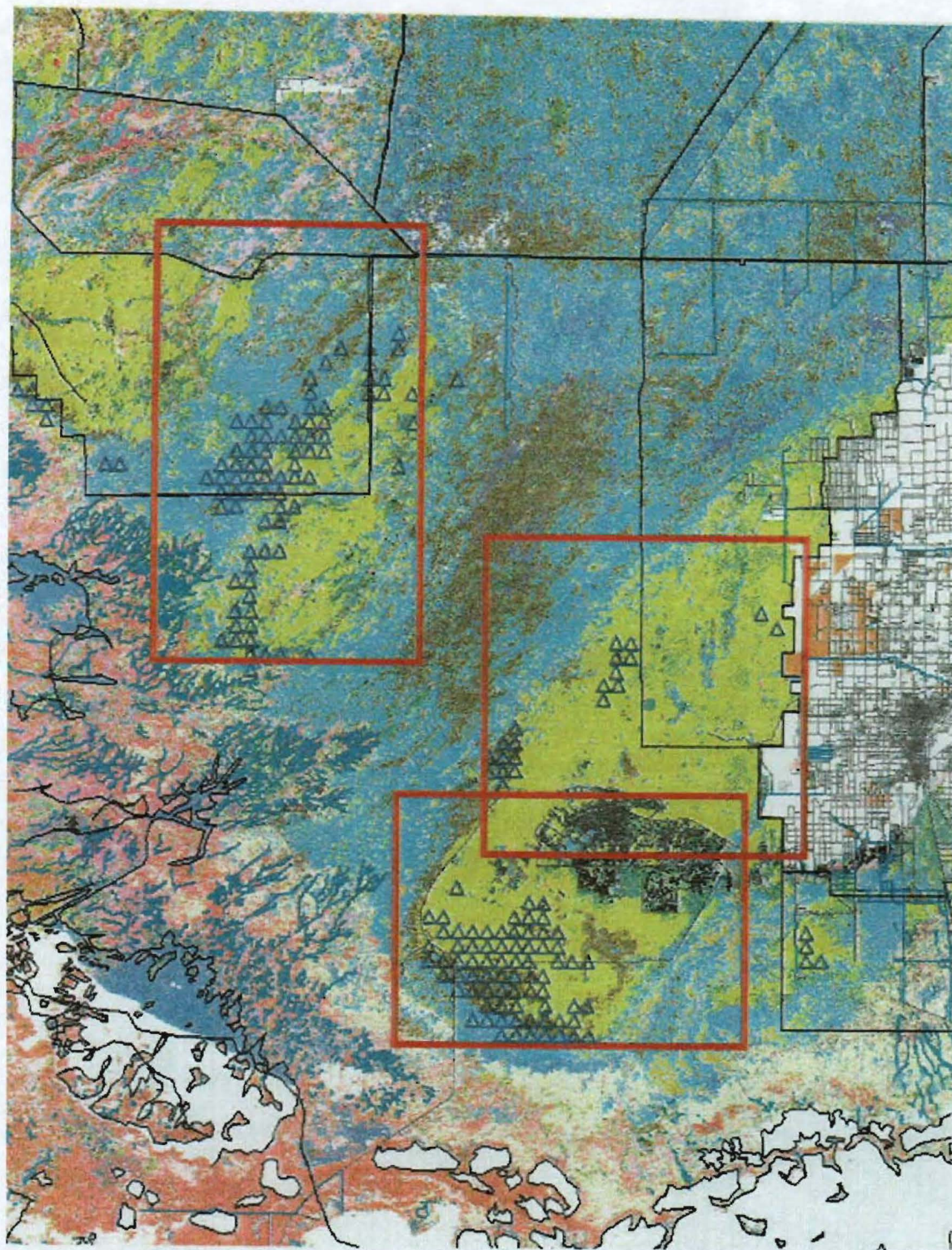


Figure B-2. False color satellite images of the sub-regions that encapsulates sub-populations of the Cape Sable Seaside Sparrow, superimposed with a 500m resolution square grid. Different colors represent different vegetation types (see Table A-2), as classified by The Nature Conservancy for thematic mapping satellite images (LANDSAT TM) taken in December 1993 and April 1994.

Map a) depicts the "Western" area. The main features include Tamiami Trail, represented by the red line roughly parallel and 2km (four squares) from the top margin of the map. Rattlesnake Ridge is the prominent system of ridges (color-coded yellow) in the southeast quadrant. This is bordered by Shark River Slough (blue) to the southeast, and by East Slough (blue) to the northwest. East Slough drains from the higher elevation, northeast corner of the map, adjacent to the South Florida Water Management District's WC3B water conservation area, down to the mangrove belt in the southwest corner of the map.

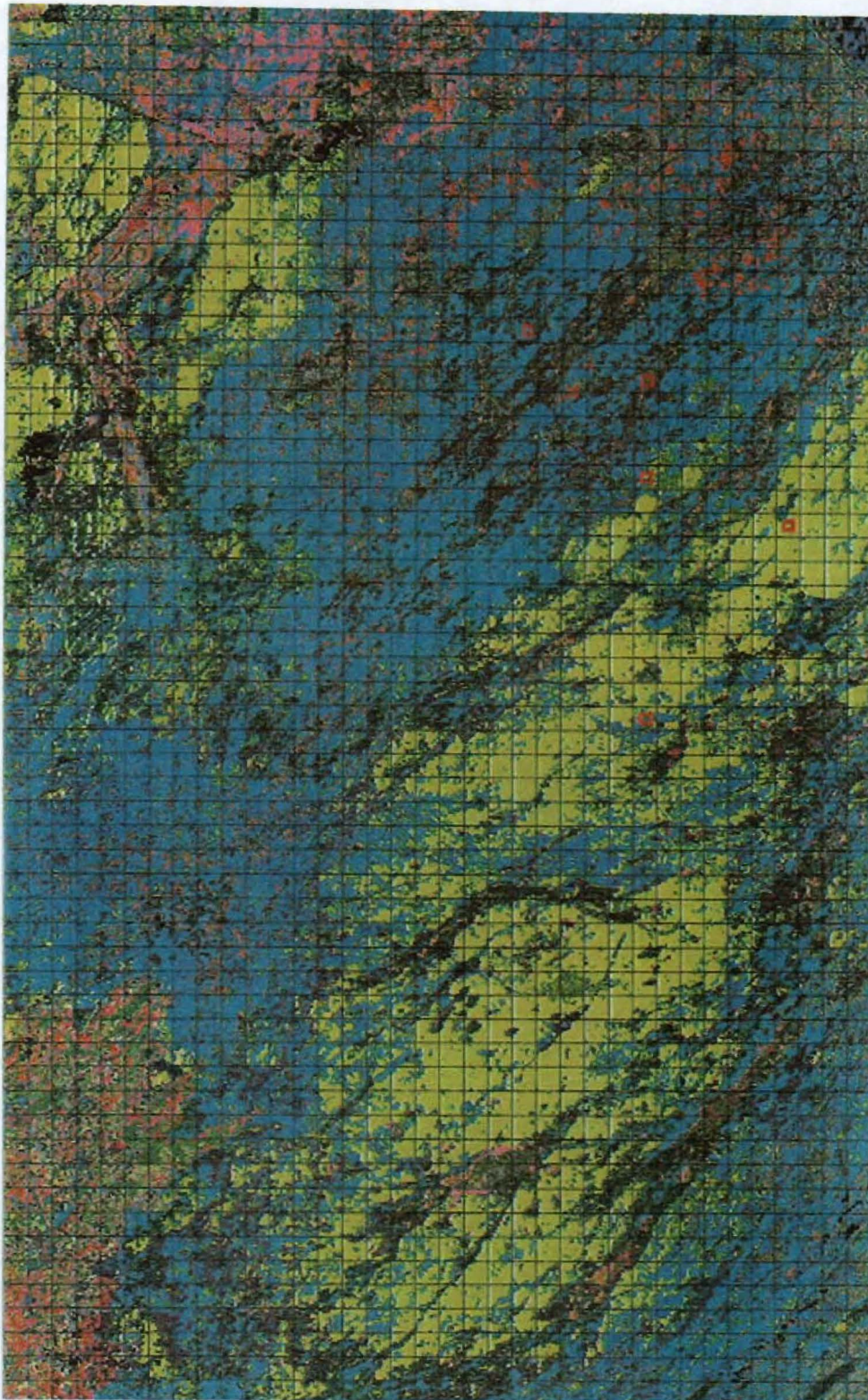


Figure B-2 (continued)

Map b) represents the "Ingraham" area. One of the main features visible is the Old Ingraham highway as a red line that parallels the west bank of Taylor Slough and then turns west to bisect the prairie (yellow). This area represents a gentle slope running from northeast to southwest. The green areas adjacent to this road are woody plant species growing on the sides of the road and on the abandoned agricultural land just to the south of it.

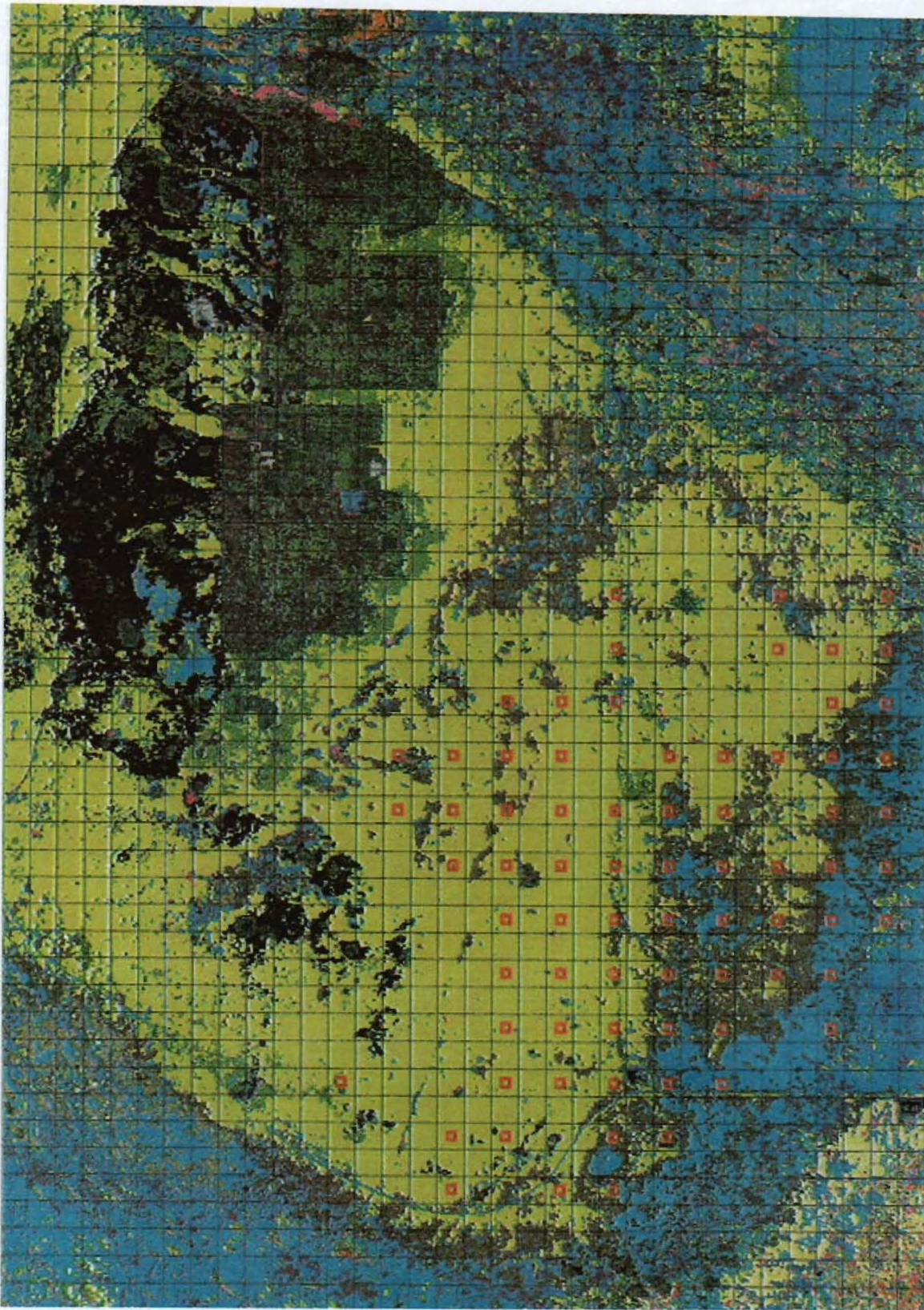


Figure B-2. (continued)

Map c) represents the "Eastern" area. The prairie areas, in which singing male Cape Sable Seaside Sparrows are found, are bounded by pinelands to the south, slough habitat (purple and brown) to the northwest (Shark River Slough) and the agricultural areas of Homestead (white) to the east.

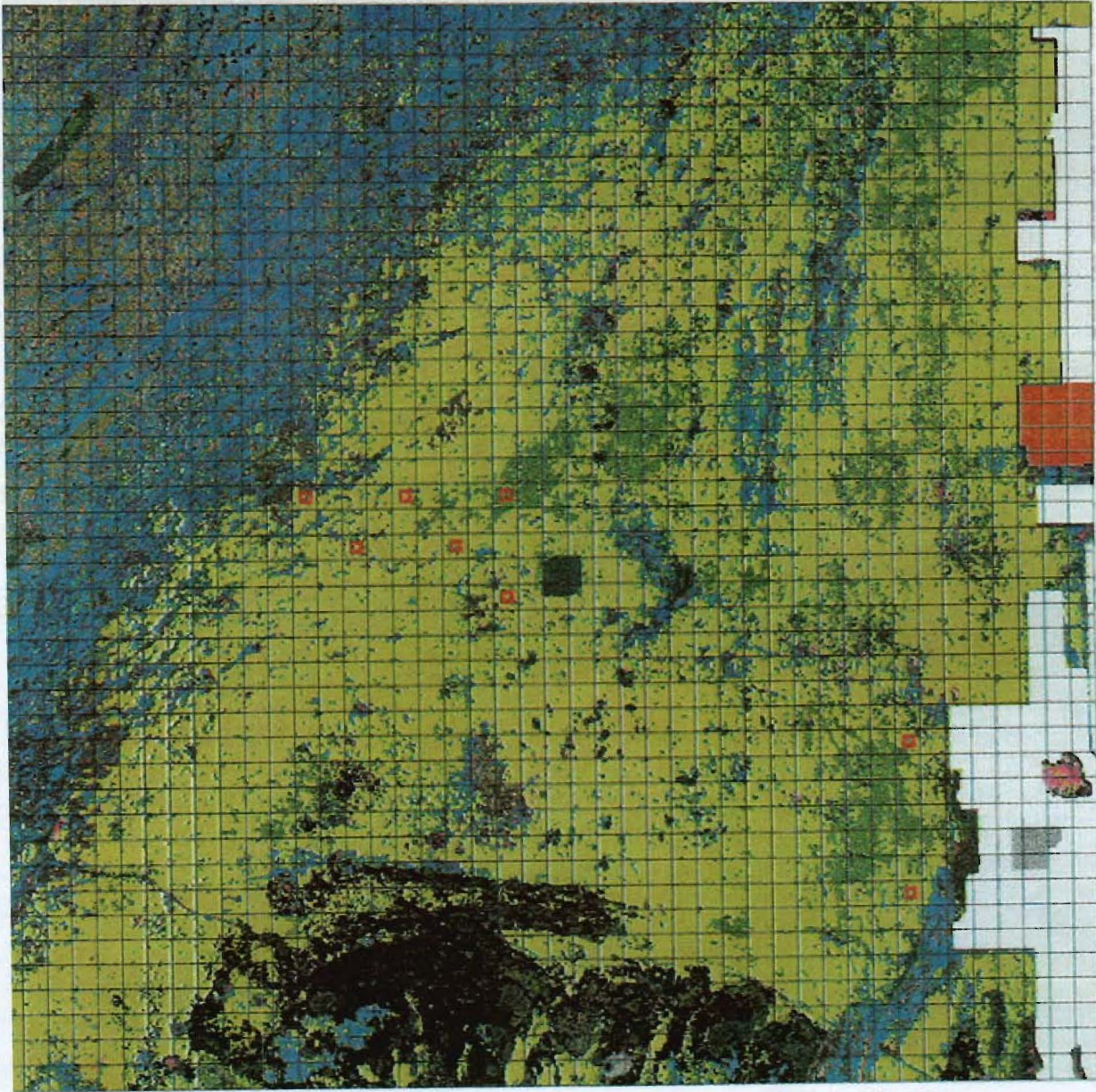


Figure B-3. Frequency distribution of cells occupied by Cape Sable Seaside Sparrows for a) the western area (for cells in which singing male sparrows were found in 1993, N=38) containing a percentage of habitat supertype coverage. These are i) dry habitat coverage, ii) marsh habitat coverage, iii) total coverage of both dry and marsh habitat, and iv) coverage of the tree supertype which includes hardwood, pine, willow, mangrove and cypress.

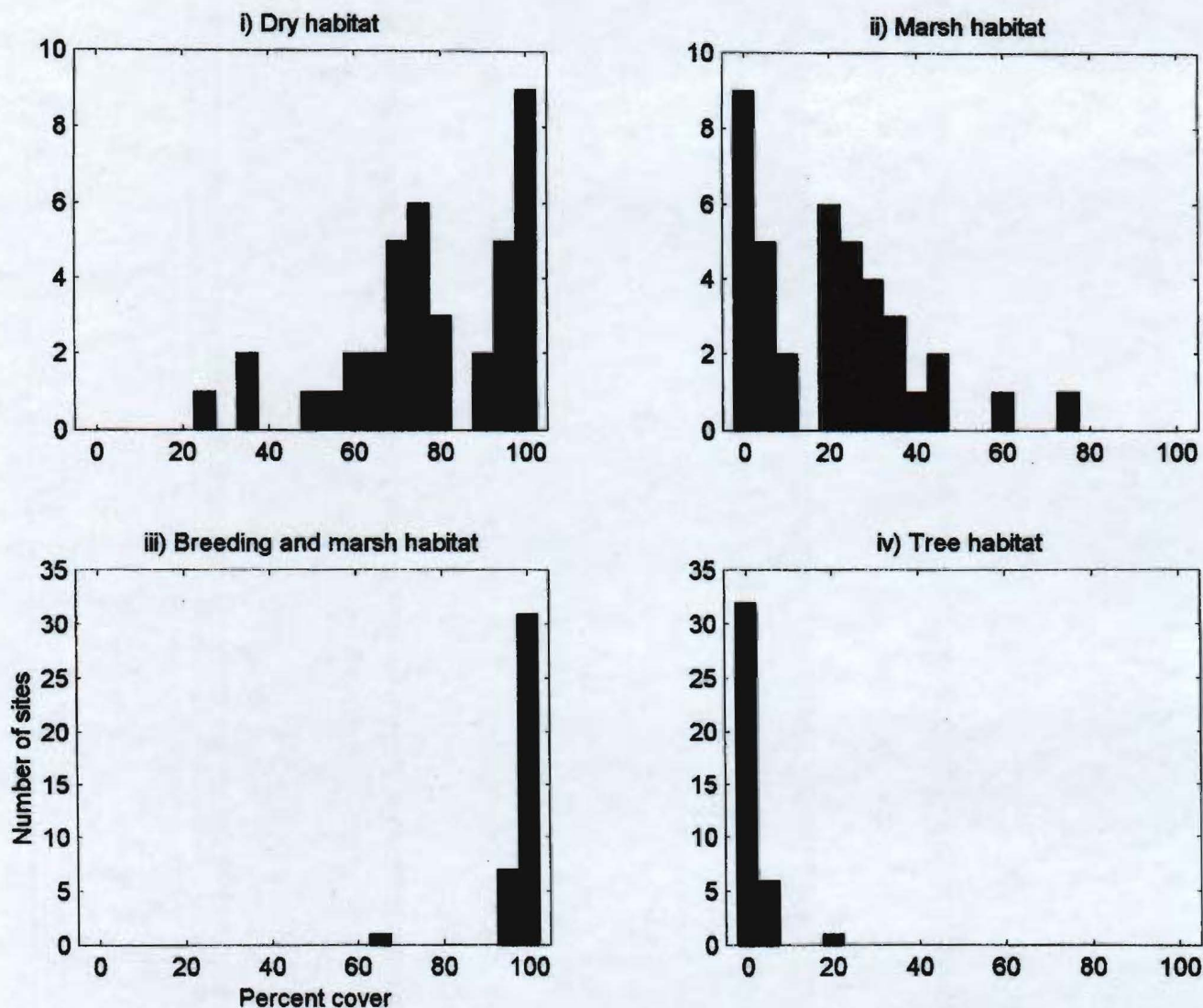


Figure B-3 (continued)

Frequency distribution of cells occupied by Cape Sable Seaside Sparrows for b) the western area (for cells in which singing male sparrows were found in 1993, N=104) containing a percentage of habitat supertype coverage.

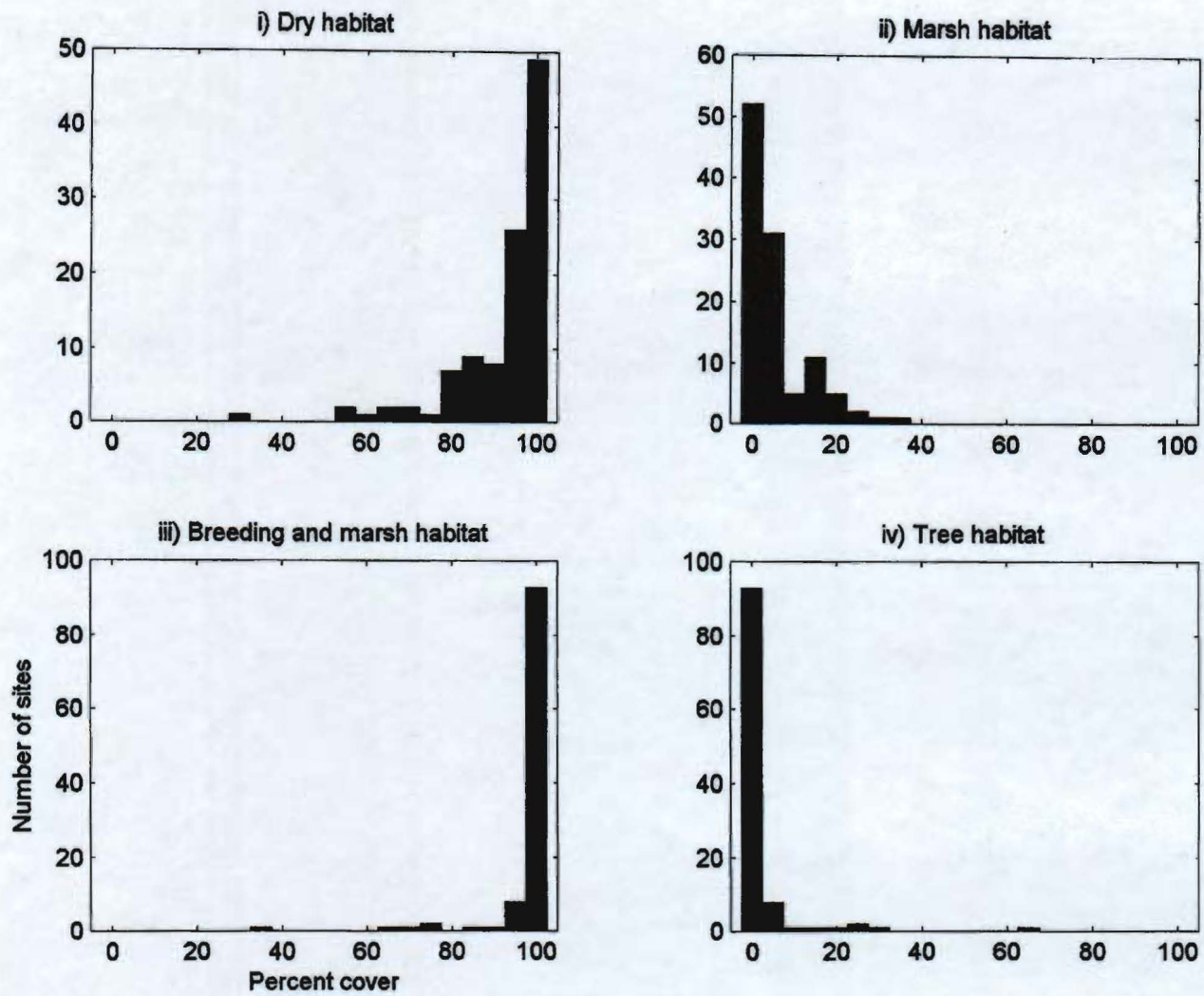


Figure B-4. Map summarizing the habitat and the 1993 Cape Sable Seaside Sparrow distribution for the western sub-region. The intensity of the background color represents the percentage of dry habitat supertype cover within each cell (see color scale). Cells for which the habitat supertype coverage thresholds are exceeded are marked with symbols to represent which threshold is exceeded. Upright crosses mark cells (+) containing more the MAXTREE percentage, diagonal crosses (x) signify excessive MAXWET percentage, and diamonds denote cells with less than MINDRY or less than the combined coverage of the wet and dry supertypes. Yellow circles denote cells in which singing males were detected in 1993. See text and Table 3 for description and values of MAXTREE, MAXWET, and MINDRY.

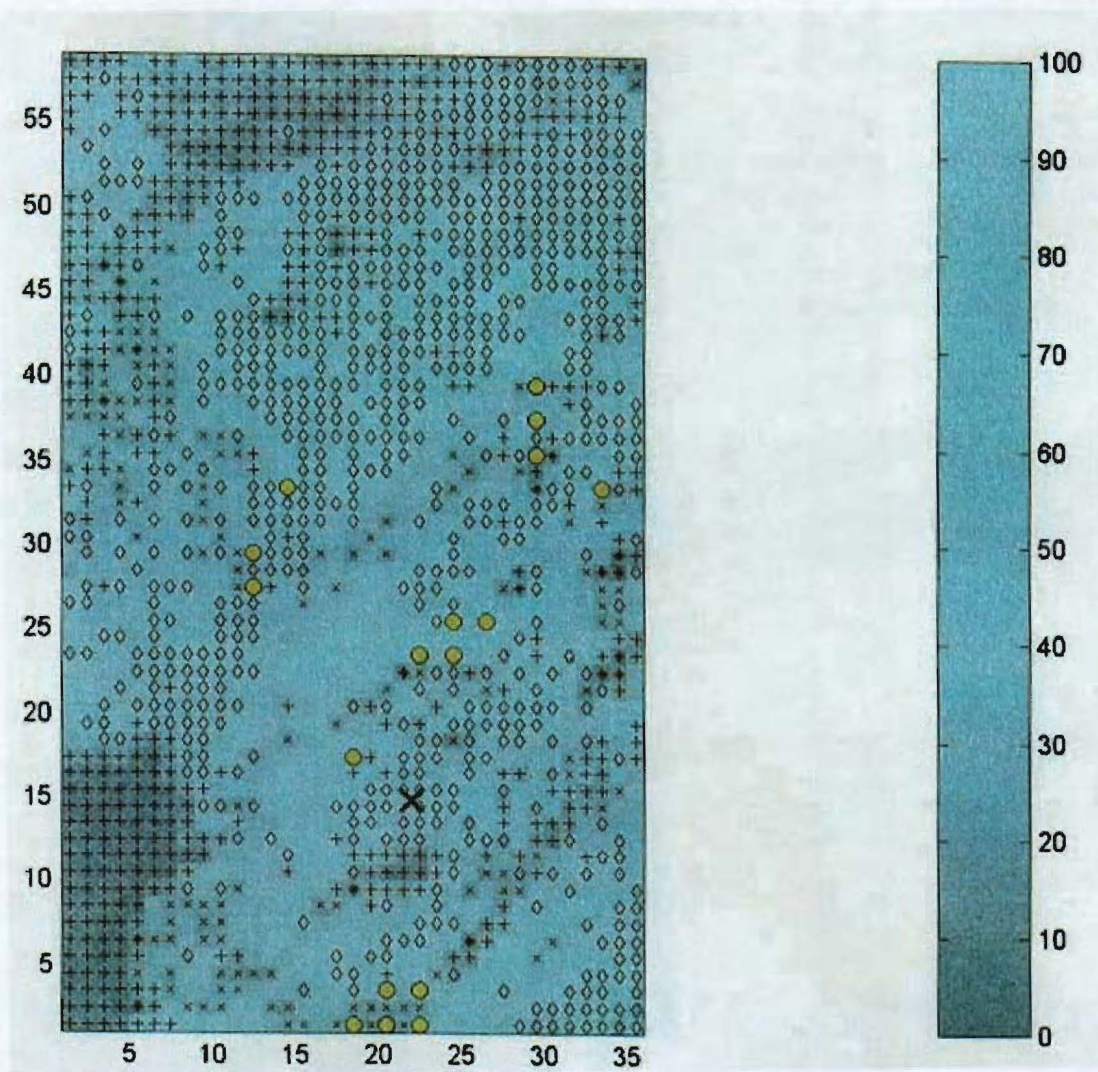


Figure B-5. Plots summarizing the relationship between Cape Sable Seaside Sparrow territorial male density and dry habitat supertype coverage for a) the western and Ingraham sub-populations. A linear regression plot of singing males (1993 survey) against estimate of breeding habitat percentage cover (of 30m cells within 500m cells).

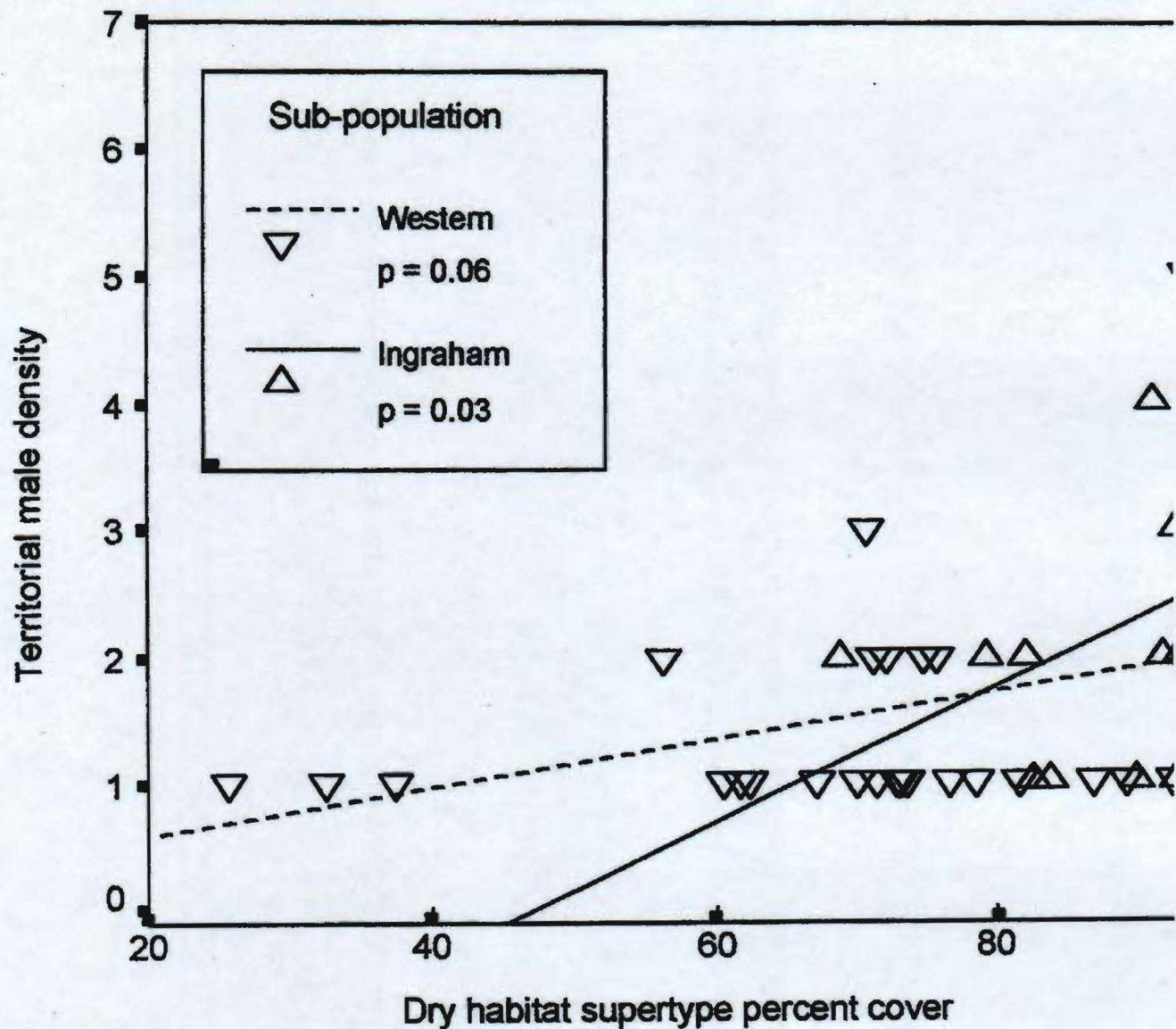


Figure B-5. (continued)

Plot of means summarizing the relationship between Cape Sable Seaside Sparrow territory density and dry habitat supertype coverage for b) the Ingraham sub-populations. A plot of means (by cell) for upper-quartile ANOVA ($N = 32$, $p = 0.001$) of the maximum number of singing males (1992-98 surveys) against category of dry habitat percentage cover (30m cells within 500m cells).

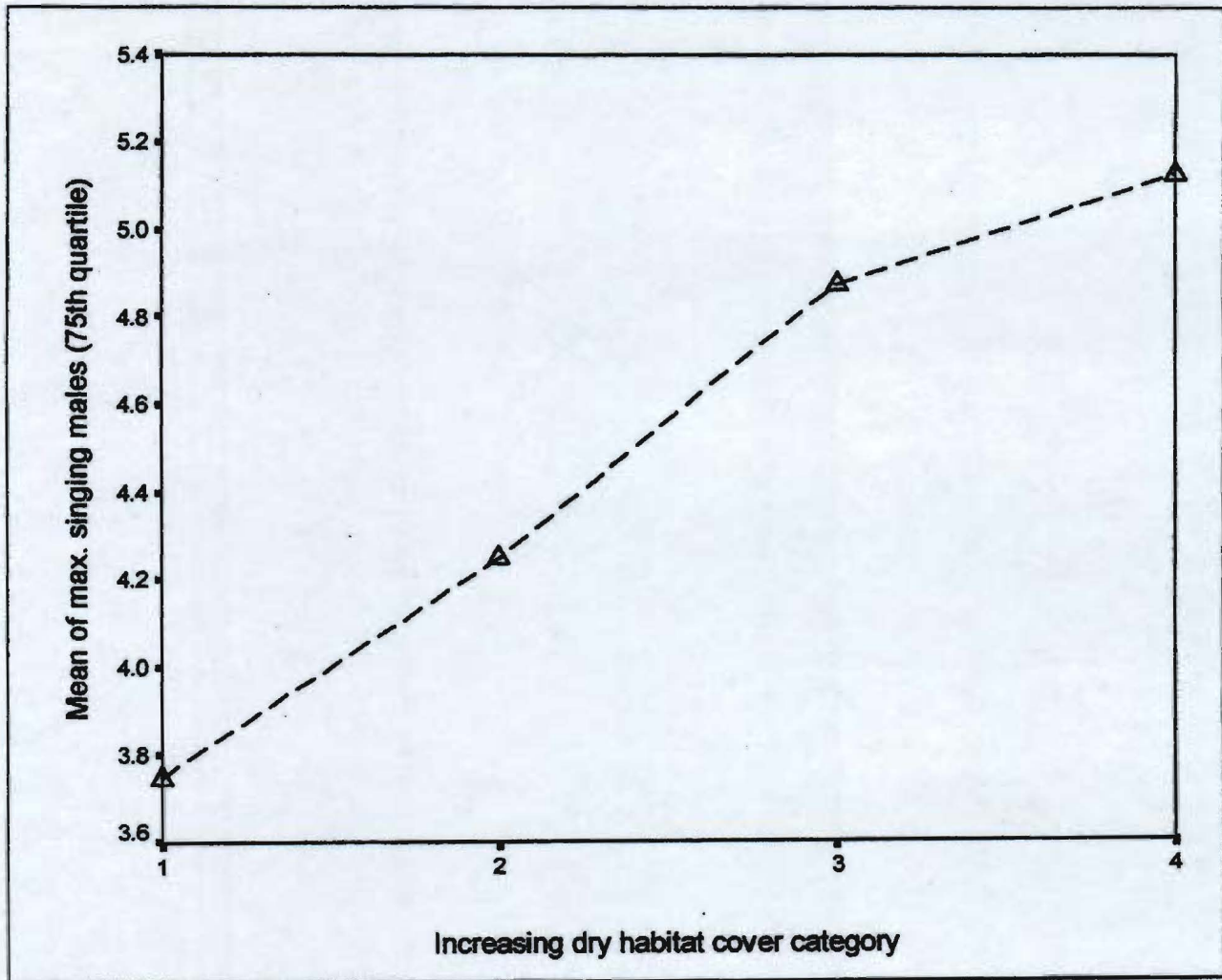


Figure B-6. Map of the habitat supertypes and pattern of Cape Sable Seaside Sparrow territory density change (1993-1998) for the Ingraham sub-region. An upward pointing green triangle indicates that the maximum number of singing males at a site (occupied for at least five of six years) increased after 1994. Decreasing maximum numbers are indicated by red triangles pointing down. Historical locations of singing males with low occupancy levels are shown as yellow circles (O). The larger X denotes the center of the distribution. Main features are Old Ingraham highway (O I Highway) that bisects the area, Taylor Slough (T S) and Shark River Slough (S R S).

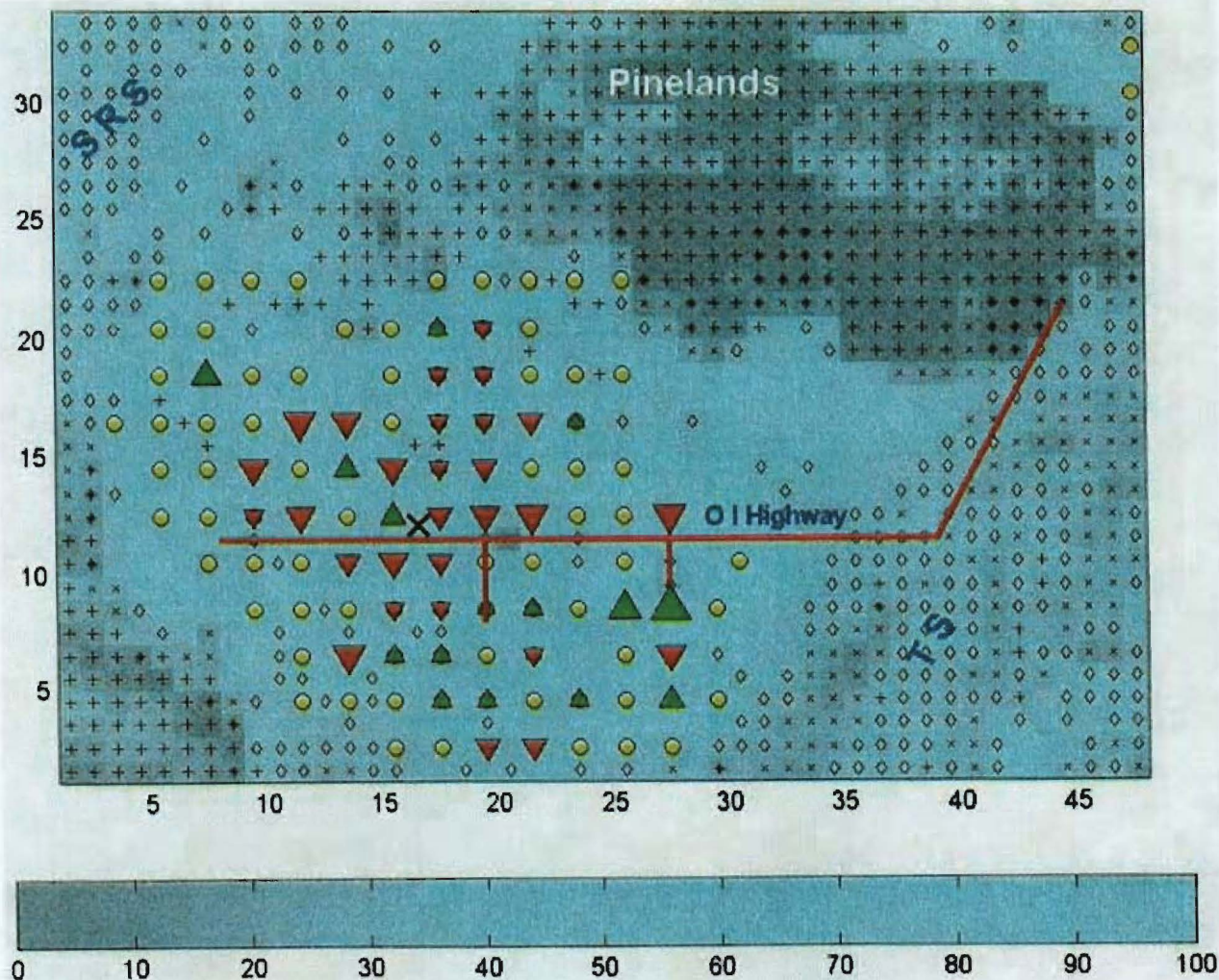
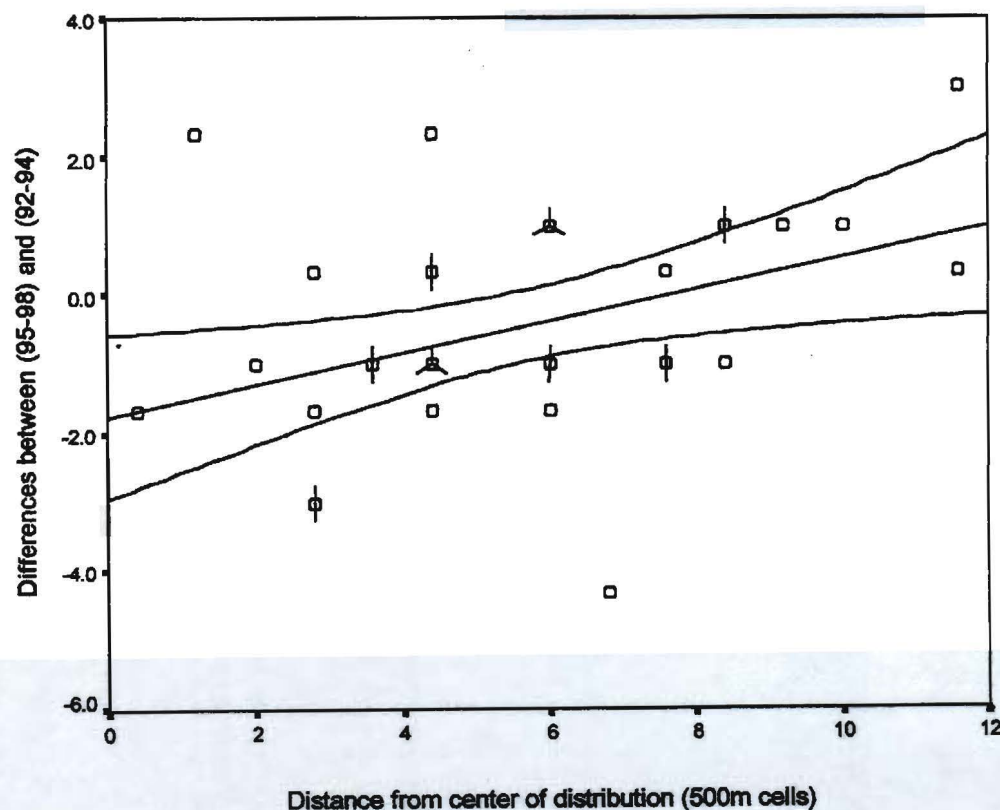


Figure B-7. Regression plot (mean and 95% confidence lines) of the change in Cape Sable Seaside Sparrow population (by cell) between the periods 1992-1994 and 1995-1998 against the distance from the center for a) the Ingraham distribution ($p < 0.05$). Only those data points for which 5 or more years of occupancy were recorded are included in the analysis ($N=33$). The number of radiating lines surrounding some data symbols indicates the number of multiple data points.



PART 3

SIMSPAR:

A Spatially-explicit Individual-based Object-oriented
Simulation Model for the Cape Sable Seaside Sparrow
in the Everglades and Big Cypress Landscapes

Abstract

A spatially explicit individual based model was designed as a management tool for the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*) of the Florida Everglades. The model includes landscape layers of habitat and topography at 500-m resolution. The population model considers each individual in a small population and its response to the changing landscape and other individuals. The life history and behavioral characteristics of model individuals are based on field observations of the species. Spatial and temporal patterns of breeding success are determined by historical daily water levels acting upon the landscape. The processes of mortality, mate choice, and dispersal are expressed stochastically; hence the model was implemented as Monte Carlo simulations. To validate the model the results of these were analyzed to allow comparison with demographic survey data. Individual mortality rate and female's ability to locate unmated males were identified as crucial factors affecting the survival of Cape Sable Seaside Sparrows in a dynamic landscape. It also represents one of the models within the Across Trophic Level System Simulation (ATLSS) Program of the U.S. Geological Survey, Biological Resources Division. This is an ecosystem-wide model designed to predict the impact of alternative hydrologic scenarios on a number of species and the resources they depend upon.

Introduction

Conservation biologists are increasingly challenged by the problems of managing species with low population levels, especially in a changing environment (Shaffer 1981). Recent advances in remote sensing techniques through satellite technology, coupled to the decreasing cost and increasing power of computers, allow ecologists to develop complex spatially explicit population models (Dunning 1995). These kinds of models are particularly useful when applied to land management problems and species conservation (Pulliam et al. 1992, Liu et al. 1995, Turner et al. 1995). These models often employ individual-based population simulators designed with reference to a comprehensive knowledge of the species' ecology and behavior (Fleming et al. 1994, Turner et al. 1994, Humphries et al. 1996, Winkler and Klotz 1997). This means each individual in the population is modeled over time and space, and responds to changing environmental inputs and encounters with other individuals, mimicking their natural behavior. Ideally, in terrestrial systems, population models should be linked to dynamic vegetation models to capture the demographic response to succession and disturbance (Holt et al. 1995). In a few cases such models are incorporated into larger scale 'ecosystem models' that integrate a number of different types of population models representing different trophic levels (DeAngelis et al. 1998).

The case for the individual based approach

Exploration of neutral landscape models, which ignore environmental variability, has taught us much about the response of "theoretical

species" to landscape patterns (With 1997). Importantly, spatially explicit, but neutral, metapopulation models reveal lower extinction thresholds (Bascompte and Sole 1996) than do spatially implicit models (Lande 1987). Perhaps the inclusion of environmental stochasticity, and differences between individuals in the model population, will also affect extinction thresholds.

Despite the recent increase in the number of useful spatially-explicit individual-based population models (Judson 1994), they are regarded as unnecessarily complex by some theoretical ecologists (Levin et al. 1997). However, it is clear that they capture the dynamics of small populations better than do alternative modeling approaches (DeAngelis and Gross 1992). Uchmanski and Grimm (1996) review a number of these modeling techniques and conclude the individual-based approach is preferable for modeling small populations that are dependent upon limited resources.

Critical parameter estimation

The estimation of particular ecological parameters is critical to the behavior of spatially-explicit population models (SEPM). The behavioral range of SEPMs is only recently emerging, but sensitivity analyses of both neutral and applied models suggest that we require a detailed knowledge of the ecology of the target species (Conroy et al. 1995). Wennergren et al. (1995) question the robustness of such models given our incomplete knowledge of dispersal behavior and rates. An spatially-explicit individual-based population models (SEIBPM) of pocket gopher populations (Anderson 1996) concludes that further research into the

gopher sensory abilities and excavation mechanics is required to build a reliable model. These conclusions reveal the importance of the individual-based approach in increasing our understanding of population dynamics in different species. Specifically, we can use such models to identify the more sensitive parameters, and possibly redirect the focus of field research. More generally, these findings highlight the need for close collaboration between theoreticians, field biologists and many other disciplines.

Developing an SEIBPM for the Cape Sable Seaside Sparrow

Concern for the endangered Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*) of the Florida Everglades centers on dwindling population levels and the development of appropriate management policies for hydrology, and fire. The sparrow is an ideal candidate for the individual-based modeling approach. Not only does a wealth of spatially explicit abiotic data exist across its geographic range, but the breeding ecology and distribution of the sub-species is well known, and it obviously has clear habitat preferences.

In this chapter we describe the construction of a spatially-explicit individual based population model that simulates the entire population of Cape Sable Seaside Sparrows. In this model each individual responds to both the effects of hydrologic patterns on the landscape it explores, and to other individual sparrows. Its breeding success is determined by the chance of finding a mate and the subsequent hydrological conditions of the location (cell) in which the pair breed.

The resultant model allows us to test the effects of increased environmental variation, or habitat fragmentation, and assess the effects of proposed management policies.

Case history

Before we describe how the model was constructed we will outline the conservation problem concerning the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*). Its range is currently restricted to freshwater marl prairies in the extreme southern portion of the Florida peninsula (Werner 1975, Bass and Kushlan 1982). Recent surveys suggest that the population size has declined from 6000+ in 1981 and 1992, to less than 3000 individuals in 1998. The entire geographic range is affected by various management agency decisions (specifically those of fire and hydrology) that affect the Everglades National Park and Big Cypress National Preserve.

We know that hydrologic management policies have a great impact on the sparrow (Nott et al. 1998). Specifically, as water levels recede during the dry season in late winter and spring, given sufficient habitat the sparrows establish territories and start nesting in dense grass tussocks. Males may produce up to three broods with the same female if their nesting sites remain dry. If water levels do not recede early enough in spring, nesting may be delayed, and if water levels subsequently rise during the nesting season, eggs or nestlings may be drowned. Although seasonal inundation varies from year to year, the spatio-temporal pattern of water levels is primarily the responsibility of South Florida Water Management District. Through a system of levees, canals, pumping stations and sluice gates they are able to redirect the

flow of water through the Everglades region. The recent declines in the sparrow population occurred across its entire range. This is due to higher water levels in recent years (Nott et al. 1998), and degradation of prairie habitat due to patterns of succession. Because the current range of the sparrow is limited to a few hundred square kilometers that is subject to flooding and fires, the population is highly vulnerable. The Everglades restoration project (Hinrichson 1995) will result in changes to the hydrology of the southern Everglades. This could increase the water levels in parts of the sparrow's range and increase the risk to the reproductive success of the sparrow. It is critical to quantify the impact of any proposed hydrologic regimes on the survival of sparrow populations. This model has already been applied to proposed hydrologic scenarios provided by South Florida Water Management District as part of the restoration effort.

Justification for developing an SEIBPM for the Cape Sable sparrow

The purpose of the modeling is to predict the future population levels of the Cape Sable sparrow under the different prospective hydrologic regimes that the sparrow's habitat may undergo in the future. There are two major factors that argue in favor of using a spatially explicit, individual-based model to predict the future population dynamics of the population.

There are only six years' worth of population estimates, not enough to derive a simple statistical model, relating year-to-year changes in mean water level to changes in sparrow population. A simple model would also not provide information at the level of spatial and temporal

detail needed to make specific management recommendations. The habitat model is essential in the construction of a spatially explicit population model, but alone is of limited use in predicting spatio-temporal population patterns. It is difficult to model time lag effects in population response using a simple habitat change model; only by incorporating it into a SEPM can those effects be visualized.

Model: Conceptual Overview

A detailed approach to modeling the population viability of the sparrow is feasible, because the main threat to the population is disruption of reproduction due to flooding (Nott et al. 1998), which can be simulated through hydrologic modeling. The behavior of the sparrows during reproduction and the influence of water levels on the initiation or continuation of reproductive behavior are relatively well known from field studies. Finally, the water levels in the sparrow's range can be predicted at a fine scale of temporal and spatial resolution as a function of rainfall regime and water management protocols. For these reasons, a predictive model relating landscape hydrology to sparrow population dynamics, based on detailed mechanisms, is possible. Conceptually, the model is designed as follows, based on empirical information.

1. The landscape of the sparrow's range is modeled explicitly as a set of spatial cells of fine enough resolution to represent areas of similar vegetation, topography, and hydrology (see Chapter 1 and 2). We identified the relationships between habitat type within a cell and its carrying capacity in terms of the density of breeding territories (Chapter 2). We also modeled water levels

by cell on a daily time step (Chapter 1). It is the temporal and spatial patterns of this 'hydroscape' that drive the demographic patterns that the model population exhibits.

2. Each individual sparrow in the population is modeled during the breeding period. In particular, the model tracks the sex, age, and breeding status of each model individual from egg to the end of its life. For mature males, the model tracks establishment of breeding territories, finding a mate, the start of nesting, and the status of eggs and nestlings on a daily basis.
3. The relationship of sparrow breeding activity to water depth is modeled. As noted above, water depth in spatial cells is kept track of daily through a hydrologic model. A spatial cell is not available for breeding activity until the water level in that cell falls below a threshold level of 5 centimeters. Any rise in the water level above 16 cm in a particular spatial cell during the nesting season is assumed to cause nest abandonment to the sparrows that have nests in that cell. One component of variability in the model occurs through stochasticity in the date and the locality of the cell in which a specific male chooses a territory and subsequently mates.
4. The sparrows are not modeled in detail during the non-breeding season, as that part of the annual cycle is probably not as sensitive to anthropogenic environmental conditions. Age-specific mortality rates are assigned during that period probabilistically, based on empirical data. The following spring,

when the next breeding season begins, older males return to their previous nesting territories. If they failed to breed successfully the year before, they move to a new habitable location where one is available in the vicinity of the site they used last year. Recent male recruits also begin their search in the area surrounding their natal site.

Model: detailed description

The following description of Version 1.0 of this model addresses the spatial and temporal aspects of the model. We also describe the behavioral and life cycle parameters relevant to the population dynamics of this species. We interpret specific examples of model output relative to our current knowledge of the biology of this species. We demonstrate the variability in behavior of the model by means of a sensitivity analysis. Finally, we suggest that certain parameters require further field research in order to increase our confidence in the model's predictive potential.

Landscape description

The Cape Sable Seaside Sparrow model operates on a 500m resolution landscape. The status of each cell is tracked through time and adjusted according to the effects of hydrology and fire. In turn, individuals in the sparrow population respond to the status of the cell that they are associated with. They may also test surrounding cells during dispersal and mating phases. Although our knowledge of the precise landscape dynamics and successional patterns is incomplete, any assumptions made in this section are based on estimates made from recent field studies. A number of landscape layers are defined that allow us to model changes in the landscape and the effect of hydrologic patterns on breeding success. Currently the model covers two areas (referred to as the "Western" and "Ingraham" areas or landscapes below) in which sparrows are known to breed and utilizes topographic and habitat suitability layers. These will be described in more detail later.

Topographic layer

Associated with each of the two areas is a 500m resolution layer describing the topography in units of centimeters above mean sea level. The topography of the western area was resolved using 1995 water depth measurements for 834 sites arranged on a 1 kilometer grid (see Part 1). The resolution was increased to 500m by interpolation (Nott et al. 1998). A similar method was used for the Ingraham landscape but based on fewer water depth samples collected in the winter of 1997.

We estimated the topography using the methods described in Part 1. We recorded water levels at various points across the landscape during the winter of 1997 and estimated elevations at those points with reference to the stage level of nearby monitoring station, NP46. These data were augmented with known elevations from National Geodetic Survey points in the area. This topography is shown in Figure A-3a.

The extent of each of the areas described below is shown in Figure B-1 and defined by the Universal Transverse Mercator (UTM) coordinates given in Part 2, Table 1.

a) 'Western' landscape

This is an area to the west of Shark River Slough covering approximately 17.5 x 27.5 km. The area historically held a population of 3000+ sparrows. This population suffered serious declines after 1992 and remained at estimated levels of below 500 individuals through 1998 (at the time of writing this document).

The updated topography for this area (derived in Part 1) is shown in Figure C-1. Inspection of these two maps reveals a series of ridges running south-southwest known as Rattlesnake Ridge. Between this ridge and higher ground to the west is East Slough, which originates at its northern end near the S12A hydrologic structure and drains into the mangrove belt at its southwest limit. The habitat map for this area (Figure B-2a) shows narrow belts of potential breeding habitat corresponding to the flanks of East Slough and its tributaries draining from Rattlesnake Ridge.

b) 'Ingraham' landscape

This is an area covering 24 x 18 km. This area holds the majority of the remaining sparrow population; between 2500 and 3000 individuals in all years it has been surveyed since 1981 (Curnutt et al. 1998). The extent of the Ingraham area with the locations of historical breeding sites is shown in Figure B-1.

This area is very different from the western region. It consists of a prairie gently sloping from the northern side (~120cm above mean sea level) towards the southern mangrove belt (~30 cm above mean sea level). Pines and adjacent marsh dominate the northern boundary, while Taylor Slough and Shark River Slough provide the southeastern and western boundaries, respectively. A small unnamed slough bisects the area along the northwest - southeast diagonal, isolating a small portion of seemingly potential breeding habitat.

Habitat suitability layer

A number of factors influence the breeding suitability of habitat for the Cape Sable Seaside Sparrow. These include hydroperiod, fire, and vegetative succession (including invasion by exotic plants). The spatial patterns of these factors influence the spatial pattern of potential breeding habitat. Although the precise relationship between these environmental factors and the resultant spatial pattern of habitat suitability is not completely understood (Nott et al. 1998, Curnutt et al. 1998), some effects are clear.

Although elevation and hydrology can be reasonably assumed as uniform within the spatial resolution of the model (500m x 500m cell), the vegetation type within a given 500m cell may be quite heterogeneous, including both suitable and unsuitable breeding habitat types. Therefore, the assignment of a particular cell to a habitat quality class (measured in terms of the density of sparrow territories it can sustain) requires using vegetation data at a finer scale. The Nature Conservancy habitat map for southern Florida provides a resolution of 28.4 meters. For each area described above, detailed maps depicting the pattern of habitat types are shown in Figure B-2a and Figure B-2b. From these data, and the results of geographic range-wide demographic surveys of the sparrow, we resolved the relationship between vegetation characteristics within a cell and the maximum attainable territory density. The results of these analyses are given in Part 2 and the resultant maps provide the habitat layer upon which this population model operates. We describe these and other factors that affect the potential density of territories within a cell.

a) Breeding habitat and territory density

We define the grassland community in which the sparrow lives and breeds as 'the prairie matrix'. Such areas are fragmented by sawgrass swatches, tree islands, anthropogenic features, and shrub invasions. The prairie matrix lies within an even more extensive mosaic of other community types that the sparrow does not utilize which we refer as 'non-habitat types'. These include pinelands, cypress, hardwood hammocks, long-hydroperiod marsh, mangroves, and anthropogenic structures.

In Part 2 we constructed a number of rules that we apply to the 28.4m resolution TNC vegetation map (The Nature Conservancy 1993/1994) for each model area. This provides a habitat layer of 500m resolution cells that contain an overall percentage of breeding habitat of which part represents nesting habitat. We aggregated four vegetation type codes (from the TNC vegetation map see Part 2, Figure B-1 and Table B-1) into a supertype representing nesting habitat. We calculated the *nesting habitat coverage* of 28.5-meter resolution cells within each 500m-resolution cell and determined the maximum number of territories each cell can support. In addition we calculated the coverage of marsh habitat supertype coverage for each cell. A cell only provides suitable breeding habitat if the combined coverage of the marsh habitat supertype and the nesting habitat supertype exceeds 90%. This is known as the *minimum breeding habitat coverage*. These values are shown in Table 1.

Table 1. Default values of habitat suitability parameters and hydrologic parameters for the Cape Sable Seaside Sparrow individual based model. See text for details.

Habitat suitability parameter	Default setting
<i>Nesting habitat type codes</i>	[29 30 33 39]
<i>Minimum nesting habitat coverage / 500m cell</i>	55%
<i>Minimum breeding habitat coverage / 500m cell</i>	90%
<i>Maximum territory density / 500m cell</i>	10
<i>Fire recovery period (years)</i>	4
<i>Hydrologic recovery period (years)</i>	3
<i>Nesting trigger day</i>	50
<i>Potential breeding season duration days</i>	210

Furthermore, we established a relationship between the number of singing males detected at a survey site and breeding habitat coverage within the 500m x 500m area surrounding it. This relationship predicted that a maximum of 5 territories would be found at a survey site containing 100% breeding habitat, but this represents only a sample within the cell. The maximum number of territories defined by the relationship must be corrected to account for the fact that a human observer has a limited hearing distance, and cannot detect all the singing males within the 500m resolution of the study. Based on observed territory densities, Bass and Kushlan (1983) suggested a correction factor of 16 (times the number of singing males) to estimate the population size within a square kilometer (this included a factor of two to account for females). This correction factor was confirmed by Curnutt et al. (1998).

In field study plots (approximately 500m x 500m) covering prime breeding habitat, in the Ingraham area, densities of 8 per cell occur but may reach densities as high as 12. Considering these facts we predicted 10 as the *maximum territory density* per 500m cell (Table 1), this implies a maximum of 40 singing males (territories) per square kilometer, given 100% breeding habitat coverage. This value is Furthermore, the results of Part 2 show that no territories are found in a cell containing less than 55% breeding habitat coverage. Given these rules, we adjusted the maximum potential territory density in proportion to the dry habitat coverage within each cell.

This process provides a layer to the model that affects the ability of dispersing males to successfully establish territories in any cell they

encounter. We can further adjust the maximum possible territory density of a cell by considering the fire history and recent hydrologic history of a 500m-resolution cell.

b) Fire effects on territory density

The effect of fire on vegetation is dependent on the intensity of the fire, the existence of standing water, and the time of year. The first component of the vegetation to burn is the dead vegetation. In sparrow breeding areas dead vegetation contributes to the overall vertical structure, which is important for nest placement and predator avoidance (Lockwood et al. 1997). Sparrows are not found nesting in recently burned areas but may return within four years (Werner 1976). There are various factors involved in the recovery of habitat after fire, which are not well understood. We assume that the maximum potential density of a 500m cell is realized 4 years post-fire and that potential territory density increases linearly after the first year (Taylor 1983). We intend to include fire history in the model that is both spatially and temporally accurate. This is possible only in areas for which detailed fire records are kept. The correction index ranges between 0 and 1 and is formally expressed below. Expressions such as $(\text{fire age} \leq 4)$ represent thresholds, the value of which 0 or 1, that may switch the following or preceding expression on or off. The following index is zero for $\text{fire age} = 1$ and rises in increments of 0.33 until $\text{fire age} = 4$, after which it remains set to 1.

post-fire suitability index =

$[(\text{fire age} \leq 4) \times (\text{fire age} > 1)]$

$\times [(\text{fire age} - 1)/(\text{fire recovery period} - 1)] + (\text{fire age} > 4)$

c) Hydrological effects on territory density

As well as directly affecting breeding by delaying or interrupting breeding, hydroperiod patterns also influence vegetation patterns within the prairie matrix. Fluctuating water levels maintain plant species assemblages at an early successional stage (Odum 1969). Prolonged wet periods have a negative effect on the breeding suitability of short-hydroperiod prairie (Nott et al. 1998). Most of the western area in which sparrows bred in 1981 and 1992 is now unoccupied and the vegetation changed dramatically between 1992 and 1996. During this period a large portion of this area was inundated with water for much of the breeding season. This resulted in a change of dominant species and less complex vertical structure, conditions that are not conducive to successful breeding. We assume that hydrologic damage to breeding habitat only takes two years of a hydroperiod longer than 275 days. Subsequent recovery of the habitat to a state suitable for breeding is possible if the length of hydro-period decreases. The dynamics of any recovery are yet to be resolved but recent observations suggest the recovery may only take 3 years (Pimm pers. comm.). The correction index ranges between 0 and 1 and is expressed formally below. In this case if the age since inundation of the cell exceeds the recovery period the index is set to 0. This and the *post-fire suitability index* defined earlier, are used to modify the number of territories a cell can support as described later.

post-inundation suitability index =

(post-inundation age >= post-inundation recovery period)

Default values for the parameters outlined above are summarized in Table 1 and allow us to set a number of rules and relationships governing the maximum nesting potential of any given cell.

Landscape cell descriptors methods and state variables.

In addition to the habitat suitability rules (methods), there are a number of parameter values, state variables and simulation results that are associated with each cell and the sparrow's occupancy of the cell. In concert these determine the response of an individual encountering the cell. These are defined below and again expressions containing inequalities (e.g. $\leq$ or $>$) are set to 0 or 1 depending on the respective values of the variables either side of them.

Location - the x-y coordinates of the geographical location of the cell.

Elevation - the absolute ground level elevation of the cell in centimeters.

Water depth - the difference between the stage height of the daily hydrologic data and the elevation = *stage height* - *elevation*.

Post-fire age - the number of years since fire damage.

Post-inundation age - the number of years since flood damage.

Hydrologic history - the hydroperiod duration (days) for each of last two years.

Potential maximum nest density - the maximum number of territories the cell can support. This is calculated using the following relationship:

maximum territory density
x (*breeding habitat coverage* >= *minimum breeding habitat coverage*)
x (*nesting habitat coverage* >= *minimum nesting habitat coverage*)
x [(*nesting habitat coverage* - *minimum nesting habitat coverage*)
/ (*100* - *minimum habitat coverage*)]
x *post-fire suitability index*
x *post-inundation index*

Actual nest density - the number of territories currently occupied by males associated with the cell. If this value is less than the maximum nest density for a cell a dispersing male encountering that cell will occupy a territory with a probability of one.

Territory owners - the unique identities of male individuals who own territories in the cell.

Annual productivity - the number of successful fledglings produced within in any year.

Hydrologic modeling

Water levels are explicitly modeled over time and space, whereby water levels in each cell are modeled on a daily time step. The model incorporates the historical hydrology from 1977 to 1996 inclusive, a two column file of decimal date (year + day/365) and *stage height* (cm), the water level above mean sea level. The model tracks the effects of these data on breeding potential in each cell of the landscape. First breeding attempts can only be successful if the duration of the dry period exceeds the duration of the breeding cycle (~45 days).

The maximum duration of the potential breeding season starts on the first day of January each year and lasts 210 days to allow for the completion of three broods (Table 1). Although this entire period is explicitly modeled, nesting attempts occur only during the period after a particular day that represents the earliest known nesting attempt from field studies. The daily water levels are tracked even before this date to assess the length of hydroperiod, which in turn is used to model effects upon vegetation. We assume that some environmental trigger such as day length triggers nesting behavior (Table 1). Even after this date water levels must be low enough to allow territorial behavior and subsequent nest building. This phenomenon is described in a later section.

Hydrology datasets

For each of the areas covered by the model, there is daily water level data for each cell. These are derived from empirical data collected at a hydrologic monitoring station within or close to the sub-populations under study. Specifically, we use historical data from two National Park Service hydrologic monitoring stations. The western area is influenced by the hydrologic patterns experienced at the station NP205 located at (Northing 2825223 Easting 515235). The core area is influenced by the hydrologic patterns experienced at the NP46 hydrologic monitoring station located at (Northing 2800176 Easting 520521).

There are a number of gaps in these data. In the case of NP205 we filled these gaps using adjusted (to ground level) sequences from the

nearby, and closely correlated, P34 station (Northing 2832200 Easting 505924). The gaps in the P46 data occur mainly when the water level is either very high or below ground level. We were safe in linearly interpolating to fill these gaps because breeding activity is not sensitive to changes in the level at these extremes.

The historical daily hydrologic data for the NP205 monitoring station are depicted in Figure A-2, showing the generally wetter conditions in the mid-1980's and recent years. The effect of this sequence on annual breeding season duration at this site (March - May inclusive) is shown in Figure 5b (from Nott et al. 1998).

Individual Cape Sable Seaside Sparrow state variables and descriptors

Each individual in the population possesses a number of state variables describing its current status. At each time step the values of these variables are checked against threshold values for a set of behavioral rules. These state variables are described below:

Identity - a unique integer used to identify an individual.

Location - a pair of x-y coordinates describing the current position of the individual within the landscape.

Age - the age of the individual in days since the start of its incubation as an egg.

Gender - a binary integer identifying the individual as male (0) or female (1).

Breeding status - a number referencing the current breeding status of an individual.

- 0 juvenile - assign gender at the end of the breeding season.
- 1 male without breeding territory (see *Territory ownership*).
- 2 female - unmated.
- 3 mated male - territorial, mated and nest building male.
- 4 mated female - mated and nest building female
- 5 nesting male - with eggs or nestlings.
- 6 nesting female - with eggs or nestlings.
- 7 male with fledglings
- 8 female with fledglings

Territory ownership - a binary integer set to 0 (bachelor/floater) or 1 (denoting territory owner).

Mate identity - the unique *identity* of an individual's mate.

Mating date - the number of days since pair bonding occurred.

Offspring identity - the unique integer *identities* of an individual's current offspring.

Mother identity - identity of an individual's mother.

Father identity - identity of an individual's father.

Annual nesting success - number of successful broods in current year.

Lifetime nesting success - number of successful broods in lifetime.

Fitness - index of an individual's fitness - not implemented.

Genotype - allelic complement of an individual - not implemented.

Life Cycle Parameters

A number of life cycle parameters that influence Cape Sable Seaside Sparrow population dynamics are included in the model. Once a pair bond is established the mean nest building period lasts 7 days. Once the nest building period is complete, it is assumed eggs are laid at the rate of 1 day per egg plus 1 day rest. For instance, if a female is destined to lay three eggs, the age of all those individuals is set to -3 at this time. This allows four days for laying the eggs before incubation starts. Clutch size is probabilistically assigned to successfully mating pairs based on a field derived distribution of clutch size. The sex ratio of the offspring is even. Juvenile mortality rates (during nest cycle) are density-dependent. This is a positive linear relationship; at the minimum density of one nest per cell the mortality rate is minimal (0.4), and at the maximum nesting density juvenile mortality is maximal (0.42).

After 23 days from the start of incubation, nestlings become 'walking fledglings' and are immune to the effects of rising water. This is two days later than the mean stage suggested by Lockwood et al. (1997) and represents a worst case scenario. Before this stage eggs and nestlings are drowned if the water level reaches the *nesting height*. After 33 days since the start of incubation individuals fledge and become independent of their parents and represents 12 days of fledgling care (Lockwood et al. 1997). A period of 3 days represents a rest period after a successful breeding attempt and before nest building activity recommences. A maximum age of five years represents the physiological limit of a sparrows life span, independent of annual mortality. The

default setting allows individuals to potentially breed for four seasons and survive to their fifth winter. The oldest individuals die of old age before their fifth breeding season, representative of the physiological limit upon their longevity.

Adult mortality may be age dependent and is represented by an age related probability table from which the daily mortality risk of each individuals is calculated. In the default case we assume there is no differential age mortality and every age has an annual mortality probability of 0.4 (equals 0.6 survivability). However we will explore the effects of differing mortality rates in later sensitivity analyses. These life cycle parameters are summarized in Table 2.

Table 2. Default values for life cycle parameters in Cape Sable Seaside Sparrow individual based model. See text for detailed description.

Life cycle parameter	Default value
<i>Nesting date (days)</i>	7
<i>Clutch probability (size:p)</i>	2:0.16 3:0.48 4:0.36
<i>Male probability</i>	0.5
<i>Juvenile mortality</i>	0.4 - 0.42
<i>Walking age (days)</i>	23
<i>Fledging age (days)</i>	33
<i>Inter-brood rest period (days)</i>	3
<i>Maximum age (years)</i>	5
<i>Age dependant mortality (year:p)</i>	1:0.4 2:0.4 3:0.4 4:0.4 5:0.4

Behavioral Parameters and life cycle logic

The model considers six distinct behavioral parameters for which the default values are described below along with their default values (Table 3). Many of these are derived from breeding season field studies (Lockwood et al. 1997). At each time step the status of each individual is referenced and compared with the status of both the landscape cell it occupies and associated individuals such as offspring, mates and parents. A number of simple rules determine whether the status of an individual changes. We describe the logic behind modeling the breeding portion of the life cycle with reference to life cycle parameters described in the preceding sections.

Males are available for mating only if they have *territory ownership*. To claim ownership young males must first encounter a cell holding fewer territorial males than the *maximum nest density* for that cell. Once a territory is claimed the male has right of ownership to it for life. If water levels are above 5cm males will not sing. If they are

Table 3. Default values of behavioral parameters in Cape Sable Seaside Sparrow individual based model. See text for detailed description.

Behavioral parameter	Default value
Nesting height (cm)	16
Mating height (cm)	5
Mating range	8 cells = 4km
Dispersal range	1 cell = 500m
Mating probability	0.1
Dispersal threshold	1 breeding season

not singing they can not attract a female or be detected by normal survey techniques. The water level in a cell must be below the *mating height* of 5cm in order for the resident male to sing and attract a female.

We assume females are mobile and can find singing males within a certain distance. A female is attracted to a territorial male within its *mating range*. We set the maximum range from which a female can be attracted to a male during the breeding season to 8 cells or 4km. Successful mating is dependent upon the *mating probability*. The probability of a female accepting a territorial male and mating with him upon encounter is 0.1. There is one attempt by a male per day and successful mating will occur on one in ten attempts. If successful mating occurs the *breeding status* and *mating date* of the male and female are updated. These rules change when a pair successfully raises a brood and attempt a second (or third) brood. In this case the *mating probability* is set to unity and an *inter-brood rest period* is assumed before nest building recommences.

Once a pair bond is established the nesting phase ensues. The size of the clutch is drawn randomly from a distribution of *clutch probability*. Familial associations (*mate, offspring, mother, father*) are assigned at this stage. If water levels rise above the height of nests before the *fledgling age*, the nest and its contents are destroyed. The mean *nesting height* above ground level is set to 16 cm. After nest abandonment a breeding pair are allowed to rest for a number of days corresponding to the *inter-brood rest period*. This resting period also applies if a brood fails when all the offspring die for reasons other

than drowning (i.e. daily juvenile mortality rate). The *breeding status* of offspring is set to 0 until the end of the breeding season, when it is assigned randomly - dependent upon the *male probability*.

A brood is considered successful if the age of one or more fledglings exceeds the *fledging age*. At this stage the offspring become independent of the parents. The parents are then able to nest again after an *inter-brood rest period* before nest building recommences, given favorable conditions. The *annual productivity* counter of the cell in which they fledge is updated with the number of fledglings produced.

Male recruits, adult bachelors, and unsuccessful breeders disperse one cell (500m) at a time (neighborhood dispersal) before the start of new breeding season. If a male fails to successfully breed in any year the individual will disperse and attempt to find a new territory the next year. A detailed description of the dispersal mechanism follows.

Inter-breeding season dispersal

After the effective breeding season (*Potential breeding season duration*) the population suffers over-wintering mortality *pro rata* the annual mortality rate. This kills both individuals older than the *maximum age* and also random individuals in accordance with age-dependent mortality rates. Before the beginning of the next breeding season individuals return to their natal sites to begin the dispersal phase.

The model distinguishes between males and females with respect to dispersal behavior; males search for vacant breeding territories and females search for unpaired males. The parameter settings for each may vary. Dispersal mechanisms are amongst the most poorly understood concepts in meta-population biology. The mechanism described here makes assumptions based on behavioral observations of this and other grassland passerine species. It incorporates strict philopatry (male exhibit fidelity to breeding territory location), an individuals perfect knowledge of the area, exhaustive search patterns and increased mortality risk with movement. All these colonization strategies and concepts are discussed from a theoretical point of view by Tonkyn and Plissner (1991) and with respect to the influence of landscape heterogeneity by Gustafson and Gardner (1996).

Male individuals without established territories (adult male floaters and male recruits) disperse at the beginning of the breeding season. Natal preference is assumed for potential recruits whereby the search pattern starts at the location of the natal territory (Wegro et al.). However, male individuals with established territories may move to another location if they failed to breed for a number of years previously (*dispersal threshold*). In either case an individual randomly chooses a new location in an area defined by *search range* and tests it for suitability. Non-habitat cells are considered as reflective boundaries and are not visited. If all the potential territories are occupied in their present cell, a male seeking a territory moves on to a neighboring cell but avoids cells it has already visited, if no unvisited cells are available the individual becomes a non-breeding "floater" and relocates to the last cell it visited. This kind of

dispersal mechanism is typically used in spatially explicit dispersal models and is generally known as a "self-avoiding random walk" (Stanley 1986). A probability of mortality, *movement mortality*, is associated with each step. This process continues until all males find a vacant territory, exhausts their search or die.

If a vacant territory exists in the cell a male visits (i.e. *nest density* is less than the *maximum nest density*) they will occupy it with a probability of 1 (Wasser 1985) and subsequently own it for life. Field observations of many avian species support this assumption; a territory that is vacated by the death, dispersal or removal of the resident male is rapidly occupied by floating male. In this way all habitable cells can potentially be saturated at their *maximum nest density*. This occurs only if the population is sufficiently large and enough recruits are available to fill those territories vacated by death or dispersal of the territory owners.

Model: Implementation and verification

We implemented the conceptual model as a Monte Carlo simulation programmed in MatLab version 5.1 (MathWorks Inc.). We applied the model to the sub-population inhabiting the western side of Shark Slough and also to the core sub-population of the Cape Sable Seaside Sparrows south of the pinelands in the Everglades (pictured in Figure 1). Both sub-populations historically held around 3000 sparrows, and the model is capable of keeping track of the locations and breeding status of this number of birds or more during the breeding season.

Initializing the population

The relevant landscape is seeded with an initial population. Each landscape cell is seeded with a number of individuals corresponding to the *maximum nest density* of breeding pairs that cell can support. In addition a number of "floaters" representing the assumed previous year's productivity are added, the number is proportional to the *maximum nest density* the cell can support. The geographical location of each individual is correspondingly assigned.

The age of an individual is chosen randomly from a decaying binomial distribution of ages representing a stable age class distribution. This distribution results from running the model under ideal breeding conditions until the carrying capacity of the landscape and a stable age class distribution is achieved. The gender of each individual is assigned randomly and is dependent upon the *male probability*. The *breeding status* of each individual is set to 1 or 2 dependent upon gender (see above) representing a population of non-breeding individuals with no pair bond associations (*mate*). Territorial ownership is established during the first breeding season of the simulation.

The *territory ownership* is initially set to 0. Ownership is assigned in the model when males encounter hydrologic conditions such that the water level is below the *mating height*. Without this ownership males fail to attract females. Familial associations (*mate*, *offspring*, *mother*, *father*) are assigned in the breeding cycle routines. If a pair

successfully fledges one or more offspring, *annual and lifetime nesting success* is updated.

Modeling the population

As in all Monte Carlo type simulation models, for each hydrologic scenario, many replicates are simulated. These replicates differ only in the 'seeds' used for the pseudo-random number generator. At the beginning of each replication the model defines an initial population of sparrows, which are subsequently tracked on a daily basis. Their actions are dependent upon their interaction with both the landscape and other individuals. The rules governing the interaction of individual state variables, life cycle parameters, behavioral parameters and landscape cell state variables were defined earlier.

Model verification

Testing the validity of this model presents a unique problem but one that is relevant, in a general way, to other studies. The problem is how do we compare the model output with the extensive survey results? As we have discussed in this and previous chapters, the survey counts singing males at the vertices of a one kilometer grid during the breeding season. The daily transects are organized in a structured random pattern so in one year a site may be wet and no breeding activity is observed on the day it is visited. In another year the site may be dry and sunny and males will be singing vigorously, or they may be less obvious due to the presence of nestlings. It is also possible, in poor breeding habitat, that territories may not be continuously

occupied from year to year. The model must produce equivalent counts if we are to validate it against historical data.

For verification purposes, we incorporated a 'virtual helicopter survey' into the model to mimic the real annual survey technique. We divided the number of survey sites in an area by the number of days the survey lasts (normally 60). We divided the survey sites into this many transects and randomized their order. Every day during April and May (the normal period of the survey) the model tests the cells that correspond spatially to the next transect in the sequence. It records the number of resident males (with 'singing status') within that cell and totals them for the year.

Importantly, by a process of trial and error we seeded the model with a number of individuals in 1977 to produce (in 1981) a model spatial pattern and virtual helicopter survey number that approximated that of the real survey data for 1981. In this way we allowed the hydrologic patterns between 1977 and 1981 to influence the demography in the hope that the resultant age class structure approximated reality given the variable productivity patterns experienced in those years. We continued simulations through 1996 and compared the results of the helicopter survey with those of the real survey to assess how well the model predicted the field data.

Model limitations

The model simulations do not consider the long-term effects of vegetation succession and fire effects. The software routines to deal

with these effects are inherent but are not yet parameterized. However, these are both important factors for the Cape Sable sparrow population and will be explored in future investigations.

Model: Sensitivity and viability analysis

Agencies using the model may construct various spatio-temporal sequences of hydrology and fire. The effects of alternative sequences, or scenarios, can be studied by using them as inputs and comparing the resultant spatial and temporal numerical responses of the population. Such comparisons may include the differences in mean population level, population variability and the probability of becoming extinct, or dropping below certain threshold population levels, which reflect minimum viable population levels. These analyses are an integral part of the model.

Sensitivity analyses

Although the model parameters are set to values derived from field studies there is always a question of error given the small sample size of most studies of rare and endangered species. For instance, bird banding data must be collected over many years before age dependent mortality rates can be estimated with a high degree of confidence. From the conservation point of view it is essential to know the sensitivity of a species to changes in predation pressure, landscape fragmentation, extreme weather and many other influences on population dynamics (Soule 1987). Models such as this one provide an ideal tool for identifying the most sensitive parameters; those that produce a great effect given a small change. Often such phenomena take the form of a critical

threshold on either side of which the magnitude of the effect is greatly different. Percolation theory provides us with a classic example of such a threshold. A drastic decrease in landscape connectivity occurs when the coverage of that landscape by a single habitat type falls below 60% (With et al. 1998). However, such thresholds also appear in empirical studies (With and Crist 1995). The previous study (Part 2) showed that no breeding sparrows were found within 500m cells where the coverage of nesting habitat was below 55%. Furthermore, dispersal behavior is critically linked with landscape complexity and the effects of fragmentation in natural populations (Schippers et al. 1996).

The concept of the minimum viable population in conservation is one that attracts considerable debate. Conservation agencies must assume that extremes of influence on populations have a finite probability of occurring. If we wish to use a model to explore extinction risk given those extremes, then we must decide upon a population level below which we consider the species to be at a high risk of extinction. By identifying any critical thresholds in the sensitivity of the species response to changing influences we may be able to predict potential sources of increased risk and manage the species accordingly.

Mortality rates can be influenced by many factors, such as competition and predation, that can be difficult to measure in bird populations. However, if we observed increasing numbers of potential nest predators such as raccoons, snakes, hawks, rodents, and introduced fire ants, then we might reasonably assume that mortality rates would increase across all age classes. Empirical evidence shows that incidental nest predation (juvenile mortality) is particularly important in grassland

birds with low densities of breeding individuals (Vickery et al. 1992). How much effect do small increases have on long term survival of this species?

Another reason for conducting sensitivity analyses is to assess the data requirements for the model. As we pointed out earlier, some parameters are difficult to quantify. If simulations indicate that these are particularly sensitive parameters, then field research effort should be increased to obtain more reliable estimates. Two such parameters are those of dispersal ability in male and female Cape Sable Seaside Sparrows. Although some estimates are available for these parameters from telemetry and banding studies (see default values), the site fidelity data only covers 3 years (Lockwood et al. 1998) and the telemetry sample size is small and from a single non-breeding season (Dean pers. comm.). Another problem is that female dispersal data is difficult to obtain because females are harder to catch and band, so it is difficult to obtain a reasonable sample size of their movements. These data are from the Ingraham area, which experienced relatively stable environmental conditions over the period of the study. They are not available for the western sub-model area, where conditions have drastically changed. If we change the values of the dispersal parameters, does the validity of the model change appreciably? If not, we might conclude the values we have are consistent across the range.

Population viability analyses

To explore the effects of changing the model parameters to mimic changing influence we must be able to compare the results of a series of simulations, in which a single parameter value is gradually changed. Conventionally, stochastic population models use population viability analyses to assess the effects of environmental variation and the values of life history parameters on demographic extinction risk (Ginzburg et al. 1982, Goodman 1987, Shaffer 1990).

We chose three measures of population viability to compare the results of sensitivity analyses:

- I) Time to quasi-extinction risk (PTQExt): the cumulative probability (based on N replicates - thus the term quasi-) that the population will drop below a specified number over time.
- II) Time to quasi-explosion risk (PTQExp): the cumulative probability (based on N replicates - thus the term quasi-) that the population will exceed a specified number over time.
- III) Interval explosion risk (PIER): the probability (based on N replicates - thus the term quasi-) that the population will reach a specified number sometime during the period of simulation.

Each of these analyses is expressed for the period following the first five years of the simulation, given historical hydrology patterns (1977-1997). This period is typified by a decrease in the population

due to the wet conditions experienced during the mid 1980's (Figure C-2), followed by a dry period during which the population recovered, followed by extremely wet years starting in 1993. The model is seeded with a population of around 500 individuals and a maximum of 4 territories per cell is set.

Results

Figure C-2 shows an example of the model population trends over the 20 year period for the western sub-population. The diamonds represent the total population estimate at the end of each breeding season. Of these a varying proportion constitute the breeding population (pair bonds). After a series of wet years the breeding population size equates to the total population. After a series of dry years the available breeding habitat is saturated and the difference between the breeding population and the total population represents the floater population size. The black line traces the total population throughout the breeding season. Sudden drops indicate mass drowning of nests. The numbers of singing males detected by the "virtual helicopter survey" are depicted as crosses.

Figure C-3 shows the correlation between the results of the virtual helicopter survey and the real helicopter survey. Despite the low number of data points the model results correlate well with the field observations ($p < 0.05$).

Figure C-4 represents a summary of the model output for a single replicate and year (1989), showing various patterns of abiotic and

population variables. Clearly, water levels were low for much of the breeding season (a), which exposed most of the available breeding habitat (b). The nestling population (c) rose quickly after the onset of breeding showing three distinct bursts of productivity. Although the virtual helicopter survey only detected 20 singing males (d) the cumulative fledgling population steadily increased over the breeding season and led to an overall threefold increase in the population (notwithstanding winter mortality). This was a very successful breeding season.

Conversely, the patterns for 1987 (Figure C-5) show the effects of season long high water (a) that left little available breeding habitat (b). The virtual helicopter survey detected nearly 20 singing males but their breeding effort was interrupted throughout the breeding season by high water that drowned nestlings. Only later in the season did the fledgling population begin to increase but hardly enough to maintain the population (net productivity of 1.10). Subtracting the effects of overwintering mortality (~ 0.2) would lead to an annual decrease in the population.

Figure C-6 shows the spatial pattern of breeding success across the western landscape for the year 1989. Black symbols superimposed on the topography (red-blue = high-low elevation) indicate non-habitat cells as determined by the habitat sub-model. Also superimposed on the topography are white circles representing cells containing territory-owning males, with black dots indicating successful breeding attempts. Although the distribution is patchy, by 1993 territorial males were

more numerous and had spread further across the landscape (Figure C-7). Unfortunately 1993 represented a very wet year and no breeding attempts succeeded. The following years were also wet years and the population had crashed by 1996 (Figure C-2) leaving small isolated pockets of territorial males at higher elevations (Figure C-8) as also indicated by the results we obtained in Part 1, Figure 4. We also show the locations of males recorded in the survey years 1993-1996 as large black circles.

The effect of changing annual mortality rates, given historical hydrology patterns acting on the population, is shown in Figure C-9a. A dramatic extinction risk threshold exists between 0.35 and 0.45 annual mortality rate. The risk of the population dropping below 100 individuals rises from 0.05 to 1 over this mortality range. At a mortality rate of 0.4 (default setting) the quasi-extinction probability is 0.55. The probability of quasi-explosion, at the level of 500 individuals, also shows a similar threshold in the opposite direction.

Female dispersal ability is also an important parameter affecting demographic patterns in the model population. Figure C-9b shows that the risk of extinction decreases as the female search range increases. The probability of explosion (exceeding 500 individuals) remains close to unity.

Discussion

These investigations clearly support the use of spatially explicit individual based models in the management of an endangered species, The Cape Sable Seaside Sparrow. Combining our knowledge of the ecology and behavior of this species with a realistic landscape, and historical hydrologic patterns allowed us to reliably predict the demographic patterns of the sparrow over the last 20 years. As a result the model has since been used in a species management role within the Everglades National Park. Specifically it is used to predict the effects of proposed hydrologic scenarios, under the Everglades Restoration Project, on sparrow demographics. It also represents one of the models within the Across Trophic Level System Simulation (ATLSS) Program of the U.S. Geological Survey, Biological Resources Division. This is an ecosystem-wide model designed to predict impact of alternative hydrologic scenarios on a number of species and the resources they depend upon.

Validating avian population models

Obviously, it is difficult to validate avian population models because of the nature of the population structure. Point count monitoring techniques miss many individuals in the population; many are floaters and some species are secretive, especially during the nesting stage. Consequently, as in this case, a ten-minute helicopter stop yields low counts that represent only the breeding population and may underestimate the true population size during periods of high productivity. On the other hand, a low count may reflect the total size of the population after periods of low productivity. The solution provided by this model is a virtual survey methodology that mimics that

of the real survey. As a result the model allows validation at two levels; virtual helicopter counts against point count data, and spatially explicit breeding population densities against local territory counts.

Without adopting exhaustive survey techniques it is impossible for managers to estimate true population sizes. Such techniques are both costly, because the entire range needs to be surveyed, and are potentially disruptive to breeding efforts. For grassland birds one technique involves dragging a rope across transects and flushing birds from the grass. The reliability of this technique is dependent upon being in the right habitat and cannot be used during the breeding season. Using spatially explicit population models, such as SIMSPAR, allows managers to predict the spatial pattern of breeding activity and population size. They can then selectively monitor sensitive areas within the species' range and validate their predictions. In this case, it would be possible to reduce the resolution of the extensive helicopter survey and concentrate more effort on those areas where the model predicts sporadic breeding success.

Implications of sensitivity

In this model, two parameters are of particular interest in terms of our confidence in empirical evidence; female mobility and annual mortality rates. The ability of female birds to disperse is crucial when a population is small because it is essential that the potential breeding population maximize their effort. In the western area, for instance, recent flooding has isolated small pockets of breeding

activity. Let us consider the implications of this type of distribution. Without a reasonably sized floater population, and assuming females do not disperse far, the chance of a territorial male attracting a mate decreases. This is because the probability of finding locally uneven sex ratios increases, as the population size decreases. Obviously, as the dispersal ability of females increases their chance of finding unmated territorial males also increases. Intuitively, given a strictly philopatric breeding system, it would be advantageous for females to be mobile and thus avoid inbreeding. The results suggest that we should obtain better estimates of the value of the female dispersal parameter.

The species is particularly sensitive to mortality rates, as we might expect given the findings of Vickery (1992). This is an important management issue and our results suggest that bird-banding efforts should continue in order to refine the mortality parameter of the model. The influence of predation pressure will also affect mortality rates and should be closely monitored. For instance, increased frequency of shrubs and trees provide perching and nesting opportunities for avian predators (hawks and nest raiding grackles). Furthermore, old roads and tracks that bisect habitat enable movement of potential terrestrial predators and the spread of exotic plant species. Although there have been no observations of sparrow nests being raided by introduced fire ants (*Solenopsis invicta*), the threat certainly exists. Polygynous ant colonies are numerous along the Old Ingraham Highway that bisects the Ingraham breeding population, and also within recently recovered muhly grass prairie north of the Park Road and West of Taylor Slough (personal observation). The destructive

impact of introduced ant species upon local arthropod density and diversity is well recorded (Vinson 1985, Cole et al. 1992). Even without the direct effects of nest raids by ants on overall sparrow mortality, they could reduce the prey base available to breeding sparrows and affect nesting success. The impact of fire ants within the Everglades National Park should be assessed for the sake of many species.

Advantages of the individual-based approach

To conclude on a more general note, the criticisms of the individual based modeling approach, that they are dependent upon reliable estimates of demographic variables and life cycle parameters, would appear to be founded. This study clearly shows high sensitivity to mortality rates. However, it suggests that maybe we should look at these issues from a different perspective. We should consider the notion that it is not the model that is sensitive, but rather the species that is sensitive. Species evolve distinct dispersal and mating strategies that allow them to exploit complex landscapes. These kinds of models allow us to reveal sensitivities and to explore the range of possible strategies, when empirical evidence is hard to obtain (Waser et al. 1994). If species evolve to exploit specialized niches then we should expect that critical thresholds in their response to changing conditions exist. These species are often rare and endangered because the niche, and the habitat type that supports it, is also rare. Unfortunately, human alteration of the landscape and its inputs can pose a sudden and widespread threat to a species' ability to adapt.

Only by identifying the critical thresholds relating to species' ecology can we hope to conserve current levels of biodiversity.

No species lives in a long-term stable environment and each must adapt to exploit changing environmental conditions and spatial patterns of habitat, or go extinct. Individual based models offer the opportunity to include behavioral adaptations into the model, and assess the effects of a changing environment. Yes, these models require reliable estimates from field data but, by considering individual variation and behavioral switching, they allow us to predict the range of possible outcomes given alternate patterns of influence. For instance, by explicitly modeling habitat change we can identify critical thresholds of fragmentation beyond which a species dispersal behavior is maladapted. In this way they provide better species management tools than simpler deterministic models, in which the predictive outcome is fixed and possibly wrong.

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Figure C-1. Flow chart representing the logic behind establishing territories and mating for individuals in the Cape Sable Seaside Sparrow model.

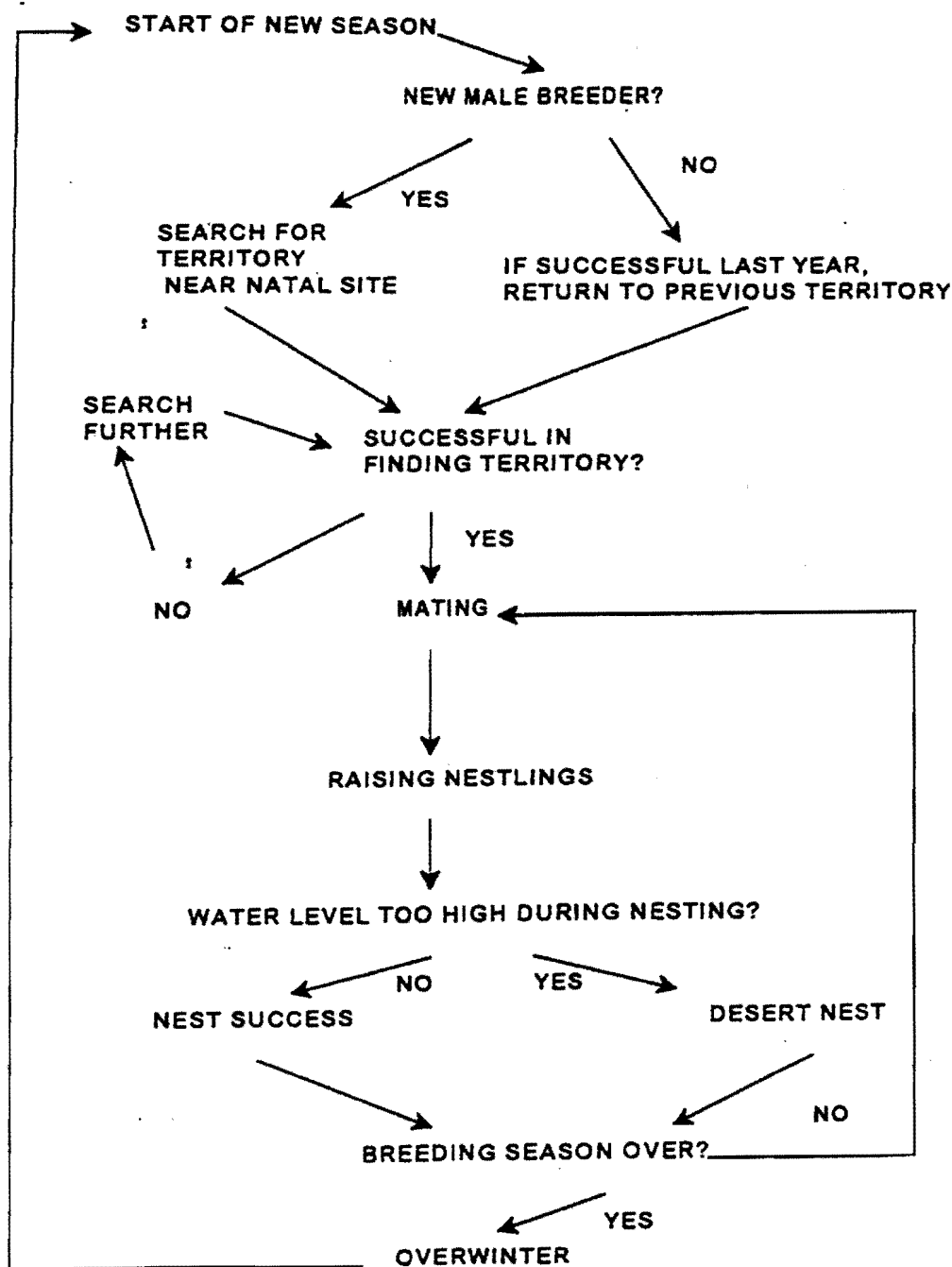
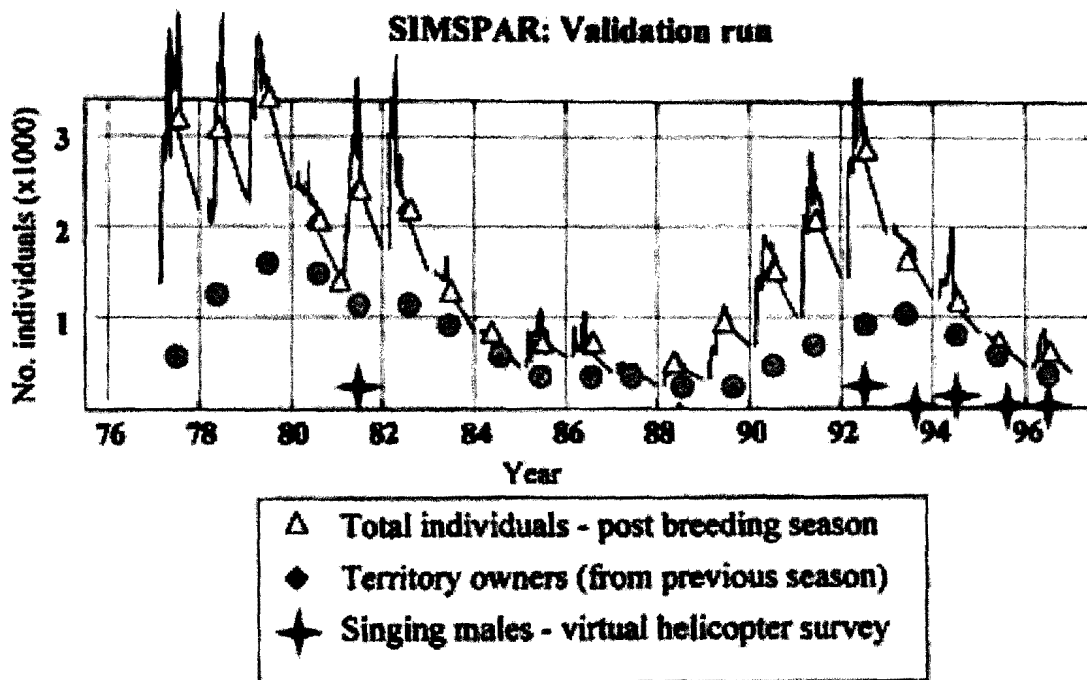


Figure C-2. Example output from SIMSPAR depicting the population estimates for a twenty-year period (1977-1996). This represents a single replicate of the Monte Carlo simulation. The triangles represent the total population estimate at the end of each breeding season. Diamonds represent the total potential breeding population (pair bonds) and crosses represent the number of singing males detected by the "virtual helicopter survey" described in the validation section of the text.



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Figure C-3. Plot of the mean number of singing males recorded by the "virtual helicopter survey" against the actual number of singing males recorded by the field based demographic survey. The correlation coefficient and significance of the fit is also shown.

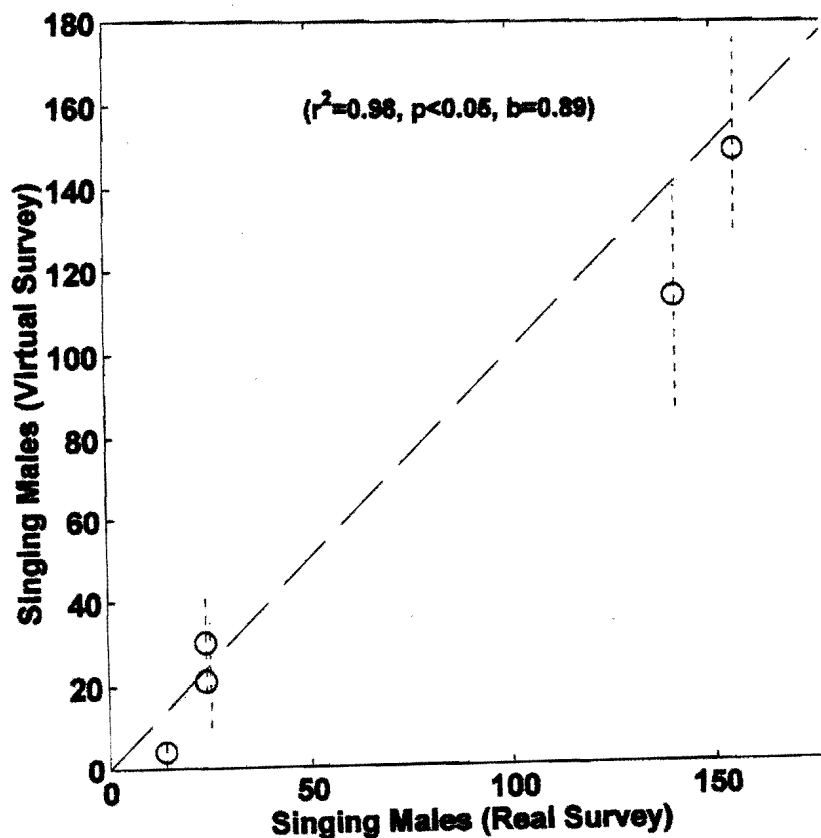


Figure C-4. Example output from SIMSPAR depicting various patterns of abiotic variables and population estimates for a single year (1989) of a single replicate in the Monte Carlo simulation; a) daily water level at NP205 hydrologic monitoring station, b) daily percentage of breeding habitat exposed and available. Pane c) shows the number of singing males recorded by the virtual helicopter survey. Pane d) shows the size of the nestling population by day, as they successfully fledge the cumulative number of this years fledglings is shown in pane e) leading to an overall threefold increase in the total population f).

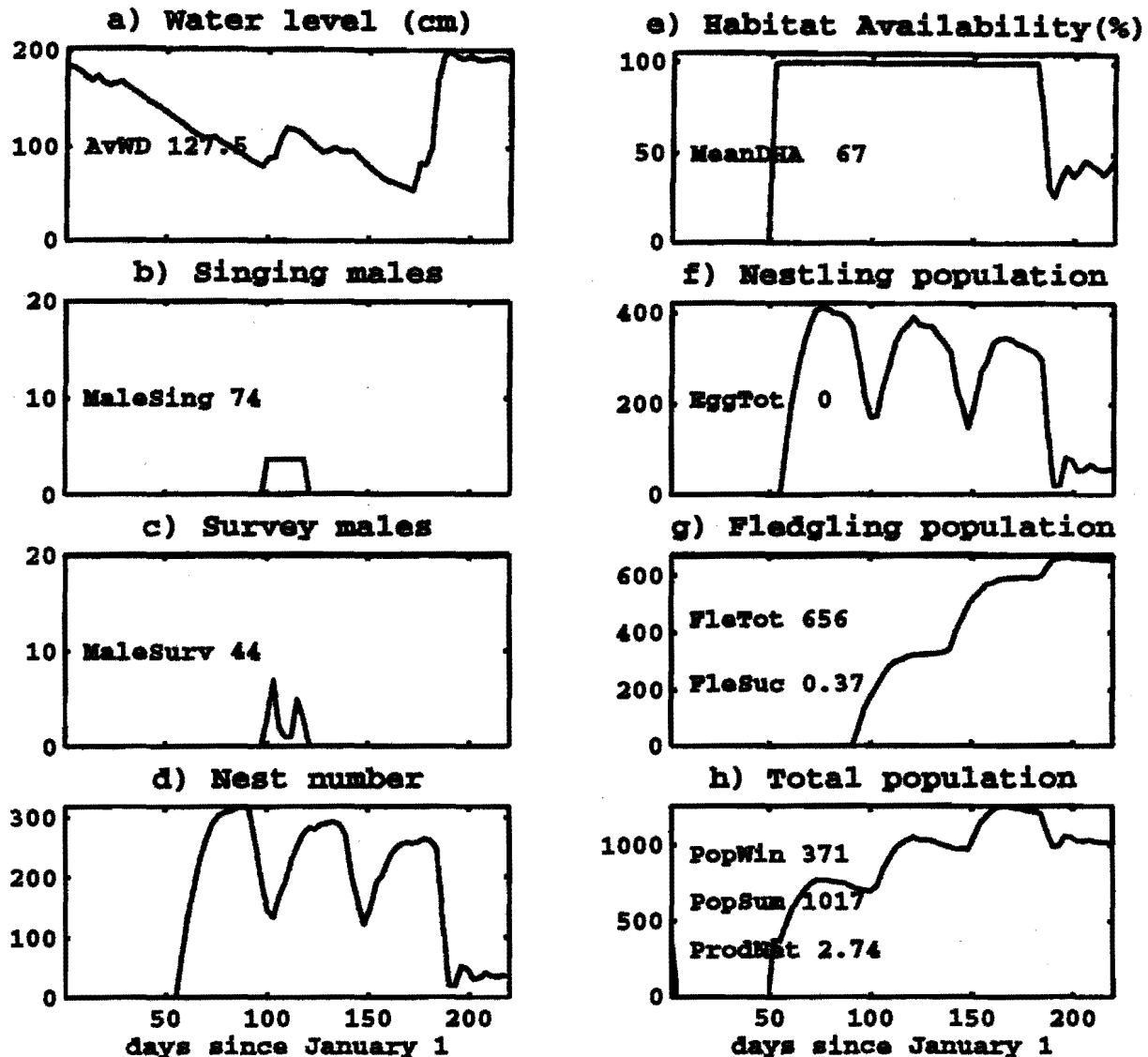


Figure C-5. Example output from SIMSPAR depicting various patterns of abiotic variables and population estimates for a single year (1987) of a single replicate in the Monte Carlo simulation; a) daily water level at NP205 hydrologic monitoring station, b) daily percentage of breeding habitat exposed and available. Pane c) shows the number of singing males recorded by the virtual helicopter survey. Pane d) shows the size of the nestling population by day, as they successfully fledge the cumulative number of this years fledglings is shown in pane e) leading to a slight increase in the total population f).

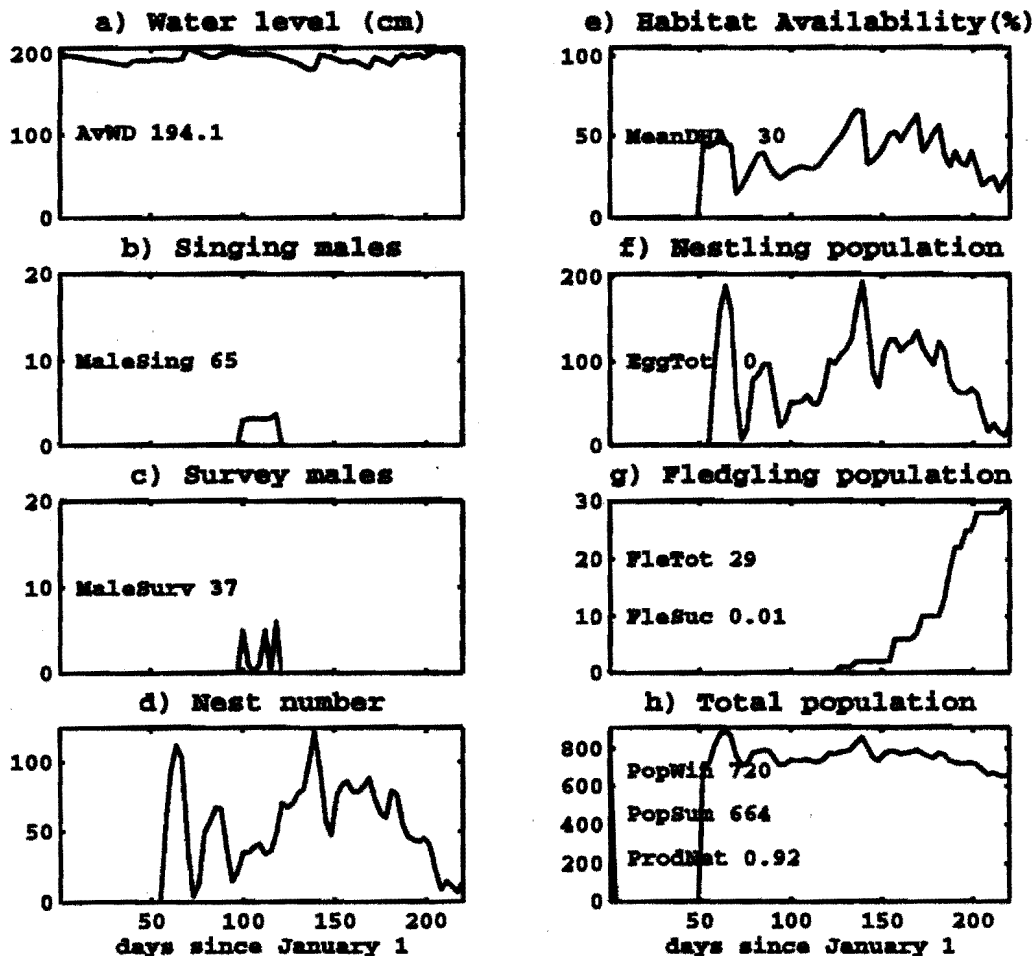


Figure C-6. Example output from SIMSPAR showing the spatial pattern of breeding success across the western landscape for a single year, 1989, for a single replicate of the Monte Carlo simulation. Black crosses superimposed on the topography (red-blue = high-low elevation) indicate non-habitat cells as determined by the habitat sub-model (see text). Also superimposed on the topography are white circles representing cells containing territory-owning males, with black dots indicating successful breeding attempts.

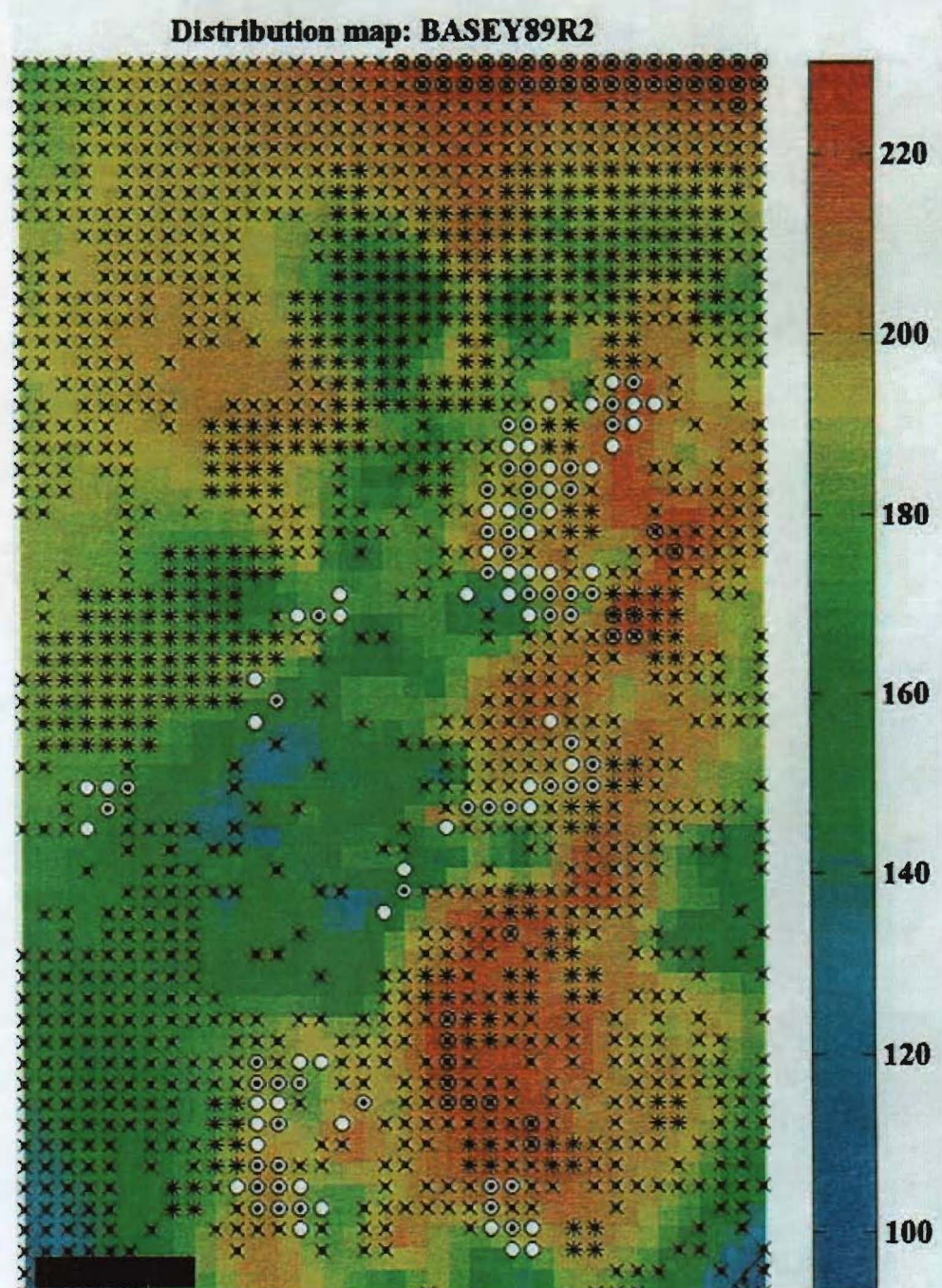


Figure C-7. Example output from SIMSPAR showing the spatial pattern of breeding success across the western landscape for a single year, 1993, for a single replicate of the Monte Carlo simulation. Black crosses superimposed on the topography (red-blue = high-low elevation) indicate non-habitat cells as determined by the habitat sub-model (see text). Also superimposed on the topography are white circles representing cells containing territory-owning males, with black dots indicating successful breeding attempts.

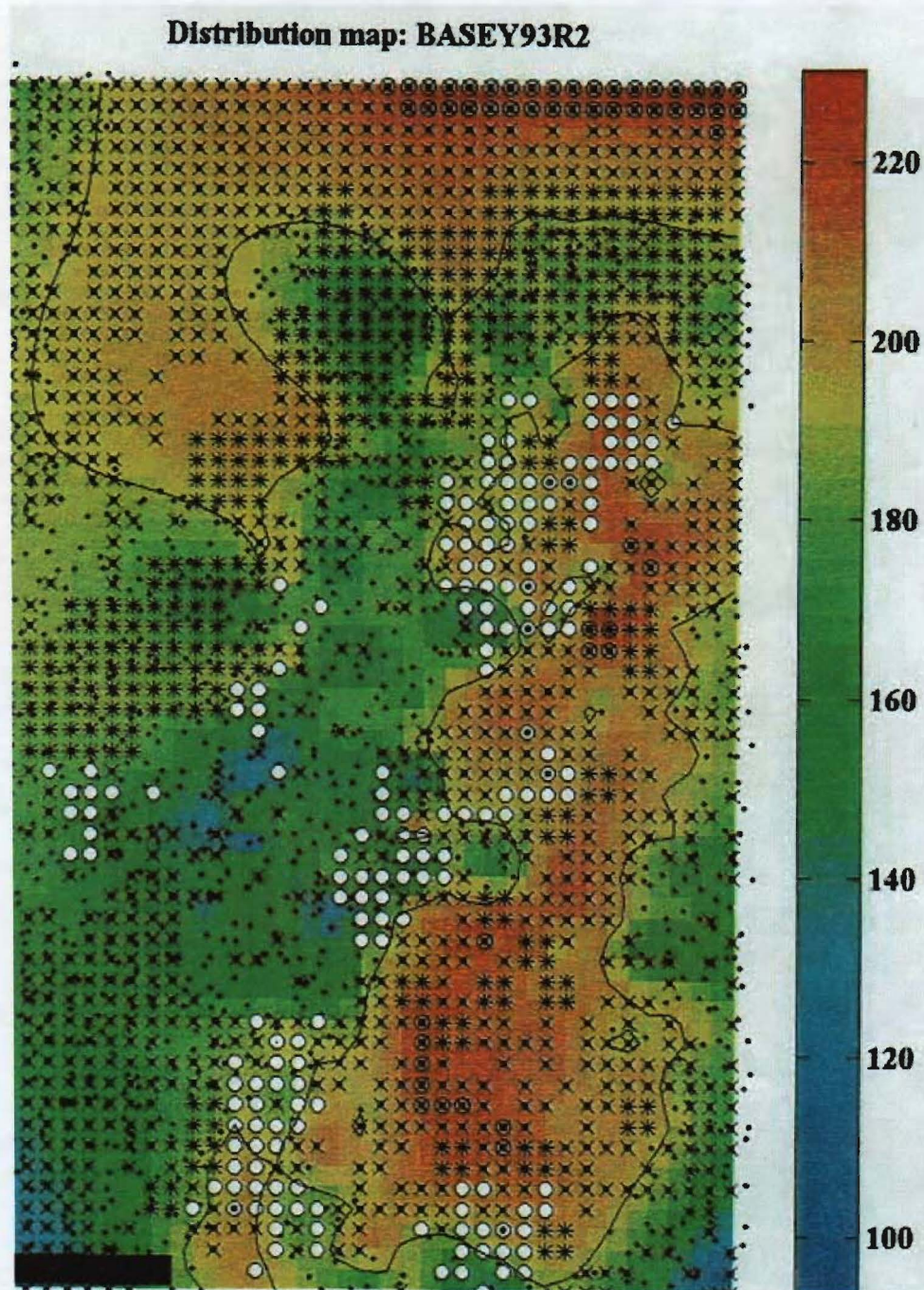


Figure C-8. Example output from SIMSPAR showing the spatial pattern of breeding success across the western landscape for a single year, 1996, for a single replicate of the Monte Carlo simulation. Black crosses superimposed on the topography (red-blue = high-low elevation) indicate non-habitat cells as determined by the habitat sub-model (see text). Also superimposed on the topography are white circles representing cells containing territory-owning males, with black dots indicating successful breeding attempts.

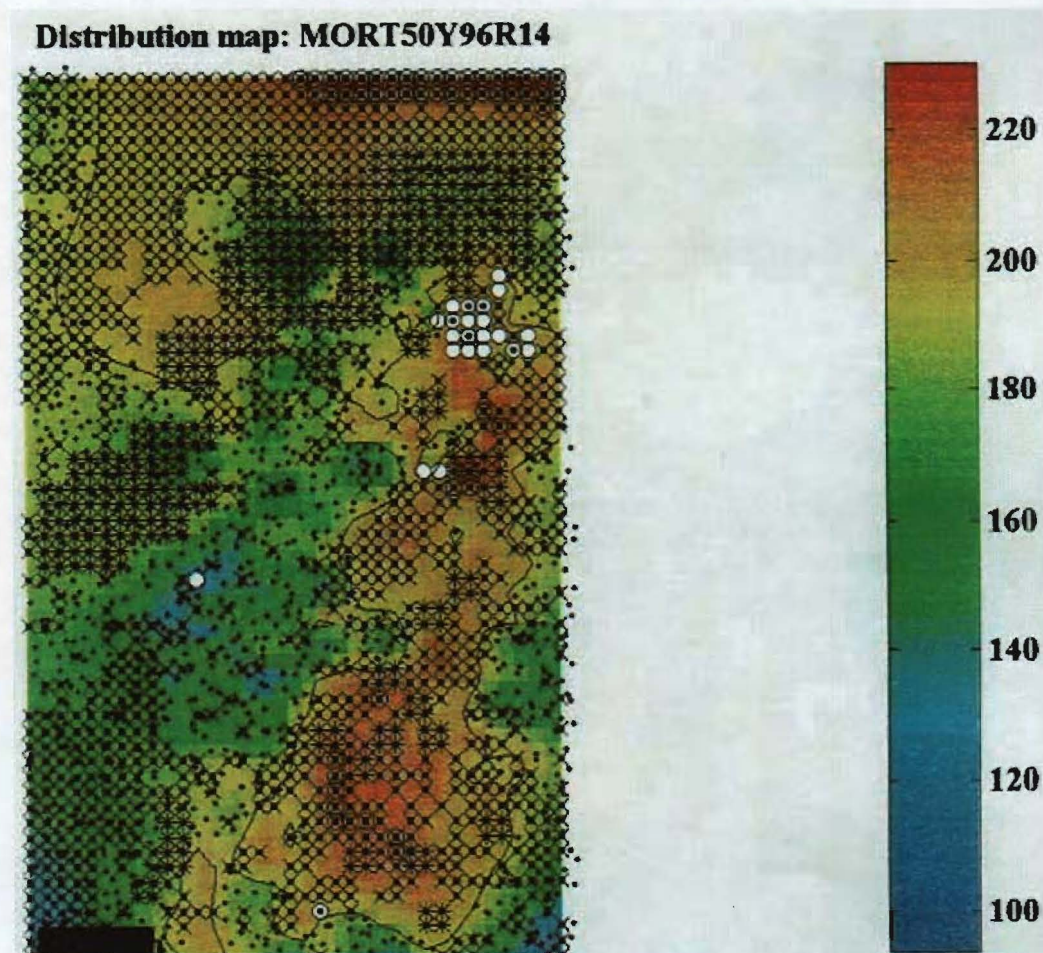
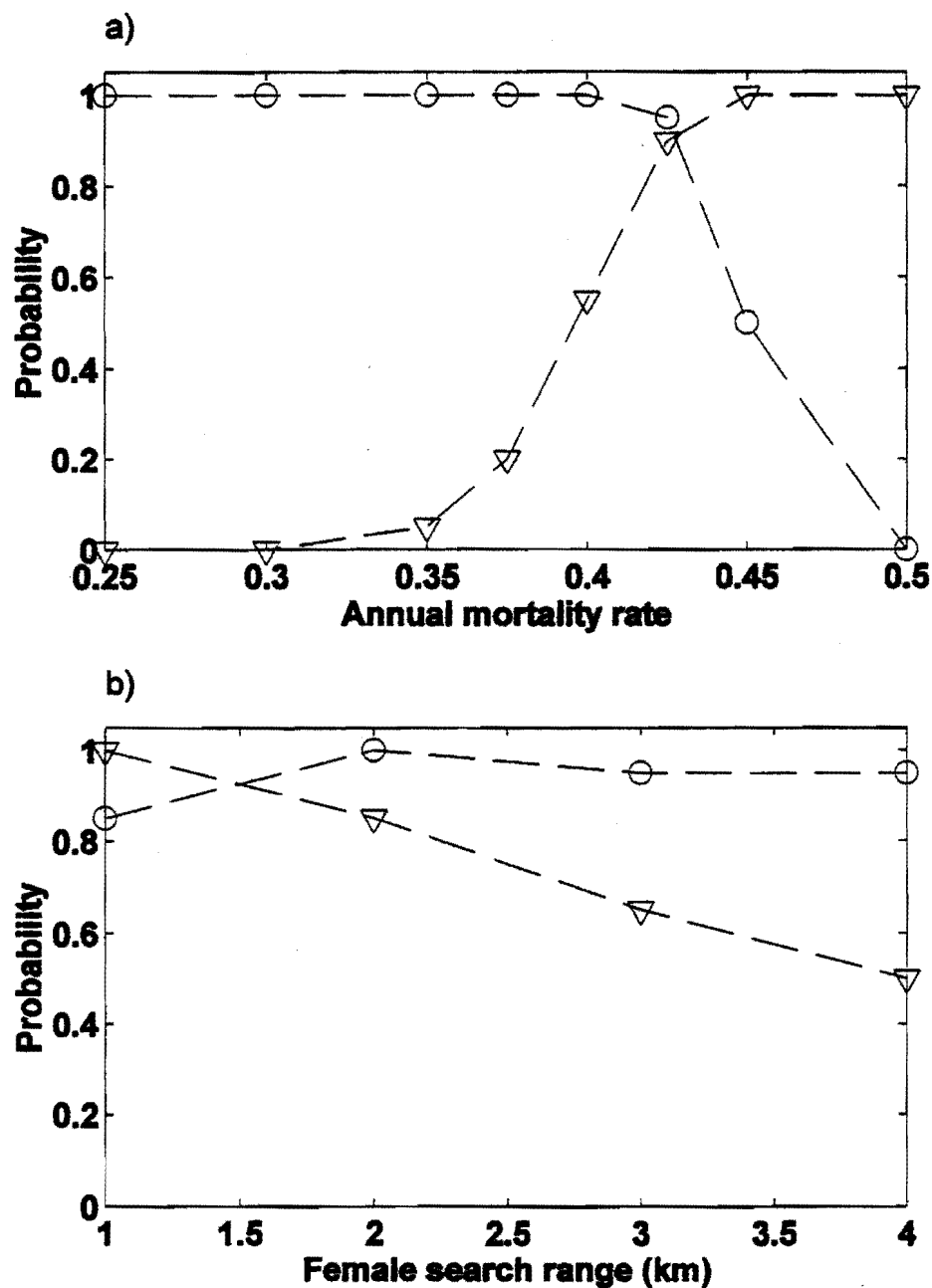


Figure C-9. Results of SIMSPAR sensitivity analyses expressed as the proportion (probability) of simulation replicates in which the population exceeds 500 individuals (triangles) or drops below 100 individuals (circles) after 20 years. These plots demonstrate sensitivity to a) annual mortality rate, and b) female dispersal range.



Identifying Cape Sable Seaside-Sparrow (*Ammodramus maritimus mirabilis*) habitat from satellite images.
Audrey L. Mayer, Robert Powell, Clinton Jenkins, Julie L. Lockwood, Katherine H. Fenn, and Stuart L. Pimm

Abstract

The Endangered Cape Sable Seaside-Sparrow (*Ammodramus maritimus mirabilis*) inhabits the freshwater marl prairies in the interior of Everglades National Park. Since 1850, hydrologic projects have affected the vegetation of South Florida, including the Cape Sable sparrow's habitat. Sparrow numbers have declined by over 50% in the past five years, when high water levels flooded one of the two core populations. Using nest locations, we produced a conservative classification scheme, and determined how much suitable habitat was available to the sparrow from 1992 to 1996. We then used vegetation data from ground surveys to identify specific vegetation characteristics that were correlated with our satellite classification. These characteristics may indicate satellite-visible habitat features. We measured the total area of suitable habitat available to sparrows in each year, and discuss implications of our study for conservation of the species.

Introduction

The Endangered Cape Sable Seaside-Sparrow (*Ammodramus maritimus mirabilis*) inhabits the freshwater marl prairies in the interior of Everglades National Park. Early researchers observed these sparrows in *Spartina* sp. marshes (Howell 1919, Semple 1936, Dietrich 1938, Nicholson 1938, Anderson 1942, Stimson 1944, 1948, 1956), although Ogden (1972) and Werner (1975) found them in *Muhlenbergia filipes* prairies beginning in the early 1970's. Since 1972, most of the Cape Sable sparrow population has utilized *Muhlenbergia* prairie, although this habitat type is believed to be a recent invader (Werner and Woolfenden 1983, Olmsted et al. 1980). *Spartina* habitat has disappeared from most of its current distribution in South Florida (Olmsted et al. 1980). Except for the extinct Dusky Seaside-Sparrow (*A. m. nigrescens*), which inhabited freshwater *Spartina* marshes as well, all other subspecies use brackish or tidal saltwater marshes along the Atlantic and Gulf coasts (Post and Greenlaw 1994).

The Swamplands Act of 1850 began the US Army Corps of Engineers' campaign to drain the Everglades for agriculture and flood control for the eastern urban area (U.S. Department of the Interior 1994). Over 2200km of canals, gates, and levees divert freshwater from Lake Okeechobee into the Atlantic Ocean, or into the western half of Everglades National Park. These structures have altered the natural hydrology and fire regimes, and consequently changed the distribution of many habitats (Loveless et al. 1970, Alexander and Crook 1973, Olmsted et al. 1980, Olmsted and Armentano 1997). Studies in Cape Sable sparrow habitat have documented vegetational changes resulting from altered hydrological and fire regimes (Werner and Woolfenden 1983, Kushlan and Bass 1983, and Curnutt et al. 1998, Nott et al. 1998). In flooded areas, *Cladium jamaicense* can form tall dense stands, which sparrows avoid. In areas that are too dry shrub invasion occurs, and sparrows abandon these areas as well.

To determine the effectiveness of management decisions on the Cape Sable sparrow population, we need to know the distribution of the sparrows, population trends, and changes in the distribution and occupancy of their habitat. In 1981, and 1992 through the present, Kushlan and Bass (1983) and Curnutt et al. (1998) conducted an extensive helicopter survey to map sparrow populations, suitable habitat and potential habitat. Observers stopped every kilometer, and recorded the number of singing sparrows heard, as well as cursory vegetation and water data. Werner and Woolfenden (1983) used aerial photography to identify potential sparrow habitat, which included clumped *Spartina*, unclumped *Spartina*, sparse *Cladium*, and *Muhlenbergia*. In areas they identified as potential habitat, subsequent ground visits determined the accuracy of their classification. Satellite imagery and Geographic Information Systems are increasingly useful for habitat mapping, especially for threatened and endangered species (Palmeirim 1988, Breininger et al. 1991, Franklin and Steadman 1991, Pereira and Itami 1991, Rickers et al. 1995, Sperduto and Congalton 1996). Paired with vegetation and life history data from the ground, satellite images become a powerful conservation tool. Here, we use this technology to map all potential Cape Sable sparrow habitat in Everglades National Park, and determine specific vegetation characteristics common to this habitat.

Study Area and Methods

Much of the Cape Sable Seaside-Sparrow's population inhabits areas that are accessible only by helicopter. We therefore collected most of our nest and vegetation data within areas on the eastern side of Everglades National Park (Figure 1). We first discuss our methods for analyzing satellite images, and then discuss our plant data collected from ground surveys.

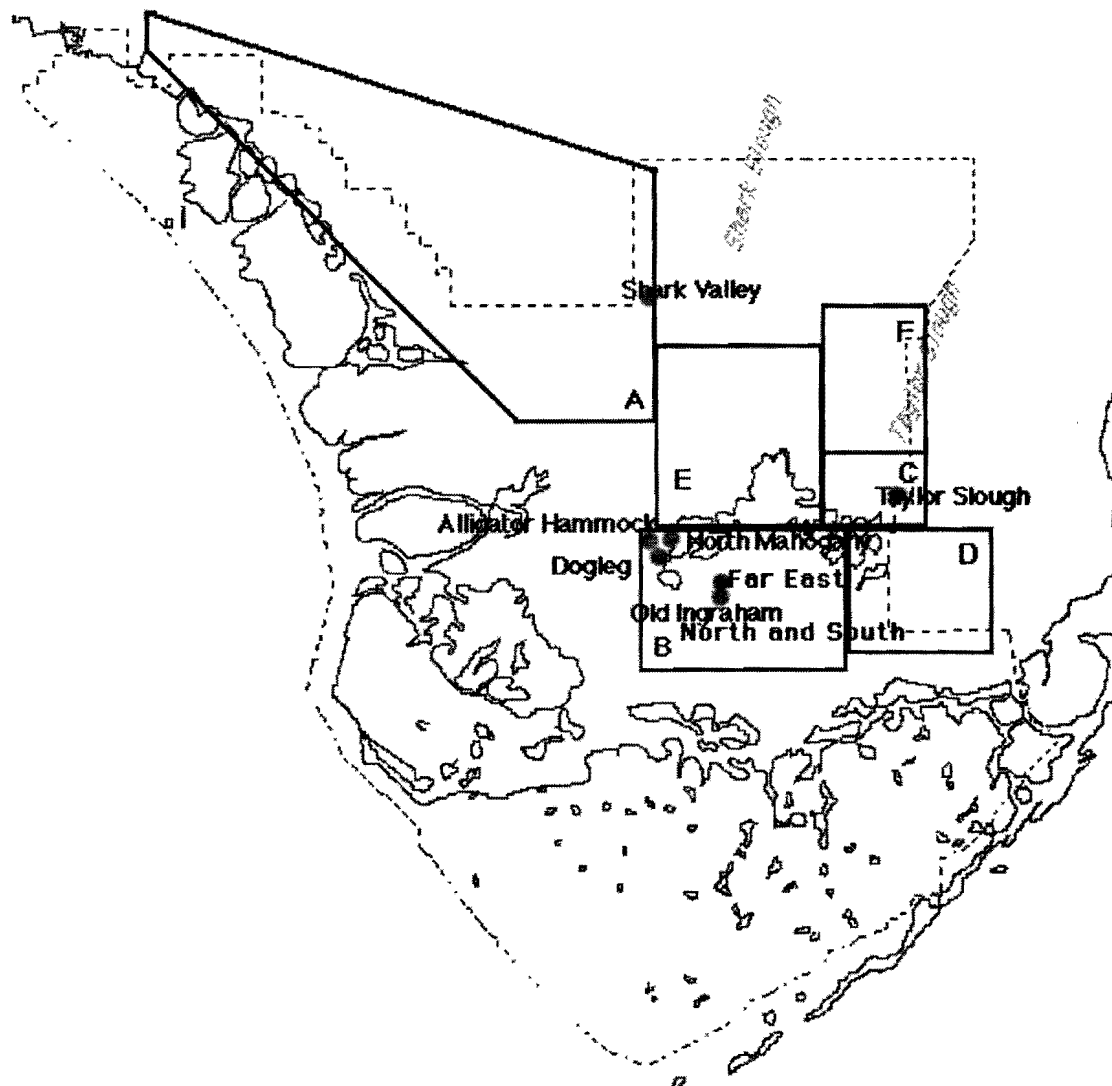


Figure 1. Map of Everglades National Park and study areas.

Satellite data

We conducted our satellite image analysis in three stages: image preparation, classification and image analysis.

Image Preparation

We classified five Landsat Thematic Mapper (TM) images to identify sparrow habitat. These TM images had a resolution of 28.5m². Table 1 gives the pertinent information on the images used.

Year	Acquisition Date	Entity ID
92	13 May	LT501504209213410
93	14 Apr	LT501504209310410
94	1 Apr	LT501504209409110
95	6 May	LT501504209512610
96	21 Mar	LT501504209608110

Although we attempted to limit our window for images from April to May, clouds obscured all available 1996 images during this period. In 1997, no image was sufficiently clear of clouds from March through June, and we were unable to make any analyses for that year.

We used nest location data from 1996 through 1998 in our classifications, concentrated in five of our study areas (Figure 1). In 1997 and 1998, we used a Trimble Pathfinder Pro Global Positioning System (GPS) receiver, and took two hundred UTM readings at each nest. We applied differential corrections later that day at the research station. With this method, our calibration runs demonstrated a receiver RMS error of slightly greater than one meter. Our UTM locations for our 1996 nest sites are less accurate, within 5-15 meters, since we used the Coast Guard beacon for real time differential correction.

We first calculated the covariance matrix for the seven layers. Bands 3 and 4 (red and near infra-red) contained the majority of the information, and band 6 (thermal infra-red) added no information to the analysis. However, retaining all seven available bands did not restrict our analysis capabilities, so we kept all of them and gained a marginal increase in generality. Since each image was over 360 megabyte, we used only a 7 megabyte subset of each image that contained our study areas. We rectified our 1996 image with 17 ground control points from 7.5 minute quadrangle maps and UTM coordinates of recognizable features on both the image and the maps. The RMS error of the rectification was a little more than one meter. We rectified the rest of the images by pixel matching with the 96 image. For this rectification, the RMS error of the pixel matches was approximately one centimeter. To determine whether this accuracy was sufficient, we randomly generated 50 test cases, each consisting of a source image, a target image and a set of coordinates. We had an 87.5 percent

probability of identifying the exact pixel of a known coordinate. We georeferenced our nest locations to the same projection as the TM imagery, and produced an ARC/INFO vector coverage of nests. We overlaid these coverages on the satellite images to identify the corresponding pixels.

Classification Techniques

An image analysis *classification* refers to an identification of a region or regions of an image with certain attributes. In our case, we wished to identify the areas of the Everglades National Park and its surrounds containing suitable nesting habitat for the Cape Sable Seaside-Sparrow. A classification is performed by finding a *signature* for the region of interest in terms of its spectral response. Each pixel of the image is then compared to the signature through a *decision rule* to decide whether to include the pixel in the classification (Jensen 1997). We performed unsupervised and supervised classifications using the ERDAS Imagine image processing software on an IBM RS/6000 workstation (Jensen, 1996; ERDAS, Inc, 1997). Our unsupervised classifications gave us an overview of the system as a whole and the degree of variation within and among our study sites. Unsupervised classifications seek a requested number of clusters in the data. This method classifies pixels according to the cluster they are "nearest" to, spectrally speaking. We used the ISODATA method to acquire 5, 10 and 20 classes in our classification (Jensen 1997). In all cases, iterations continued until less than one percent of the pixels in the scene changed class, which took less than 25 iterations.

We then developed a supervised classification technique to identify sparrow habitat. We first used the rectified 1996 image, then applied this technique to all other images. Training samples "grown" from the nest locations generated habitat signatures. We used one nest to pick a seed pixel, then examined all pixels within a physical radius of 20 pixels. The training sample included all pixels within a Euclidean spectral distance of 30 from the seed pixel. This technique produced training samples of about 1,000 pixels.

A series of trials used nest site capture as the measure of merit to establish our parameters. We grew a training sample for a given physical limit and spectral distance, with spectral distance as a parameter of particular interest. We scored the samples by comparing the number of nests captured in the training sample with the total number of nests in a square of a side equal to twice the radius constraint. The results were insensitive to the value of the physical radius on the region growing process. We found that a value of 20 pixels gave a sample size that generated sufficient margins of errors.

Every pixel on every band had a brightness value (BV) scaled to the range of an unsigned eight-bit integer (0-255). The seven-dimensional Euclidean distance gives us the spectral distance d between two pixels A and B:

$$d = \left(\sum_{i=1}^7 (BV_{Ai} - BV_{Bi})^2 \right)^{\frac{1}{2}}$$

As the spectral distance increases, so does the variability of the sample. A useful spectral distance should produce a training sample with a variability roughly equal to the variability in nest sites. If the spectral distance is too small, the training sample will not reach a plateau and the sample size will be too small. The proportion of nest sites captured will also be small. As the spectral distance goes up, the samples increase until the plateau is reached, and the proportion of nest sites captured also increases. Beyond this point, the sample size remains constant but the spectral variability of the included pixels continues to increase, as does the proportion of nests captured continues. At large spectral distances, the sample encompasses the whole spectrum and every pixel (and every nest) within the physical radius. The number of nests captured increased linearly with spectral distance until a plateau near 29-31BV. Above this "knee" in the curve, the range of the signature increases disproportionately for every nest captured. A spectral distance of 30 consistently produced nest captures in the range of 90-95 percent.

Since we had very accurate nest locations in 1997 and 1998, but only had usable imagery from 1996 through 1995, we compared many supervised signatures. In the next section, we discuss our method for identifying sparrow habitat, that could be applied to all images.

Image Analysis

The most stable and productive sparrow communities are in our Ingraham North (IN) and Far East (FE) study areas (Pimm et al. 1998). We have extensive data from these sites from 1995 through 1998, and hoped the signatures produced in these sites would be applicable to the entire Park. These areas are fairly insulated from the effects of water management decisions outside the park, and have a history of modest burn frequency (REFS). The work proceeded in three phases. First, we produced unsupervised classifications of all our study areas, from the Main Park Road and Sweetbay Pond, and ranging eastward along the Old Ingraham Highway. We knew from ground surveys that these areas supported different vegetation communities, and wanted to test the ability of the satellite imagery to differentiate between them as well. This work established the essential homogeneity of the area.

Second, we produced many signatures based in IN and FE in a wide variety of ways. We tested the ability of the signatures to capture nest sites across all the study areas, and concluded that we could reliably identify sparrow habitat based on the characteristics of the core areas. Finally, we extended the methodology and made identifications of suitable sparrow nesting habitat throughout the park for all years for which we had imagery. We compared these identifications to data previously gathered

through helicopter surveys taken in previous years, as part of the National Park Service Systematic Reconnaissance Flights project.

Analyses of Unsupervised Classifications

As noted above, we produced three unsupervised classifications on the 96 image. Using field data and a set of 1:10,000 scale color-infrared aerial photos (National Aerial Photo Project, 1994), we assigned interpretations to each of the classes. The classification with only five classes proved to be too coarse, as only two classes could be related to grasslands. A ten-category classification produced five categories that could be related to grasslands, four in the prairie area and one on the periphery which we assigned to wet prairie. This classification method proved to be the most useful. The twenty-category classification produced 12 grassland categories, three or four each in four major groups differentiated by appearance: bright grass, prairie grass, dark grass, and wet grass. Although this classification was too detailed to be useful for analyses without extensive ground truthing, it did lead to a deeper understanding of the structure of the grassland community in the study areas. Briefly, the groups can be described as follows:

Bright grass areas were stands of relatively sparse vegetation cover and higher exposure of periphyton and limestone. The latter reflect energy very well, leading to higher BVs and a brighter appearance in the image. This group had the biodensity (biomass per unit area).

Prairie grass signatures correspond to areas of moderate density and height, mainly mixtures of sawgrass (*Cladium jamaicense*) and other graminoids, particularly *Muhlenbergia filipes*. These grasses do not completely obstruct the underlying periphyton and limestone. We estimated the biodensity to be considerably higher in prairie grass areas than in bright grasses, but less than in dark grass areas.

Dark grass areas were tall dense stands of sawgrass and other dense monocots. Sawgrass inflorescences were often over six feet high. Most of the other graminoids were absent. In the denser areas, other sedges and rushes such as needlerush and even cattails were abundant. The vegetation covers all of the ground, eliminating any exposure of the periphyton or the limestone. Biodensity was much higher than in any of the other areas.

Wet grass areas were common to the periphery of the region as the elevation decreases toward sea level. In these areas, there was usually a certain amount of standing water, which shifted the signature to the darker end of the range. Sawgrass, swamp lily (*Crinum americanum*), and other hydrophilic species dominated these areas, while other prairie graminoids decreased. Biodensity in these areas is highly variable, but never as high as in the dark grass areas.

In general, the wet grass areas are highly variable and occur in strips to the west and south of the core areas. The wet grass classes may comprise a more or less continuous change from the prairie grass communities to the very wet areas in Shark Slough to the north, and the mangrove swamps that dominate the lower areas of the Everglades. The amount of water in the area seems to be the dominating variable of this group.

The other three groups, however appear to exist on another continuum characterized by variation in structure. At one end is the bright grass group with smaller clumps of grass and much exposed ground. At the other end is the dark grass group consisting of heavy vegetation with little or no ground visible. The prairie grass group is intermediate to these, and is moderately dense stands of taller grasses with moderate ground visibility. The sparrow may prefer this habitat because it frequently travels along the ground to and from its nest. The sparrow also need sufficient grass structure to support its nests. The presence of *Muhlenbergia*, long associated with sparrow nesting areas, is an indicator of correct proportions of critical habitat characteristics. *Muhlenbergia*, then, would seem to be a sufficient condition for sparrow breeding, though not a necessary one.

We performed several tests on the ten-category classification. First we counted up the number of pixels corresponding to each of the categories in each of the study areas. We then ran a chi-square test to see if the distribution of categories was independent of the study area. Our analysis overwhelmingly rejected this hypothesis ($\chi^2=2195$, $P=.05$, $df=56$). This supported our qualitative conclusion that IN and FE were much more uniformly dominated by prairie grasses, while the Ingraham South (IS), Sweet Bay (SB) and Alligator Hammock (AH) study areas possess a larger proportion of the other grass classes.

We performed similar tests for the distribution of nests over the classes. We found nests in four to seven classes, depending on the year. Chi square tests showed that for any given year structure was present in these distributions ($\chi^2=22.2$, $P=.05$, $df=12$). Preference was shown for three of the prairie grasses classes; however, a significant number of nests were found in one of the dark grass classes. These nests were on the periphery of prairie grass regions which hosted vigorous nesting communities. Another chi square test demonstrated that the distribution of nests in each class did not differ significantly from one year to the next ($\chi^2=4.46$, $P > 0.05$, $df=8$). We therefore concluded that nest locations of later years could be used as seed pixels for classifications on images from earlier years.

The greater variability of the grassland signatures, compared to the other elements of the image, limited the utility of the twenty-category classification. Features such as water, hardwood hammocks, and bayheads, had well defined signatures. When generating more classes, the ISODATA algorithm subdivided the more highly variable grass classes into narrower classifications before splitting tighter

classes. This gave an unrealistic picture of the overall homogeneity of the grasses. The supervised classifications gave a much different view.

Analyses and Results of the Supervised Classifications

We obtained many signatures using nest sites in IN and FE as seed pixels. These signatures classified almost the whole of the IN and FE study areas as suitable habitat, except for those areas that were obviously unsuitable (hammocks, open water, bayheads, road edge shrubbery, etc.). This opposed the results of the unsupervised classifications, which indicated great heterogeneity in the grassland communities. Our statistics tests demonstrated the following:

The signatures generated in IN and FE were applicable generally over all the prairie study areas. When we used the signatures to classify the other study areas, the percentage of nests captured were about the same as in the areas where the signatures were generated (90-95 percent).

A chi square test on the distribution on captured nests over the study areas for ten randomly generated signatures failed to detect any structure ($\chi^2=32.88$, $P=0.05$, 54 DOF). Thus, there was no significant difference between the signatures in their ability to capture nests in the seven study areas.

We lumped all nest captures from all the areas and tested the signatures for significant differences in nest capture. A t-test showed that none was evident even at well below the 0.10 level ($t=.033$, $P=.05$, $df=9$).

We found no significant differences on 1996 images among signatures based on nest data from 1996, 1997 or 1998 ($t=.231$, $P>.2$, $df=8$).

To test whether we could identify habitat by eye based on interpretive skill alone, we generated five signatures each from nests. From the IN/FE area, we chose the pixels, and generated a stratified random sample of pixels (we eliminated obvious non-habitat). For each signature, we counted the the number of nests captured in all seven of the applicable areas. An analysis of variance showed no significant difference. ($F_{.05}(2,df=12) = 3.88$).

We concluded that sparrows use a broader pattern of habitat characteristics than the unsupervised classifications had led us to believe. Quite simply, the sparrows are less choosy than the ISODATA algorithm. Furthermore, we can use almost any part of the core area to generate a signature for sparrow habitat, and no signature so generated differs significantly from any other.

Identifying Sparrow Habitat

We then used the signatures generated in the core areas to identify sparrow habitat across space and time. We applied the signature to 70 megabyte images that included all of the Everglades National Park and the southern portion of Big Cypress National Preserve. We used a parallelepiped decision

rule leaving all unclassified pixels unclassified (in lieu of specifying some kind of tie-breaker, Jensen 1997). This gave a monochrome image consisting of just those pixels that complied with the signature. We overlaid this image on the 96 image of the park. The overlay identified 13-15 percent of the park area as suitable for sparrows. We identified all the known major sparrow populations.

To standardize the identification, we used the intersection of three signatures generated from the locations of random nests in IN and FE. This method provides a conservative estimate of sparrow habitat, and showed that intersecting the third signature caused a change of one percent or less of the number of pixels identified. For example, on the 1996 image, the intersection of first two signatures classified 12 percent of the park. The addition of the third signature did not result in any decrease in the number of pixels included in the classification. When we increased the overlay to four signatures, the pixels lost in the intersection were almost all located on the periphery of the identified regions. Geographically marginal areas are also spectrally marginal. Mathematically, there is no reason why this should be so, but we suspect that it makes sense ecologically. Unfortunately, such an exploration was not possible under the present limitations of time and funding.

With the goal of gauging the accuracy of the identification, we compared these classifications with the 1996 helicopter survey (REF). The survey covered the major sparrow breeding areas on a 1 km grid, and observers recored all sparrows seen and heard for ten minutes. In 1996, sparrows were recorded at 76 points. Identified sparrow habitat occurred within 500m of 69 of these points, which gives our classification about a 91 percent accuracy.

However, this accuracy may be decreased with a decrease in helicopter navigation precision. Also, the survey results were plotted on an unrectified image. The rectification error is about 250 m in areas where we have made accurate measurements. The navigation accuracy of the helicopter survey is certainly no better than this. Because of the uniformity of vast areas of the Everglades and the lack of precise landmarks discernable on the satellite images, rectification of the whole of the park area is a challenging task that is still in progress. Nevertheless, these errors must to a certain extent be offsetting. In summary, while we cannot quantify the error, we can only be encouraged by such good agreement between the helicopter data and the habitat classification.

We extended sparrow habitat identification to the rest of the images by applying the same technique. It was not always possible to find a signature that is valid from one year to the next, and we had to generate new signatures for each image. This may at first seem to contradict our previous conclusion that it is possible to use the locations of nests from one year to predict habitat in another, but the relationship is not really reflexive. The birds do return to the same areas year after year, the

vegetation components do remain very much the same (at least on the Ingraham prairies), but the spectral response of those components may well be different due to seasonal variation, weather changes, water levels and instrument drift (Peplies, 1998).

We made a preliminary investigation in the changes in the histograms of the images. The shape of the distribution is similar from one year to the next, but the distribution is shifted up or down the scale. Further work might elicit a transformation to normalize seasonal and other variations, and provide a useful baseline for finer analyses. Such a project would require many more images than in our possession.

We then calculated the amount of area classified as "suitable" habitat in all of Everglades National Park in the 1992 through 1996 satellite images (Table 2).

Table 2. Amount of Everglades National Park classified as sparrow habitat from satellite images.	
1992	760,528ha
1993	290,119ha
1994	653,763ha
1995	196,509ha
1996	433,469ha

Figure 2 shows a composite of our habitat identifications for 1992-96.

Plant data

From March to May 1997, we performed 20 transects in five of our study sites; four in subpopulation B, and one in subpopulation C. We used a stratified random sampling technique to place these 50m-strip transects, and took vegetation measurements from 10 1m² quadrats, one every 5 meters of the transect. All transects have associated UTM coordinates. In each 1 m² quadrat we collected floristic and structural data. Floristic data included:

- Species composition – We took presence/absence data and cover estimates (see scale below) for every species in each quadrat. Here, we only report the cover data for the four dominant graminoids in the areas we surveyed: *Cladium jamaicense*, *Muhlenbergia filipes*, *Rhynchospora* sp., and *Schizachyrium rhizomatum*.

Structural data included:

- Cover – We used a Braun-Blanquet method (from 1 (0 to 1.0%) to 6 (75-100%) Phillips 1959, Mueller-Dombois and Ellenberg 1974), and estimated total live plant cover, dead matter cover, and periphyton cover. To assure that our estimates were consistent, we compared our cover estimate to actual stem densities for one quadrat of each transect (chosen at random).

- Stem density – For each plant species, we counted the number of stems per quadrat. Using data from our plant removal study in 1995 and 1996, we found a direct relationship between stem density and standing biomass (adjusted for species composition and abundance). We used this relationship in this year's data to indirectly measure biomass in each quadrat.
- Maximum vegetation height (cm)
- Effective height (cm, Wiens 1969) – Using a field notebook, we recorded the maximum height at which 90% of the side of the notebook is obscured by vegetation. Werner (1975) used a similar measurement, which he called "vertical obscurity profile". While this is a crude measurement, it allows us to quantify an aspect of the habitat that may be important to the sparrow for nest locations, predator evasion and thermal regulation.

We used a nonparametric Mann-Whitney U test to compare vegetation characteristics between transects in suitable versus unsuitable pixels, and used an alpha level of .05 to determine significance. We also used this test and parameters for comparing transects burned in the last 10 years, with those that have not burned. We conducted all tests using SPSS 8.0 for Windows (SPSS Inc.).

Results

We detected significant trends in most of our structural measurements and two of our floristic measurements when classified into suitable and unsuitable pixel groups (Table 1, Figure 2). Maximum vegetation height and dead matter cover were lower in suitable pixels, whereas effective height, periphyton cover, biomass, percent cover of *Muhlenbergia filipes* and *Rhynchospora* sp. were higher in suitable pixels.

Table 1. Mann-Whitney U comparison of vegetation transect data in pixels classified as suitable or unsuitable from satellite imagery (bolded characteristics are significant).			
<u>Vegetation characteristic</u>	<u>Mean unsuitable pixels</u>	<u>Mean suitable pixels</u>	<u>Mann-Whitney U sig. (2-tailed)</u>
Total live plant cover	1.96	1.86	.244
Maximum vegetation height (cm)	103.64	93.52	.002
Effective height (cm)	1.77	2.93	.006
Dead matter cover	2.00	1.73	.002
Periphyton cover	4.39	4.69	.003
Species Richness	7.80	8.02	.543
Biomass (dry grams)	1711.49	2014.00	.004
% cover <i>Cladium</i>	2.00	1.92	.583
% cover <i>Muhlenbergia</i>	1.03	1.37	.007
% cover <i>Rhynchospora</i>	.86	1.20	.022
% cover <i>Schizachyrium</i>	1.06	1.23	.125

We suspected that the dominant graminoids create some of the structural characteristics we observed in the habitat. Although we cannot say for certain that these species do create the structure, we can at least determine whether or not particular species are correlated with particular structural features. We used Kendall's tau-b nonparametric correlation test with an alpha level of .05 or lower. Percent cover of *Cladium jamaicense* was positively correlated with maximum vegetation height and biomass (correlation coefficient = .393 and .367 respectively, $p=.000$ for both), but negatively correlated with effective height (coefficient = -.169, $p = .014$). Effective height and percent cover of *Muhlenbergia* were positively correlated (coefficient = .356, $p = .000$), while the percent cover of *Muhlenbergia* and *Cladium* were negatively correlated (coefficient = -.216, $p = .002$). Percent cover of both *Rhynchospora* and *Schizachyrium* were negatively correlated with maximum vegetation height (coefficient = -.252 and -.180, $p = .000$ and .008 respectively). *Rhynchospora* was also positively correlated with effective height (coefficient = .256, $p = .000$). Our observations in the field agree with these results. *Cladium* is by far the tallest growing graminoid in these prairies, and its thick, wide leaves may also account for a significant portion of the biomass in areas where it dominates. *Muhlenbergia*, and to some extent *Rhynchospora* (especially *R. tracyi*), typically grow in small bunches, and never grow taller than .7cm (pers. obs.).

Fire

Plant cover and effective height were higher in areas that have burned once the past 10 years, while periphyton cover and percent cover of *Rhynchospora* sp. were lower in these areas. An analysis of vegetation characteristics and years post fire is in progress.

Table 3. Mann-Whitney U comparison of vegetation transect data in areas burned once since 1987, and those not burned (bolded characteristics are significant).			
<u>Vegetation characteristic</u>	<u>Burned once</u>	<u>Not burned</u>	<u>Mann-Whitney U sig. (2-tailed)</u>
Total live plant cover	1.73	2.03	.001
Maximum vegetation height (cm)	94.87	98.65	.270
Effective height (cm)	2.08	2.90	.048
Dead matter cover	1.74	1.88	.660
Periphyton cover	4.69	4.51	.016
Species Richness	7.82	8.11	.839
Biomass (dry grams)	1867.45	1947.75	.247
% cover <i>Cladium</i>	1.99	1.91	.518
% cover <i>Muhlenbergia</i>	1.21	1.28	.558
% cover <i>Rhynchospora</i>	1.36	.88	.003
%cover <i>Schizachyrium</i>	.90	1.37	.000

Discussion

The variation in the amount of available habitat agrees with the results of the helicopter surveys for the applicable years. Figure 4 shows a composite of helicopter survey points that found sparrows with identified habitat. Table X.X-X summarizes the agreement. This is the principal independent confirmation of the ability of signatures generated in the core areas to predict habitat over the rest of the park.

In addition, the effect of water discharges over the S-12 gates as reported elsewhere (Curnutt *et al.*, 1998; Nott *et al.*, 1998) is clearly seen in the fluctuation of the amount of available habitat in the Rattlesnake Ridge area (just south of 40-Mile Bend on the Tamiami trail, roughly between gauging stations NP-205 and P-34). Note the large reduction in identified habitat in 1993 and the almost complete disappearance of habitat in 1995 due to inundation. Note, too, that the available habitat in 1996 is much less than that of 1992 or 1994. Water level records for the period (Curnutt, *et al.*, 1998) indicate that the area was no wetter at the time the image was taken in 1996 than the corresponding time for the 1994 image. The significant loss in habitat in 1996 is consistent with a conclusion of damage to the vegetation system on which the sparrow critically depends. Presumably, the habitat is recovering, but we will have to wait for the 98 imagery before we can make any definite statements.

Finally, we have included a composite (Figure 3) with overlaid fire data for each year from 19XX to 19XX. Figure X.X-X gives a cumulative picture of the fire frequency. Each pixel is colored to show how many times the pixel has burned in the past 18 years. The area east of Shark Slough and north of the Main Park Road has been burned much more frequently than other parts of the park. Curnutt *et al.* (1998) and Nott *et al.* (1998) discuss the ecological effect of burn frequency, and the contribution of water management decisions. The elevated rate of burning in this area is a principal contributor to the decline in what was once a thriving population of sparrows.

The technique for identifying sparrow habitat finds correlations in the type and structure of the vegetation preferred by the sparrow. However, this method also has immediate value as a tool for evaluating management policy, especially related to water delivery and the protection of productive sparrow breeding areas. Above all, it gives a vivid picture of the vulnerability of the Cape Sable sparrow. The west side population is directly affected by the amount of water entering the park. The east side population has been severely reduced by overburning. The Ingraham prairie population appears to be healthy and resilient, but one only has to look at the great Ingraham fire of 1989 to see the risk to that population as well. If the sparrow habitat were reduced to just the Ingraham area, extirpation by some catastrophe would be only a matter of time.

Maximum vegetation height is lower in "suitable" pixels. Sparrows may require a high perch above their nest for territory defense, but the effectiveness of this perch is decreased if a majority of the

surrounding vegetation is also high (such as in dense stands of *Cladium*). Effective height and the percent cover of two plant species that may provide it (*Muhlenbergia filipes* and *Rhynchospora* sp.), were higher in pixels of suitable habitat. Transects in suitable pixels had lower dead matter cover and higher periphyton cover and biomass. On transects that burned in the past ten years, fire may have decreased the plant cover and effective height, but favored *Rhynchospora* and periphyton growth. Our analysis of years since fire and effect on habitat characteristics is still in progress.

Most of these results agree with previous findings by Lockwood et al. (in prep) and Mayer et al. (in prep). Maximum vegetation height decreased in transects further from sparrow territories, but was highest in the 1m area immediately surrounding the nest. These studies also found effective height to be highest in suitable habitat and around nests. Sparrows may require these clumps for nest sites. Dead vegetation may also provide this structure. Lockwood et al. (in prep) found higher dead vegetation cover at nest sites than in areas further away (but still within a territory), and Mayer et al. (in prep) found dead cover to be highest in transects closest to sparrow territories. We found periphyton cover to be higher in suitable habitat pixels, while Mayer et al. (in prep) found periphyton cover to increase with distance from a sparrow territory.

Muhlenbergia filipes cover was considerably higher in suitable pixels, which is what we expected. The majority of the Cape Sable sparrow population now exists in one habitat type; *Muhlenbergia* prairies. In areas, such as Taylor Slough, where the hydroperiod has become longer and the area wetter, *Cladium jamaicense* can replace *Muhlenbergia* (Olmsted et al. 1980, Kushlan and Bass 1983, Nott et al. 1998, Mayer et al in prep). Since the percent cover of *Cladium* was highly correlated with maximum vegetation height, we would expect that as *Cladium* increases and *Muhlenbergia* decreases in an area, the area would support fewer sparrows. These changes can be picked up by satellite images, and can be tracked spatially and over time.

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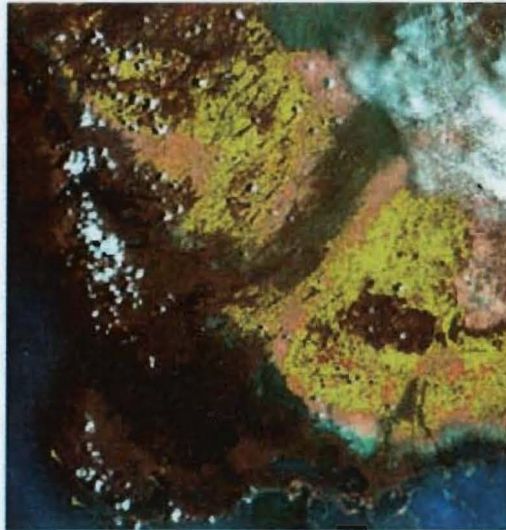
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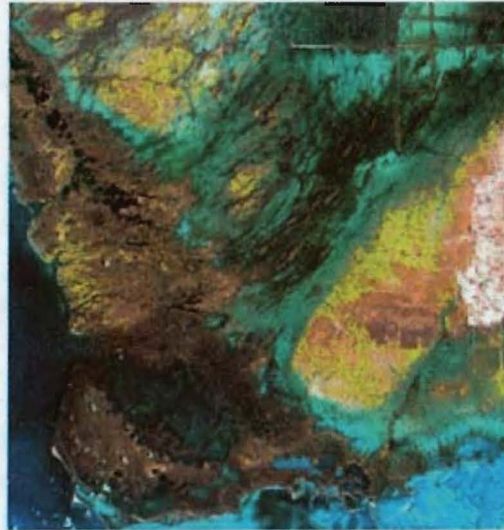
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Cape Sable Seaside Sparrow Habitat

13 May 1992



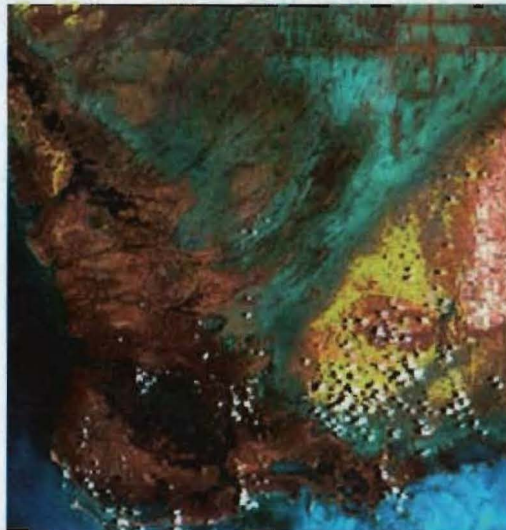
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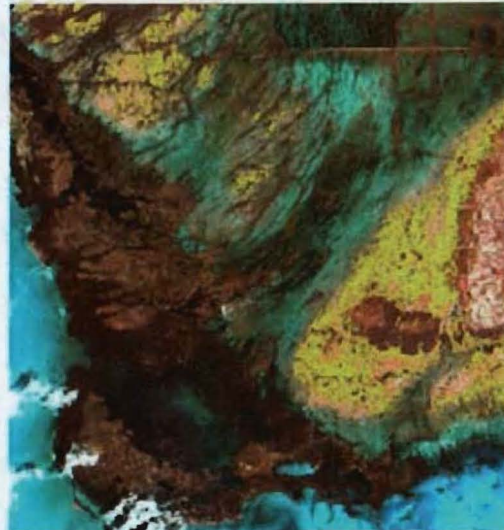
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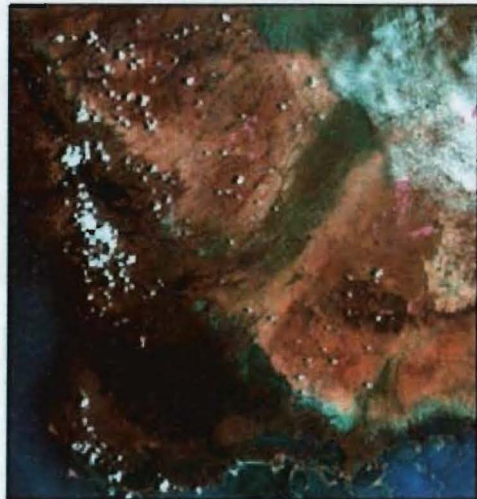


21 March 1996



Fire History of Everglades National Park

1992



1993



1994



1995

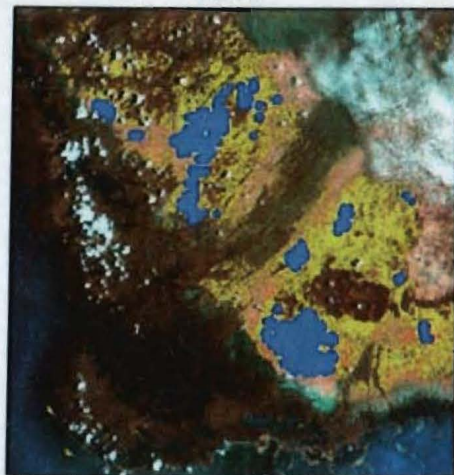


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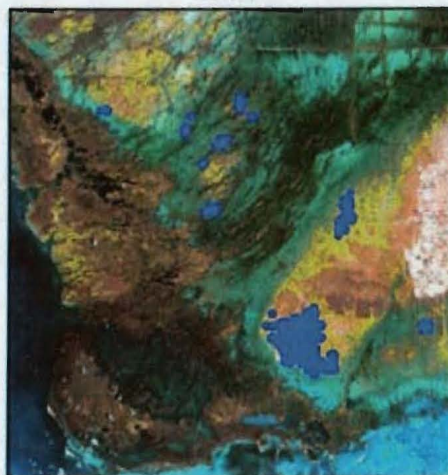


Helicopter Survey Results (1992-1996)

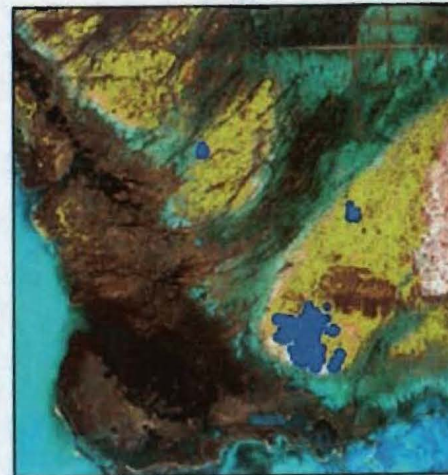
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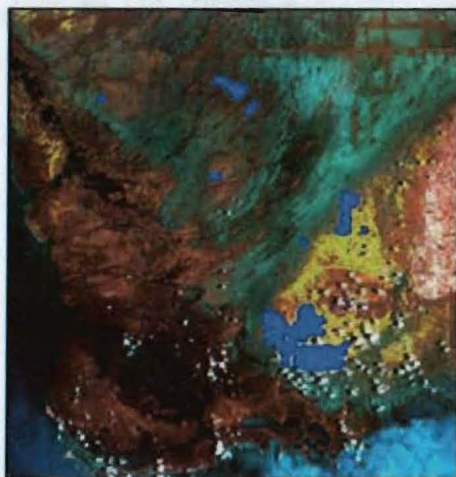
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