Sparrow in the Grass

A report on the first ten years of research on the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*)

Stuart L. Pimm, Julie L. Lockwood, Clinton N. Jenkins,
John L. Curnutt, M. Philip Nott, Robert D. Powell,
Oron L. Bass Jr.

Preface

This year's annual report is fundamentally different from previous ones. First, this year marks the end of a major funding cycle and we are obligated to provide a summary of the work completed to date. Second, and not coincidentally, it is a year when most of our research to date has been published in major journals (or is in the final stages of that process).

These facts mean that we need to produce a self-contained synthesis. In previous years, we have collected papers in various stages of preparation — from first drafts to journal publications — and written a brief introductory account of how papers have moved from one to the other from year to year. That choice required separate advice to new readers who had not followed the story so far and to experienced readers who would encounter chapters that were now publications, but which they had seen in previous year's reports as drafts. This year's report completely replaces previous reports. It can be read without reference to earlier work, since it summarizes all earlier work. Our intent is to convert this report into a monograph for publication by a major U.S. university press.

Writing a single, cohesive document is not an easy task. The original papers on which this document is based cross-reference other published papers. Moreover, those papers inevitably must repeat sufficient introductory material to be self-contained. By contrast, this report should cross-reference material that appears within it. Its arguments should develop logically so as to minimize repetition. We hope we have succeeded in these tasks, but recognize that far more cross-referencing will be necessary before this report can be considered for publication.

Finally, here is the list of authors of previously published (or accepted) parts of this document.

- Chapter 1 was written by John Curnutt; it is an original work for which he retains copyright. It was not produced as part of this project, nor funded by it. It appears here, with his permission, to facilitate discussion of the sparrow.

- Chapter 2 was written by Julie Lockwood. Parts of this have been published as Lockwood, J. L., K. H. Fenn, J. L. Curnutt, D. Rosenthall, K. L. Balent, and A. L. Mayer. 1997. Life history of the endangered Cape Sable Seaside Sparrow. Wilson Bulletin 109:234–237.

- Chapter 3 was written by Julie Lockwood. Parts of this have been published as Lockwood, J. L., K. H. Fenn, J. M. Caudill, D. Okines, O. L. Bass, Jr., J. R. Duncan, and S. L. Pimm. 2001. The implications of Cape Sable Seaside Sparrow demography for Everglades restoration. Animal Conservation 4:275–281.
- Chapter 4 was written by Julie Lockwood.
- Chapter 5 was written by Stuart Pimm.
- Chapter 6 was written by Stuart Pimm and Julie Lockwood. Parts of this chapter have appeared in three publications:
  - Curnutt, J. L., A. L. Mayer, T. M. Brooks, L. Manne, O. L. Bass, Jr., D. M. Fleming, M. P. Nott, and S. L. Pimm. 1998. Population dynamics of the endangered Cape Sable Seaside-Sparrow. Animal Conservation 1:11–20.
  - Curnutt, J. L., S. L. Pimm, and B. Maurer. 1995. Population variability of sparrows in space and time. Oikos 76:131–144.
  - Nott, M. P., O. L. Bass, Jr., D. M. Fleming, S. E. Killeffer, N. Fraley, L. Manne, J. L. Curnutt, T. M. Brooks, R. Powell, and S. L. Pimm. 1998. Water levels, rapid vegetational changes, and the endangered Cape Sable Seaside Sparrow. Animal Conservation 1:23–32.
- Chapter 7 was written by Clinton Jenkins. It combines the text of two papers provisionally accepted by Animal Conservation:
  - Jenkins, C. N., R. D. Powell, O. L. Bass, Jr., and S. L. Pimm. Demonstrating the destruction of the habitat of the Cape Sable Seaside Sparrow.
  - Jenkins, C. N., R. D. Powell, O. L. Bass, Jr., and S. L. Pimm. When good birds make bad choices.
- Chapter 8 was written by Stuart Pimm and Oron Bass Jr. Most of this text appears as Pimm, S. L., and O. L. Bass, Jr. 2002. Range-wide risks to large populations: the Cape Sable Sparrow as a case history. Pp. 406–424 in S. Beissinger and D. R. McCullough (eds.), Population viability analysis. University of Chicago Press, Chicago.

In addition, Col. Robert Powell assembled the pieces and compiled the first draft of this report.

Executive Summary

0.1 History

In 1918, A. Howell discovered the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*), the last new "species" ever recorded in the continental United States. He found it in the saltmarshes of Cape Sable, the south-eastern tip of the Everglades. This population must always have been tiny — there was never enough habitat on Cape Sable to support a viable population — and it was almost certainly only a peripheral and perhaps ephemeral subpopulation. The 1935 Labor Day hurricane, which devastated the Cape, almost certainly eliminated it.

In 1954, L. A. Stimson rediscovered the sparrow in the vast *freshwater* prairies of the Everglades. He realized then that the true range of the sparrow must cover an area much larger than the scattered saltmarshes near the coast. In fact, the distribution of the sparrow belies its appellation of "seaside", being found as far as 40 km inland from the Gulf of Mexico. There is no evidence that it only recently moved into freshwater marshes. Stimson understood that the sparrow has likely been a freshwater sparrow over geological time spans.

The Cape Sable Seaside Sparrow was among the first group of species listed as endangered by the U.S. Fish and Wildlife Service on March 11, 1967. The sparrow was listed because of its limited distribution and threats to its habitat posed by large-scale conversion of land in southern Florida to agricultural uses.

Surveys of the sparrow, employing helicopters to ferry observers to its remote locations, began with Harold Werner in 1974. In 1981 the first range-wide survey was undertaken. This was repeated in 1992, and range-wide surveys have continued every year since. The surveys show that sparrows are found in a set of populations (A through F) separated to various degrees by unsuitable vegetation.

0.2 Breeding biology

Sparrows maintain territories within which all nesting and feeding activities occur. Territories are mutually exclusive such that no two males share a substantial proportion of their

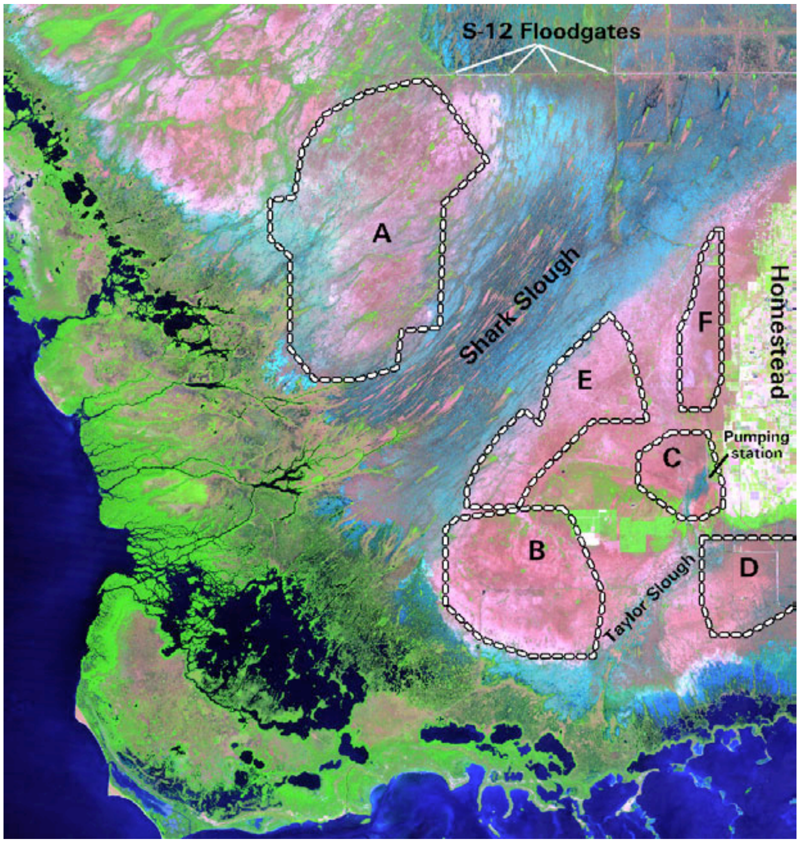

Figure 1: Location of sparrow populations (A–F) in Everglades National Park and Big Cypress National Preserve. Water enters the park from two sources, the S-12 floodgates and a pumping station north of Taylor Slough. From there, the water flows south-west. The pink, teardrop-shaped features in Shark Slough are tree islands; they align to the Slough's natural flow path, which enters at the northeast of this image. The S-12 floodgates are west of this natural entry point.

territorial space. Males establish territories beginning in late January and February. Males establish and defend territories by singing, but occasionally aggressively chase males and females that violate territory boundaries. The territory size is approximately 2 ha.

We gathered information concerning incubation, egg laying, and brooding from 329 nests found and monitored from 1996 to 2000. Female sparrows initiate clutches (i.e., lay the first egg of a clutch) an average of 2.7 days after nest completion. Females lay eggs every day until the clutch is complete, laying an average of 3.1 eggs per nest. (This average did not vary between years in our studies. There was also no difference in the number of eggs laid per nest across populations.) Incubation lasts for 12.1 days. On average, we found 0.4 unhatched eggs per nest. Out of the 31 nests that we followed from the initiation of the clutch to hatching, we never observed a reduction in clutch size through the removal of an egg. Hatch rates varied from a low of 90% (1999 nests) to a high of 100% (1997 nests).

The average nestling period for nests was 9.2 days. The sparrows average 2.7 nestlings per nest. Post-hoc comparisons between years revealed that the number of nestlings per nest decreased in 2000. Nests held an average of 2.2 nestlings in 2000, a value significantly lower than all other years. The number of nestlings per nest also varied according to population.

We estimated the nest cycle of sparrows to be 34 to 44 days in length. This varies according to the number of eggs laid and the length of postfledging care. Since nesting appears to begin in mid-March, a pair that successfully triple brooded (requiring at least 44 days multiplied by 3) would maintain breeding activity into early August.

The earliest we discovered a nest was on 20 March 1997. This nest had two eggs, but was lost to predation seven days later. Within our records, the latest sparrow nest was found on 10 July 1999. This nest eventually fledged young on 26 July. This information, independent from the above calculations, shows that some sparrows can nest from March until at least early August (122 to 142 days), though likely most are not afforded such opportunities.

Of the 240 nests to which we could assign a definitive fate, 117 successfully fledged young (48.8%). Of the failed nests, 61 failed during incubation and 62 failed during the brooding of nestlings. Predation accounted for the vast majority of all losses of young or eggs.

Predation rates (risk of predation per day) varied from 0 to 0.118 with an average value of 0.0342. In an effort to understand how predation rate is affected by hydrology, we compared the above daily rates to water levels at a nearby water monitoring station. The average water level at the P46 hydrological station varied from 5.5 cm above mean sea level (MSL) to 53.4 cm MSL with an average of 31.8 cm MSL. When we plotted predation rate within the population B study area against water levels at the P46 station, the data substantiated our assertion that predation pressure increases after the onset of summer rains, and indicated that this increase is due, in part, to the presence of water. However, not all high predation rates involved late-season nests. High water levels increase predation pressure no matter when they occur.

We banded 247 adult sparrows from 1994 to 1998 inclusive. A Cormack-Jolly-Seber model that assumes constant survivorship and recapture probability provided the best fit to our data. We estimated that 66% of all adult breeding males survive from one year to the next. *This is an upper bound.* Females likely survive less well because of the rigors of egg laying, and birds without territories (especially young of the year) will also fare less well.

0.3 Demography

Any demographic model has to address two questions. The first is: What fraction of the population is breeding? Large fractions of some sparrow populations cannot breed each year because of high water levels or other factors. The second question is: How successful are those birds that do breed? We explored various scenarios, and we will summarize the results here.

First, we assumed that all breeding individuals produce large clutches (3.8 eggs; the observed average plus one standard deviation) and that these clutches fledge equal to the maximum observed, discounted over the length of time eggs and nestlings are in the nest (0.60). Further, we assumed that late breeding attempts have the same clutch size and success rate as early attempts and that all breeding individuals that produce an early nest will also produce a late nest. Finally, we assume that adults have a high survival rate of 0.72 (the average plus one standard error) and that juveniles survive nearly as well as adults (0.50). With these parameters, we estimated a per-capita annual increase of 1.86. *These assumptions are clearly unreasonably optimistic.* It is unlikely that all individuals in every segment of the sparrow population would enjoy the conditions that would produce this annual rate of increase. Even under this scenario, *a sparrow population cannot double in one year.*

Next, we changed each variable in turn to its lowest recorded value and recalculated annual growth rate. When we changed adult survivorship to the average minus one standard error, per-capita annual increase was 1.74, 12% below the unreasonably optimistic scenario of 1.86.

Changing clutch size to its lowest recorded level resulted in a per-capita annual increase of 1.44. Reducing juvenile annual survivorship rates to a value more typical of small landbirds (0.30) resulted in a per-capita annual increase of 1.47. Changing the frequency of late-season nesting attempts to their lowest observed value (9% in population A) resulted in a per-capita annual increase of 1.34. Finally, changing nest success rates to their lowest observed value (13% in Population A) results in a negative growth rate of 0.97; a 3% decline in numbers per year.

We conclude that unless *all* breeding pairs in a population can breed *at least twice* in one year and *with a good measure of success*, then the population cannot increase quickly and (under a range of likely circumstances) cannot increase at all.

0.4 Habitat selection

Our results suggest that Cape Sable Seaside Sparrows are selecting habitats on a scale < 50 ha, and are basing these decisions on the inherently limited available habitat variation seen with Everglades marl prairies. They show distinct habitat preferences at two spatial scales. The first is that they occupy habitat that is dominated by muhly grass (*Muhlenbergia filipes*) and is relatively species rich, and do not occupy habitat that is dominated by sawgrass (*Cladium jamaicense*) and is species poor. Once this decision is made, individuals must defend a territory and select a nest site within it. Our results are inconclusive about the role of habitat variables in territory selection. However, we demonstrate that individuals will select nest sites that have high levels of muhly, litter, *Rhynchospora* spp. and *Schizachyrium rhizomatum* coverage; as well as high effective and maximum vegetation heights. This result is relative to habitat available within the territory.

Higher sparrow densities are associated with high coverage of muhly grass and litter, as well as high vegetation heights. Successful nests are more often associated with high muhly coverage and high vegetation heights.

0.5 Sparrow population numbers

We surveyed the sparrow in 1981, every year since 1992, and twice in 2000. Over this period there have been substantial changes in many of the six populations. In 1981, population A inhabited the marl prairies west of Shark River Slough, interlaced between drier, shrub-dominated areas, and wetter, sawgrass-dominated areas. It extended into Big Cypress National Preserve, and held an estimated 2688 individuals. Population B held 2352 individuals near the center of Everglades National Park. Population E, just north of B, held 672 sparrows, while C and D, located along the Park's eastern boundary, held about 400 individuals each. F was the smallest population at 112 individuals.

The subsequent changes are many and complex. For simplicity, we draw some key inferences and number them for convenience.

Population A, inference 1. This population suffered the most dramatic sparrow population change we observed. The population decreased by 84% from 1992 to 1993 — a decline from over 2600 birds to just over 400 birds. In 1995, we found that the population had decreased again, to just over half of the 1993 abundance. It has remained low ever since. The important *ecological* question is whether a decline of this size is remarkable given the normal year-to-year variation in population densities found in comparable species. In fact, it is not only remarkable, but unprecedented.

Population A, inference 2. Population A made some modest gains after the floods of 1993 to 1995, but the 2001 and 2002 counts (eight and six singing males respectively, for estimated populations of 128 and 96) is clearly cause for concern. Is this also an ecologically significant event? Other evidence suggests that it likely is. During the winter of 1999–2000, water levels were very high until just prior to the 2000 breeding season. We noticed a precipitous decline in the numbers of sparrows breeding on the intensive survey plot located in the northeast of this population. Numbers on the plot were also low in 2001. That the decline was not obvious in the 2000 count is likely a consequence of the birds being present and attempting to nest during the brief dry spell, but failing to produce sufficient young.

Population B, inference 3. Population B has remained more or less constant, the range in numbers being encompassed by the two survey estimates in 2000.

Populations C and F, inference 4. The two northeastern populations C and F held an estimated 544 birds in 1981; since 1992, the estimate has never reached 200. We conclude that the underlying mechanism is fire. (With one caveat: a small area in C, south of pumping station S-332 and downstream of Taylor Slough bridge, has changed from muhly-dominated prairie to sawgrass marsh as a consequence of higher water levels. Though a small area, it is very well studied.)

Population D, inference 5. Population D held 400 birds in 1981, numbers that it has not seen since. This area too has suffered high water levels that have precluded birds from nesting there successfully.

Population E, inference 6. This population has a particularly complex history. It may be best understood by splitting the population into two pieces: E (North) and E (South). Although the numbers are small, it appears that E (South) held roughly 300 birds in 1992, but after that there were only sporadic sightings until 2000 and 2001, when the area may have held > 100 birds. These numbers add to the evidence for flooding harming the birds.

Population E, inference 7. Population E (North) had relatively low numbers in 1992 through 1996, but since 1997 has held at least 600 birds. It is possible that this increase is a recovery from the 1989 Ingraham fire that burned this area.

These population changes have legal ramifications, because the Endangered Species Act prohibits actions that will harm endangered species, both directly and indirectly (through changes to their habitats). It remains to explain these changes and to identify the factors that caused them.

0.6 Causes of population changes

With so many events occurring in more or less the same time frame, we must be careful in assigning cause and effect. Some of the hypotheses that have been suggested include:

- *The sparrows did not disappear; we just haven't been looking for them in the right places.* This is the least credible hypothesis. It has never been accompanied by plausible suggestions of where the missing birds may be hiding.

- *Population fluctuations are a normal part of the ecology of all small birds, especially those with small, restricted populations.* The changes in bird numbers are not only statistically significant, but fall outside the range expected for normal populations.

- *Flooding is a natural part of the Everglades hydrology. We have always had wet years and dry years.* That may be correct, but the flooding that has caused the population declines is the result of deliberate management decisions. The flooding is far in excess of what would be expected from natural variability.
- *Flooding causes only temporary damage to the habitat on which the sparrows critically depend.* We reject this hypothesis, demonstrating that the habitat has been modified over the long term. We consider this in more detail later.
- *Colonists from the healthy eastern populations will quickly restore the western population.* This was not a credible hypothesis when it was first proposed. The birds are highly philopatric, the distances between populations are great, and the hypothesis does not address whether the eastern populations have a sufficient excess of individuals to export. Most telling of all is that the western population has not, in fact, recovered.
- *The eastern areas suffer from a much higher frequency of fires, mostly anthropogenic, accounting for repeated extirpations in population F and the upper part of population C.* We have confirmed this hypothesis.
- *Habitat in the lower part of population C has been permanently altered by the change in water regimes due to pumping of water into Everglades National Park, just north of Taylor Slough Bridge.* This is confirmed by detailed vegetation analyses. A similar hypothesis seems to be the best explanation for the changes in population D.
- *Three years of almost continual flood conditions caused significant damage to sparrow habitat that is only now, six years later, regaining its former extent.* We have confirmed this hypothesis and will expand on it in the next section.
- *Sparrow numbers are recovering slowly, as their breeding ecology suggests.* Only when the great majority of the nesting pairs in a population can all rear two or more broods can the population grow significantly from one year to the next. The observed failure of the western population, A, matches what we expect from this demographic analysis.

0.7 The long-term destruction of essential habitat

The Endangered Species Act prohibits direct take — the killing or harming — of federally listed endangered species. From its inception there has also been the implication that it prohibits take indirectly through the destruction of the ecosystems on which species depend. That provision was challenged in a legal case, *Sweet Home vs. Babbitt*, argued in front of the Supreme Court. In the particular context of the Spotted Owl, an Oregon group argued that only direct take violated the law, and not habitat destruction. Scientists argued that habitat destruction is most often the cause of species endangerment and extinction. The Supreme Court agreed with the scientists.

This report demonstrates direct take. The unnatural flooding of the sparrow's breeding habitat directly caused its precipitous decline in the western half of its range. The flooding resulted from the diversion of the area's drainage, Shark River Slough, to the west of its natural path, and a change in the timing of its seasonal ebb and flow. Concomitant with those changes, areas in the east became overdrained and more susceptible to anthropogenic fires. Bird numbers are significantly reduced in burned areas for two years after a burn.

The report also demonstrates indirect take. Unnatural, prolonged flooding has modified the Everglades landscape, converting the birds' preferred habitat (mixed prairie, often with a substantial percentage of muhly grass) into less suitable habitats dominated by sawgrass. Inevitably, this was first demonstrated using a combination of small-scale, detailed studies (our intensive plots, typically no more than a few tens of square meters) and larger scale, quick assessments of vegetation cover (made during the helicopter survey). The ideal seemed impossible: we needed spatially detailed yet spatially extensive and frequent observations of habitat. More recently, we achieved this by employing remote sensing. There are two key results.

First, across the eight years of the study, large year-to-year fluctuations in predicted habitat (based on satellite images) confirm the culpability of water managers. Flooding in 1993, 1994, and 1995 greatly reduced the habitat predicted to be suitable for the sparrow compared to 1992.

Second, the predicted suitable habitat west of Shark River Slough was at a low ebb in 1995 and has recovered slowly, but consistently, in the years from then until 2000, when the amount dropped again. By 1999, the predicted suitable habitat had not yet recovered to its pre-flood state. Even so, the habitat is recovering faster than the bird populations.

Water management practices have damaged huge areas of vegetation across Everglades National Park, have done so for extensive periods, and in a way that jeopardizes the survival of a federally listed species. This constitutes a "take." Moreover, its demonstration is independent of, and shows an effect lasting longer than, the direct effects of flooding.

0.8 Risk assessment

Dynamic models show that the population west of Shark River Slough will decline to extinction if the pattern of managed flows over the S-12 structures for the last 20 years repeats. If these unnatural breeding season flows over the S-12s are stopped, this population will flourish. The populations in the northeast have already declined to near extinction. These declines will continue unless the fire regimes are changed. On its own, the population in the southeast runs the risk of extinction because of episodic, large-scale fires. The fate of population E (now the second largest population) is interesting because it may illustrate a population that was burned to oblivion in 1989 and is still recovering.

Our models omit obvious features. They exclude the effects of prolonged inundation or frequent fires on the vegetation. These processes alter the vegetation in ways that preclude the birds' use of areas for several years (see above). Incorporating these impacts would likely lead to even greater concerns about the sparrow's future.

Our models are not "curve fitting" exercises to the census data. They are based on our knowledge of the sparrow's breeding biology, and of the area's water and fire regimes. But they do predict the timing and magnitude of the changes in the census data. This confirms that the models are both sensible and sufficiently complete to capture the essential features of the population dynamics of the sparrow.

The Cape Sable Seaside Sparrow will only survive if it has at least three healthy populations. To implement this requirement, the breeding areas west of Shark River Slough must not be flooded in the breeding season, and water levels should be raised in the northeast of Shark River Slough to reduce the incidence of fires.

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Because the sparrow's range is largely within Everglades National Park, we have worked very closely with their field biologists and resource managers. Significantly, park biologists conducted the majority of each year's rangewide extensive helicopter survey. These individuals include Lori Oberhoffer, Jason Osborne, Mario Alvarado, and the late Bill Robertson. The time we have all logged within helicopters warrants special mention of our experienced and trustworthy pilots. In particular we would like to mention Reed Robbins and "Dave," as they helped us through some of the more difficult years of setting up backcountry camps, including executing several long-line sling load drops and rescuing us from tornados and hordes of mosquitoes. The field crews have relied on the able hands of Everglades Fire Cache, the hydrology group, and Everglades dispatch for our physical safety while in the backcountry or conducting the extensive survey. These groups also provided technical expertise in setting up camps, and annual personal and air safety training. We owe a special debt of gratitude to Gary Carnell, Bob Panko, and Bob Zepp. Similarly, our logistical needs have been cheerfully met by the staff of the South Florida Natural Resource Center, in particular Ruth Franklin. Occasionally we have sought the advice of biologists within the Center, and they have always been forthcoming with their expertise and advice (not to mention occasional housing and barroom debriefings). Gor-

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Michelle Davis drew the picture of the sparrow that graces the cover.

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Chapter 1

History

1.1 Discovery

In 1918, Arthur Howell , a biologist with the United States Biological Survey, received a commission that would invite the envy of any modern day ecologist. He was charged with undertaking a systematic and complete survey of the bird life of Florida (Howell 1932). After considering travel arrangements, the time of year, and the threats of heat and violent storms that sweep the southern end of the state, Howell decided to begin his journey in midwinter in southern Florida and move northward. His first stop was Royal Palm, Dade County, a place that later became Royal Palm State Park and ultimately part of Everglades National Park. After thoroughly surveying this already famous ornithological mecca he proceeded to Cape Sable , at the extreme southwest corner of the Florida mainland.

It is a testament to Howell's skill that on his visit, which postdated those of countless amateur and professional ornithologists, including John James Audubon, he discovered the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*), the last new "species" recorded in the continental United States. The surprise at finding a new species in the already well-documented bird life of the U.S. prompted Howell to give it the specific name *mirabilis* (Howell 1919).

That countless birders missed this drab and unassuming little bird is not surprising. Audubon stopped only on the beach of Cape Sable while freshwater was loaded onto his ship (Buchanan 1915). Even had he ventured beyond the thick wall of trees, shrub, and cactus into the elongated, 1×9 km swale of coastal prairie, he may have, as many had doubtless done before, mistaken the Cape Sable Seaside Sparrow for the more numerous Savannah Sparrows (*Passerculus sandwichensis*) and Saltmarsh Sharp-tailed Sparrows (*Ammodramus caudacutis*) which winter in the area. Howell, however, was observant and either meticulous or fortunate. He must have caught a glimpse of the unique olive tint of the soon-to-be-named sparrow, which proved novel to his already broad experience with birds of the southeastern U.S. (Anon. 1940).

The adult Cape Sable Seaside Sparrow is a medium-sized sparrow (ca. 14 cm long) with a dull olive-gray back and head, olive-brown wings and tail, and light-gray breast and sides streaked with dark olive-gray. The legs and bill are gray. The chin is white; lores are yellow; and a white stripe over a dark whisker stripe extends from the jaw. Immatures exhibit an even more subdued appearance. The back is streaked with brown to light buff, the breast is light gray to light buff with reduced streaking relative to adults, and the whisker mark and yellow of the lores are absent (Howell 1919, Werner 1978). Based on its appearance and its isolation relative to the distribution of the other seaside sparrow species, Howell (1919:87) successfully argued for full species status of the Cape Sable Seaside Sparrow (which he named *Thryospiza mirabilis*), stating "This species differs so strikingly from all the other Seaside Sparrows that intergradation with any of the forms seems very improbable." The Cape Sable Seaside Sparrow was to enjoy this status until 1973, when it was reduced to subspecies status by the American Ornithologists' Union (Eisenmann 1973).

Howell (1919) does not state the extent of his traverse of the cape's coastal prairie on his first visit. If he did not cover it in its entirety he was lucky to see a bird that, as would become evident over the next five decades, is not always where it is supposed to be or where it has been in the past. He discovered the sparrow in the narrow linear swale of prairie typically found just inside the first vegetated berm of sandy shorelines. This prairie, dominated by *Spartina* spp., had dimensions of "about six miles in length and not more than half a mile in breadth" (Howell 1932:462). Howell was doubtful that the range of the species could be so restricted and suggested that "further search in this region may show that the species has a wider range than our present knowledge indicates" (Howell 1919:87). Indeed, less than 1 km inland lay a great expanse of prairie covering most of the cape, but we have no indication as to whether Howell ventured there.

As late as 1932 the known range of the Cape Sable Seaside Sparrow was restricted to the above-mentioned strip of prairie. Howell revisited the area in 1926 and, after much searching, found a colony of sparrows "several miles distant from the spot where they had been discovered" (Howell 1932:462). Again, Howell made no mention of any efforts to find the sparrow outside of the original location. More intriguing is a visit by famed ornithologist George Miksch Sutton who, on a bird collecting expedition in 1924, traveled on foot from Flamingo to the Gulf of Mexico (Holt and Sutton 1928). Sutton eventually found the sparrow, complaining that

> "More downright labor was required to find this rare and little-known species than any other encountered. Many hours were spent before even the right environment was located. Then, when it was decided that a certain area ought to harbor the birds, if they were to be found anywhere, it took great strength of conviction to keep plowing through the tall grass in the full sun."
> (Holt and Sutton 1928:435)

Sutton's description of the location indicates that it was the same prairie Howell visited (Holt and Sutton 1928). To get to that location, Sutton had to traverse the large inland prairie that made up most of the cape proper. By all accounts, this should have been prime Cape Sable Seaside Sparrow habitat, but Sutton mentions only the birds at Howell's site. We are left with no evidence for or against scenarios of ignorance, inattention, or accidents of biogeography.

1.2 Destruction

Holt and Sutton's (1928) was the last published report of the Cape Sable Seaside Sparrow on the cape before a devastating hurricane pummeled the area beyond recognition in 1935. The Labor Day Hurricane of 1935 has been called "the storm of the century" and "the most powerful storm to ever strike the U. S. coastline. . . on record" (Barnes and Frank 1998). The storm developed over the Bahamas and in four days struck the Florida Keys as a Category 5 hurricane. Winds were in excess of 380 km/hr and, before the barometer at the Key West weather station was lost in the rage of the storm, the barometric pressure of 26.35" (669.3 mm Hg) became the lowest ever recorded in the United States. A "wall of water" perhaps as high as 6 to 7 m washed over parts of the Keys; "the destruction of buildings, roads, viaducts, and bridges was practically complete" (McDonald 1935:269). Over 400 deaths were attributed to the storm: 244 known dead and 165 reported missing, assumed dead. Many of those who lost their lives were residents of three relief-work camps inhabited by veterans of World War I (McDonald 1935). Stimson (1956:490) relates his impressions of the hurricane's effects on Cape Sable:

> "[The hurricane] must have reached the vicinity of Cape Sable about midnight [2 September 1935]. The center of the storm passed Cape Sable at an undetermined distance at sea, but supposedly within a few miles. . . . Cape Sable was buried under a wave of eight feet or more.
>
> Members of the Roberts family then living at Flamingo had received radio warning and started to walk out just prior to the arrival of the hurricane wave. On December 6, 1935, the elder Mrs. Roberts told me that when they reached the road along the bank of the Flamingo canal the water in the canal was very low, but within a few minutes the water was up to their armpits; and the only thing that saved their lives was the recent elevation, of about two feet, of the road along the canal bank. Going westward from Flamingo that same day I found a line of bleached seaweed festooned for long distances in the trees about eight feet or more above the normal high water mark."

Stimson goes on to state that it is inconceivable that a population of small, ground-nesting birds could have survived the catastrophe. This was apparently the case. Expeditions to Cape Sable with the express intention of finding the Cape Sable Seaside Sparrow were launched in 1937, 1938, and 1949; none were found (Stimson 1956). There was, however, one published account of the sparrow observed at Cape Sable in April of 1936 (Semple

1936). Could it be that this celebrated population of sparrows survived the hurricane only to be driven to extinction within a year? Or was this simply a case of misidentification?

Semple is known to the field of ornithology by a few short descriptive notes on Florida birds that appeared in the *Auk*, and by the following editor's note that appears in Holt and Sutton (1928:409): "Mr. Sutton went to Florida as the guest of Mr. John B. Semple of Pittsburgh, who has done much to increase the ornithological collections of the Carnegie Museum." In a letter to Arthur Howell dated January 1930, Semple wrote that the Cape Sable Seaside Sparrows were still in "their old haunts" after an October storm "pushed five feet of saltwater over the entire region" (Howell 1932:463). The only recorded hurricane that may have affected southwest Florida in 1930 occurred in October, but its closest approach to the cape was ca. 300 km to the west; the claim of five feet of saltwater may be an exaggeration. In Semple's only other published account regarding the Cape Sable Seaside Sparrow, he claims to have observed the sparrow in April 1936, eight months after the Labor Day Hurricane, "pursuing, manifestly, its normal, unbroken cause of life." (Semple 1936:341). However, when Semple accompanied Arthur Howell and others on the above-mentioned expedition to find the sparrow in May 1937 none were found (Stimson 1956). It seems probable that Semple, visiting the cape at a time of year when wintering Savannah and Sharp-tailed sparrows and, possibly, eastern Seaside Sparrows (*Ammodramus maritimus maritimus*) would have been present, mistook these for the Cape Sable Seaside Sparrow. It is safe to say that the hurricane in 1935 did, in fact, obliterate the Cape Sable Seaside Sparrow from its known range on the cape for at least a few decades.

A knowledgeable visitor to the Cape Sable of today would be hard pressed to find accordance between the habitat he observes and that described by Holt and Sutton (1928). At the time Howell made his discovery, the cape was primarily a vast coastal prairie consisting mostly of sparse cordgrass (*Distichlis spicata* and *Sesuvium portulacastrum*), *Spartina* spp., and the requisite fringe of mangrove (Harshberger 1914, Holt and Sutton 1928). By the early 1940s, mangrove encroachment had diminished the extent of prairie to roughly half the area of the cape (Davis 1943). Currently, of the roughly 180 km^2 that the cape covers, less than 10 km^2 remain in any sort of prairie habitat (FGAP 1994); the remainder consists of mangroves and halophytic forbs interspersed with bare mudflats (Bass and Kushlan 1982). As for the swale of prairie where the Cape Sable Seaside Sparrow was discovered, it has changed from primarily *Spartina* to more salt-tolerant species, most notably *Batis* spp.

The initial cause of this drastic conversion of habitat was undoubtedly the Labor Day Hurricane of 1935. However, one would expect that with time the cape would revert to its previous state. Although very severe, the 1935 hurricane was surely only one of a series of storms that have raked the cape from time immemorial. The apparent permanence of the habitat conversion suggests that more insidious agents were at work. Two possible causes are sea level rise and the alteration of freshwater flows in the Everglades, already well underway in the early 1930s. The effects of neither of these phenomena have been investigated in relation to the vegetation dynamics of Cape Sable.

The mystery remains as to whether the Cape Sable Seaside Sparrow inhabited the interior prairie of the cape. A consideration of biogeography would lead one to suppose that the sparrows that inhabited the thin strip of coastal prairie where Howell discovered them formed a satellite population of sorts to a larger population in the interior cape. In support of this supposition, sparrows were eventually found in this area. In 1971 Werner located a small population near the Fox Lakes in a remnant *Spartina* marsh (Werner 1975). As for earlier records, we have only Sutton's expedition (Holt and Sutton 1928) which does not mention the sparrow outside of the swale cited by Howell (1919). Stimson (1966:154) states that after the discovery of the sparrow, "Further investigation on the Cape Sable prairies showed that the bird occupied a range from a few miles west of Flamingo to well up behind Northwest Cape." As this is the only published mention of the sparrow in the area and no supporting references are given, we are left to wonder if common knowledge superseded scientific publication.

1.3 Extinction

After it became certain that the Cape Sable Seaside Sparrow had disappeared from the cape, many believed that this newest species to the United States was lost to oblivion (Stimson 1956). Before the sparrow was accorded this fate, however, there remained one dim hope. On 3 May 1928, Donald J. Nicholson , an avid and prolific ornithologist whose publications span four decades, stood on a large prairie in Collier County, "lying between pine forests and an extensive cypress swamp" (Nicholson 1934:389). A prolonged drought had made the prairie "as dry as powder." Nicholson spotted a single bird that he believed to be a Cape Sable Seaside Sparrow, a species he knew only by published accounts (Nicholson 1934). Four years later, on 21 April 1932, he returned to the same spot and found 15 to 20 pairs over a ca. 8-km^2 area. He reported the site as being "6 miles northeast of Pinecrest" (Nicholson 1934:389). If a sparrow population persisted here, far inland from the cape, the species may have survived the hurricane after all.

Pinecrest was, and is, something less than a hamlet in southern Collier County. It lies on the Loop Road, a secondary road originally constructed to be part of the great Tamiami Trail that links the two coasts of southern Florida. When the Trail was built, however, it passed north of Pinecrest, leaving the Loop Road nothing more than a handy access point to the wilderness of the Everglades and the Big Cypress.

Nicholson's report was given little attention; however, it did receive a short mention in Howell's (1932) definitive book. A glance at a map explains the lack of confidence in what should have been surprising news. Six miles northeast of Pinecrest lay the Tamiami Trail, completed in 1926. That the author would report the location relative to Pinecrest instead of the much closer town of Fifty-mile Bend must have cast some suspicion. More importantly, the area was in the middle of an extensive cypress forest — not Seaside Sparrow habitat by any means. Later correspondence between Stimson and Nicholson established the actual location to be southwest of Pinecrest in a savannah near the Lostman's Pine area, the error in direction apparently being caused by the windings of the Loop Road, which was used as a reference point (Stimson 1956). Nicholson persevered and, after accompanying Arthur Howell and others on a trip to the cape in March 1937 in a fruitless search for Cape Sable Seaside Sparrows, he guided the party to the location where he had found sparrows in 1928 and 1932 (Nicholson 1938). After a half-day of searching, no sparrows were found. The time for the eulogy of the Cape Sable Seaside Sparrow had arrived, and it was delivered by Nicholson (1938:44) in the ethnocentric language of the day:

> "And while I would like to think some [Cape Sable Seaside Sparrows] may still exist in some isolated place rarely frequented by white men, I can entertain no great hope that this is the case. It may be that another of our most interesting birds has gone forever, known only to modern science for the short span of twenty years."

1.4 Interlude

The Cape Sable Seaside Sparrow was rediscovered four years after its eulogy was published. Let's make use of this hiatus in the annals to review the perceptions of the major players concerning the distribution of the sparrow. Howell suspected that the sparrow's range must extend beyond the ca. 1 × 9 km swale where he discovered the species. Sutton agreed: "Though the birds were very rare, or at least were very rarely flushed, it is hardly conceivable that the species is restricted to so extremely small a range" (Holt and Sutton 1928:435). But the common belief that the sparrow had a ridiculously small range seems to have held sway. Why else would Stimson (1956:492), after reviewing the corrected reports of Nicholson's find in Collier County, feel compelled to write "...we now know that the sparrows were in the presently known range long before the [1935] hurricane. They were not blown up there by the storm."

The dynamic nature of the sparrow's habitat was also hinted at in early reports. Howell (1932:464) wrote:

> "Conditions in their habitat vary from year to year...occasionally flooded by heavy rains and tidal waves at other times becoming practically dry and having the vegetation destroyed by frequent fires. For this reason the birds are forced to move from time to time and find suitable breeding places, and quite possibly their numbers are kept down by these agencies."

How Howell surmised all of this from the small range he was aware of is peculiar, but, more importantly, he was proven right by future investigations. Sutton again echoed Howell's view, albeit in a more alarming fashion, by mentioning the danger of fire to the only known colony of sparrows: "It is quite possible that the whole area might be devastated by a single blaze" (Holt and Sutton 1928:436).

So, even before the 1935 hurricane obliterated the Cape Sable Seaside Sparrow population on the cape, there existed the intuition, if not the knowledge, that the search for the sparrow would prove to be a sort of ecological shell game. The sparrow's low population densities and its dynamic habitat, not to mention its secretive and unassuming habits, repeatedly confounded efforts to delineate range and status. In hindsight this is not surprising, for the searchers were not going to the best possible place. Howell, Nicholson, and the other early surveyors of the Cape Sable Seaside Sparrow were unknowingly nibbling at the edges of the species' range. The range dynamics of grassland birds vary across space and time (Curnutt *et al.* 1995). Typically, species of grassland birds have a high abundance, low variability, core population. Proceeding from the core toward the edges of the range, abundance decreases and variability increases. The edges of ranges are constituted of ephemeral, widely dispersed pockets of individuals. This continental-scale model of population dynamics applies as well to the regional scale in which the Cape Sable Seaside Sparrow exists (Curnutt *et al.* 1998). A clear understanding of the sparrow and its temporal and spatial dynamics would only come with the discovery of a core population, and this would have to wait until the 1970s.

1.5 Resurrection

Given what appeared to be universal acceptance that the Cape Sable Seaside Sparrow was extinct, its rediscovery was unsought and unexpected. On 28 June 1942, a young William Anderson was making observations on Swallow-tailed Kites (*Elanoides forficatus*) "in a little savannah next to the Big Cypress" (Collier County) when he heard, then saw, two or three Cape Sable Seaside Sparrows (Anderson 1942) . Soon after this surprising discovery, Anderson enlisted with the U.S. Army to fight in World War II. He took the time while in boot camp to write to Stimson and ask that he confirm the sighting (Stimson 1944). On 22 May 1943, Stimson, A. J. Dietrich, and Bob Woodmansee followed Anderson's directions to the spot. For a bird that had always been reported as scarce, low in numbers, and difficult to observe, what Stimson found must have astounded him. "Within a hundred yard circle there were at least ten male birds. More distant songs indicated the presence of still more" (Stimson 1944:31). This new location was "many miles from Pinecrest, and many more from Cape Sable." The sparrow lived and, moreover, in larger numbers and in a more accessible location than the cape afforded.

Five years later this was still the only known site with Cape Sable Seaside Sparrows. Even though reaching the area required an arduous 2-hr walk, the exact location was a sworn secret among the four men who knew it. "To publish or divulge the location of this one known spot might well lead to the extermination of the species," Stimson wrote (1948:69). He continued, "May this rare and miraculous species continue to live safe from any collector's gun." Nevertheless, Stimson suspected more than ever that the sparrow could be found in other locations. The publication of Davis' (1943) *The Natural Features of*

Southern Florida provided the first relatively accurate vegetation map of the little-explored Everglades. On it Stimson saw that saltmarsh prairies were scattered from near Naples all the way south to the Shark River Basin and that these sites seemed no different from the ones that he knew held sparrows (Stimson 1948). The problem was getting there. After relating an episode involving a cottonmouth (*Agkistrodon piscivorus*), Stimson wrote: "Most of the possible area where the Cape Sable sparrow might thus nest would be very difficult to access and perhaps also slightly dangerous" (1948:69).

Stimson was a tenacious and thorough ornithologist, known to disappear into the wilds of the Everglades on foot or in a canoe for days at a time, without telling anyone where he was going or when he might return (W. B. Robertson, Jr.; pers. comm.). In the spring of 1953 Stimson's efforts paid off (Stimson 1956). He found sparrows at two separate locations, one about 2 km southwest of Ochopee and the other near the Turner River. Both sites were saltmarsh prairie, dominated by *Spartina* spp. On 25 April 1954, Stimson accompanied Everglades National Park rangers on a trek via swamp buggy to check on a water gauge inside the park boundary. As they entered the extensive sawgrass (*Cladium jamaicensis*) prairie, Stimson saw a Cape Sable Seaside Sparrow flush. This sighting was followed by two or three singing sparrows heard at the water gauge, another site dominated by sawgrass. Sawgrass, unlike *Spartina*, is found in long-hydroperiod freshwater marshes. Stimson had, if not an epiphany, at least a realization that the sparrow could be found in the vast freshwater prairies of the Everglades. If this proved to be the case, the potential range of the sparrow would cover an area much larger than the scattered saltmarshes near the coast presented.

Over the next year, and through the exertion of many 30 to 50 km treks, Stimson (1956:501) determined the range of the Cape Sable Seaside Sparrow to be "the salt marshes lying to landward of the mangrove fringe along the southwest coast of Florida from northwest of Everglades City to near the headwaters of the Huston River; and in salt marsh and fresh water marsh prairie from the mouth of Gum Slough to the Shark River Basin." The distribution of the sparrow was beginning to belie its appellation of "seaside," being found by Stimson (1961) as far as 40 km inland from the Gulf of Mexico.

For 15 years, from 1956 to 1971, the known range of the Cape Sable Seaside Sparrow was vast and, for the most part, inaccessible. There are no other published reports of sparrow observations as far into the Everglades as Stimson ventured. Near Ochopee, which lies on the Tamiami Trail, one could easily access a few sites that regularly held sparrows, but encroaching human activity was beginning to adversely affect the birds (Stimson 1961). Altered hydrology, road construction, and saltwater intrusion had severely altered Cape Sable Seaside Sparrow habitat by the mid-1970s (Werner 1975), but this process probably began in 1926 with the construction of the Tamiami Trail and its accompanying canal. The completion of the Turner River Canal in the mid-1950s must have exacerbated the problem. With less surface water came more frequent and intense fires. Stimson (1961) reported on the status of three areas in Collier County that held sparrows; all three had recently burned. A site near Ochopee was intentionally burned by "snake hunters" in late May 1961. Stimson could find no sparrows there two weeks later. The more divine agent of lightning caused a fire at a site near Lostman's Pines in April or May 1957; again Stimson could find no birds there even four years after the blaze. The third area was the "secret" location discovered by Anderson (1942). This area burned in the early part of 1959 and Stimson found sparrows there in June of that year. On returning in 1961, however, Stimson found no sparrows.

The complex relationship between sparrows and fire will be addressed later in this volume. It is sufficient here to say that Stimson and others who followed the drama of the Cape Sable Seaside Sparrow were alarmed that colonies of sparrows were disappearing more rapidly than new ones were being discovered. The fact that the interior prairies of the Everglades held sparrows must have been of little consolation, since the population there had never been enumerated.

The Cape Sable Seaside Sparrow was in the first group of species listed as endangered by the U.S. Fish and Wildlife Service, on 11 March 1967, pursuant to the Endangered Species Preservation Act of 1966 (32 FR 4001, Title 16, Chapter 5a, Section 2). The sparrow retained that unenviable distinction under the Endangered Species Conservation Act of 1969 (Title 16, Chapter 5a, Section 668) and the Endangered Species Act of 1973 (Title 16, Chapter 35, Section 1531), as amended. The Cape Sable Seaside Sparrow was listed because of its limited distribution and threats to its habitat posed by large-scale conversion of land in southern Florida to agriculture. This latter reason may seem odd until one remembers that previous to the establishment of Big Cypress National Preserve in 1974, a large portion of the known population of sparrows was found on private land.

In 1970, Harold Werner, a graduate student of Glen Woolfenden, undertook the task of determining the status of the sparrow. Werner revisited all of the locations in which the sparrow had been found in the past (Werner 1975). What he found was at once surprising and disheartening. Werner found sparrows at six sites in and around the Ochopee area, but over his five years of observation (1970–1975) he noticed a marked decline in the number of sparrows and the quality of their habitat. Werner also found a few birds in the southern Big Cypress area, near the location where Nicholson (1928) made the first off-cape observations of the species. The sparrow was reported as very rare in this area in the early 1970s (Werner and Woolfenden 1983). The most surprising find made by Werner was of four singing male sparrows and five juveniles in the remnant cordgrass marshes of the interior of Cape Sable in 1970; in 1975, Werner found only one sparrow there (Werner 1975). In effect, the known boundaries of the Cape Sable Seaside Sparrow's range had changed little from the 1950s to 1970. The numbers of birds at those boundaries, however, were frighteningly low. The cape population could hardly be thought of as self-sustaining, the Ochopee populations were visibly declining, and the southern Big Cypress populations had never been very numerous.

1.6 Revelation

The first inkling of the true distribution of the Cape Sable Seaside Sparrow came in 1972 and, in keeping with the sparrow's enigmatic history, it arrived unexpectedly. In that year a wildlife technician at Everglades National Park took advantage of the doubly rare circumstance of a Short-tailed Hawk (*Buteo brachyurus*) nesting in an accessible place, just off the Main Park Road west of Taylor Slough. To investigate the food habits of the hawk, the technician climbed to the nest and retrieved a mangled ball of feathers. The remains were not identifiable in the field, and the story would have ended there but for the work of Roxie Laybourne of the Smithsonian Museum of Natural History. Laybourne was a pioneer in the science of species identification by feather structure. From a sample she was sent, she determined that the Short-tailed Hawk's meal was a Cape Sable Seaside Sparrow (Ogden 1972).

The discovery of a Cape Sable Seaside Sparrow, even a dead one, east of Shark River Slough opened up a new venue for discovery. Werner (1975) surveyed the prairies of Taylor Slough and found sparrows there. He continued searching and found sparrows as far north as the east Everglades and south on both sides of Taylor Slough to near the northern limit of mangroves. The mother lode had been discovered. Over a ca. 10,000-ha area, Werner (1978) estimated the Cape Sable Seaside Sparrow population to be between 1900 and 2800 birds.

That the sparrow inhabited the eastern prairies of the Everglades and went undetected for so long gives one pause. The northern reaches of Taylor Slough had been surveyed in the early 1950s by William Robertson, Jr., an outstanding ornithologist, and no sparrows were found. In 1957 a tourist reported seeing a Cape Sable Seaside Sparrow in the area, but park staff did not investigate (Bass and Kushlan 1982). It may be that this area was home to an ephemeral edge population similar to the one that produced the discovery of the species. More puzzling is the population between the Taylor and Shark River Sloughs south of Long Pine Key. This area, which currently holds the lion's share of sparrows, has been accessible to birders since the creation of the road to Flamingo. Indeed, countless birders, including Howell, traversed the Old Ingraham Highway, which bisects the present heart of the sparrow population, on their pilgrimages to Flamingo. It seems incredible that these avid ornithologists never stopped to look over the vast prairies in an attempt to find, if not Cape Sable Seaside Sparrows, at least some bird of interest. There remains the possibility that the sparrows simply were not there and that their current distribution is the result of ecological changes over the last 50 years. The reduction of freshwater flow into the southern Everglades began with the Central and Southern Florida Project, which commenced in 1948 (House Document No. 643, 80th Congress, Second Session) . The Flood Control Acts of 1958 and 1965 allowed the destruction of the head of Taylor Slough and the subsequent drying of the eastern Everglades. It is possible that the sparrow recently increased in abundance in the prairies east of Shark River Slough as the available habitat was augmented by water management actions.

1.7 Investigation

The discovery in 1972 of Cape Sable Seaside Sparrows east of Shark River Slough was fortunate in that it allowed scientists easy access to the sparrows via the Main Park Road. Before that date anyone interested in studying the sparrow had to face the problem of accessing the wilderness south and east of the Loop Road. In the 1970s, science did not come to the Cape Sable Seaside Sparrow; the sparrow came to science.

Werner (1975) established an intensive study plot straddling the western edge of Taylor Slough. The area was dominated by *Muhlenbergia filipes* and was home to the greatest known density of sparrows. Here he set out to find out as much he could about the ecology of the sparrow. Most of what Werner observed about the autecology of the sparrow we will discuss in later chapters of this volume. We will address here only his work on the relationship of fire and the sparrow, because this topic was of interest to the Park Service and it spawned one other short-term study of interest.

Werner collected reams of data not only on the sparrow, but also on the vegetation, hydrology, and fire history of his plot in Taylor Slough (Werner 1976). He found that a site burned shortly before the breeding season held no sparrows that year, but sparrow density increased each subsequent year until maximum density was reached the third year. Sparrow densities at sites that had burned four years previous were low, and Werner found no sparrows at sites that had burned five or more years earlier. Werner (1976) correlated this orderly sequence of sparrow behavior with the more predetermined dynamics of prairie vegetation. A burned prairie has an aboveground biomass of essentially zero immediately following the fire. At Werner's sites this biomass increased steadily until three years postfire. After that point the total biomass fluctuated but the percent live biomass decreased (Werner 1976). From these observations, Werner and Woolfenden (1983:63) concluded that: "...in *Muhlenbergia* prairie, decreased sparrow density and increased territory size may be related to decreasing ratios of live biomass and increasing amounts of old dead biomass after 3 years."

Of course, nature rarely abides by such unambiguous rules, and sparrows do inhabit sites that have burned five and more years previously (Taylor 1983, Curnutt *et al.* 1998). Beginning in 1978, Dale Taylor conducted a study designed to determine the impact of fire on the Cape Sable Seaside Sparrow (Taylor 1983). Taylor worked west of Werner's study plot in an area that encompassed a wider variety of habitat types. Specifically, Taylor included both shallow and deep soil sites, whereas Werner's site included only the latter. Taylor (1983) found that sparrow population response depended on soil depth and rate of vegetation recovery. On deeper soils ($>$ 40 cm) vegetation recovered rapidly, sparrows reinvaded within two years of a fire and increased in density until four years postfire; after that sparrows inhabited marginal sites at relatively low numbers. This concurs with Werner's (1976) findings. On shallow soil sites ($<$ 20 cm), however, reinvasion by sparrows was delayed for up to four years. After colonization, sparrow numbers remained lower than the peak numbers found on deep soil sites, but the sites remained occupied longer (up to 10 years).

Werner's and Taylor's work proved invaluable to the National Park Service personnel who developed a management plan for the Cape Sable Seaside Sparrow. It should be remembered, however, that Werner and Taylor were investigating the ecology of a bird for which neither range nor population estimates had been determined. As unsettling as this uncertainty was, by the late 1970s tragic events were occurring 300 km north of the Cape Sable Seaside Sparrow's range involving a close relative, the Dusky Seaside Sparrow (*Ammodramus maritimus nigrescens*).

The Dusky Seaside Sparrow shared many attributes with the Cape Sable Seaside Sparrow. Like the Cape Sable, the Dusky had a range isolated from other seaside sparrows by geographic barriers, it lived in brackish to freshwater marshes, and its habitat was heavily influenced by natural disturbance (Baker 1978). Unlike the Cape Sable, the Dusky had the misfortune of living in the path of a relentless drive for "progress." The decline and ultimate extinction of the Dusky Seaside Sparrow happened with alarming rapidity. Beginning in the 1940s, its habitat was heavily dosed with DDT in an effort to control mosquitoes. This led to an estimated decrease of 70% in the sparrow population by 1957 (Trost 1968). As the mosquitoes developed resistance to chemical control, the Florida Board of Health launched an ambitious project of ditching and impounding coastal marshes. By the late 1960s all coastal marshes within the Dusky Seaside Sparrow's range were thus altered (Sykes 1980). Within the remnants of the Dusky's range the decade of the 1970s was witness to the following assaults: (1) the construction of a major expressway to link Walt Disney World in Orlando to the Kennedy Space Center; (2) the digging of a large drainage canal to allow residential construction in a wetland; and, (3) repeated uncontrolled fires set by ranchers for land management (Kale 1996). The drop in sparrow numbers was precipitous: in 1972 a survey of the total population detected 110 males; in 1973, 54 males; in 1978, 23 males (Baker 1978). When only four Dusky Seaside Sparrows could be found they were taken into captivity for breeding (Delany *et al.* 1981). Since all of the birds were male, back-crossing was used in an attempt to develop a population of "mostly" Dusky Seaside Sparrows (Kale 1996). The last Dusky died in captivity on 16 June 1987; ironically, it was housed at Disney World.

News of the Dusky Seaside Sparrow's imminent demise and the legal responsibility of the National Park Service to protect and increase populations of endangered species on their lands intensified the call for better estimates of the status of the Cape Sable Seaside Sparrow. The situation was all the more urgent given the dynamic nature of sparrow habitat and the sparrow's enigmatic history (H. Kale, II, pers. comm.).

Oron "Sonny" Bass, Jr., and James Kushlan, biologists at Everglades National Park, undertook the daunting task of characterizing the distribution and habitat use of the Cape Sable Seaside Sparrow by conducting extensive surveys from 1978 to 1980. Their efforts culminated with a census of all available sparrow habitat in 1981 (Bass and Kushlan 1982).

The principal difficulty in surveying Cape Sable Seaside Sparrows lies in reaching areas nestled deep inside the nearly 1,000-km^2 wilderness of Everglades National Park and Big Cypress National Preserve. For their 1978 through 1980 surveys, Bass and Kushlan covered easily accessible areas on foot and used a Bell C-47 helicopter outfitted with pontoons to reach the more remote areas (Bass and Kushlan 1982). In reference to the sparrow's coastal marsh habitat, Stimson (1956:494) commented: "In years of normal rainfall this whole. . . area is accessible only by airboat, or perhaps helicopter. Neither is hardly [sic] the type of conveyance from which to seek a small bird." Bass and Kushlan had, in fact, developed a novel method of using a helicopter to conduct sparrow surveys. The method entailed landing at a predetermined census site and turning off the helicopter engine. Surveyors then watched and listened for sparrows for 7 min while making observations on the vegetation and surface-water conditions before reboarding the helicopter and advancing to the next site (Bass and Kushlan 1982). To the uninitiated this may seem somewhat bizarre. Wouldn't the sparrows simply fly away on the approach of the roaring machine? The authors can attest to the fact that the birds do not scatter (although one hopes that they have enough sense to get out from under the pontoons before it's too late). If singing sparrows are present, they are usually heard within a few minutes of the engine being cut (and we have seen some singing as the helicopter lands).

Bass and Kushlan's (1982) preliminary censuses showed the continuing constriction of the sparrow's range as outlined by Werner (1976). In 1978, sparrows were observed at two sites on Cape Sable, but none were found there in 1979 or 1980. Sparrows have not been seen on Cape Sable since 1978, marking the end of the sparrow's occupancy of its place of discovery and namesake. In 1978 and 1979, sparrows were found at one and two sites, respectively, near Ochopee, but none were found there in 1980. In 1980, Bass and Kushlan intensified their search of the prairies on either side of Shark River Slough, including north of Taylor Slough and south of Long Pine Key. They found substantially more sparrows than expected. These preliminary censuses set the stage for the extensive survey of 1981.

In 1981, Bass and Kushlan's goal was to systematically census all potential sparrow habitat (Bass and Kushlan 1982). Census points were determined by gridding U.S. Geological Survey 7.5-minute orthophoto quadrangles into 1-km^2 blocks. The intersections of the grid lines that fell in prairie habitats that were not monotypic stands of sawgrass were designated as census sites. Using the above-described helicopter method, Bass and Kushlan surveyed 864 sites from 31 March through 16 June 1981. The results were staggering. Cape Sable Seaside Sparrows were found in virtually all prairies of considerable size that were not dotted by trees or exposed to long hydroperiods. These "dry prairies" are typically dominated by *Muhlenbergia* grass or have this species as a major component (Bass and Kushlan 1982).

West of Shark River Slough, a small cluster of six sites just south of Gum Slough held sparrows, but the greatest part of the sparrow population was found in a more or less continuous prairie that stretched over 20 km south of the Tamiami Trail and bordered the slough itself. Here over 150 sparrows were seen at 117 sites. East of Shark River Slough the pattern was more complex. Of 396 sites surveyed, 155 held a total of 248 birds. About a third of the sites with sparrows formed a contiguous block south of Long Pine Key that stretched nearly the entire distance between Shark River Slough and Taylor Slough. The remaining sites were north and east of Long Pine Key, with an isolated group east of Taylor Slough near the Aerojet canal, and a small cluster of sites isolated to the north in the East Everglades.

The estimation of population numbers from census data is a difficult task (Ralph and Scott 1981). Nonetheless, Bass and Kushlan were compelled to make such an estimate. They estimated the detection distance of a singing sparrow at 200 m and consequently assumed a census coverage of 12.6 ha at each site visited. The number of singing birds at each site was used to calculate a density for the 1 km^2 surrounding the census point. Bass and Kushlan obtained a population estimate by multiplying the average density of birds per 1 km^2 by the number of occupied sites, then doubling that number to include uncounted (non-singing) females. This rough estimate of the number of Cape Sable Seaside Sparrows served two important functions. First, it gave a ballpark figure of the population size. Second, it established a baseline for detecting population changes by comparison with results of future surveys.

Bass and Kushlan (1982) estimated the minimum population of the Cape Sable Seaside Sparrow to be ca. 6,600 birds: 3,700 east of Shark River Slough and the remainder west. The final discovery of the size and spatial distribution of the sparrow population was as surprising as it was welcome. Those who may have harbored a crisis mentality toward the status of the sparrow could now be assuaged. The optimism produced by the 1981 results was tempered, however, by the realization that peripheral populations of sparrows had disappeared (Bass and Kushlan 1982). Furthermore, the sparrow, though currently numerous, was subject to the vagaries of fire and the exploits of the water managers who controlled the timing and amount of freshwater flow into the sparrow's range.

1.8 Complacency?

For a species that was thought to number in the hundreds throughout its history, the realization that the Cape Sable Seaside Sparrow actually had a population of greater than 6,000 was a source of relief and, perhaps, complacency. After the 1981 census Kushlan *et al.* (1982) produced a management plan, the objectives of which were "to determine and maintain the present distribution of the Cape Sable sparrow, and to prevent it from becoming in danger of extinction" (p. 19). The plan called for increased censusing, intensive research on habitat use and reproduction, studies on the relationship of fire, water management, and sparrows, and management activities to maintain the peripheral population of Ochopee. The management plan was well developed and scientifically sound, but none of the actions were carried out until a decade after they were proposed. The proposed research would cost a considerable sum of money — especially if it entailed repeating the extensive census — and the funds, although requested annually, were not made available. Crises get funding, and 6,000 sparrows was not a crisis.

This prompts the question: how many sparrows are enough? Is a population of 6,000 small-bodied, short-lived birds that breed in a dynamic habitat driven by fire and water, and subject to the occasional hurricane, big enough to ensure against extinction? And for how long? A detailed investigation into the viability of the sparrow population falls outside the scope of this chapter. Instead, we will consider the original extent of sparrow habitat: where the Cape Sable Seaside Sparrows could have lived before agricultural and residential development fragmented the ecosystems of southern Florida. A glance at the results of the 1981 extensive sparrow census reveals the coincidence of sparrow distribution limits with manmade features. The population west of Shark River Slough abruptly ends with the Tamiami Trail; except for the small population found in East Everglades, the sparrow's distribution east of the slough follows suspiciously the boundary of Everglades National Park. Davis' (1943) vegetation map shows the original extent of marl prairie in southern Florida. East and west of Shark River Slough the prairies extended north of their current distribution. On the west side the prairie extended 45 km due north of Tamiami Trail , squeezed between the Big Cypress and the slough itself and covering an area of about 130 km^2. East of the slough the prairie spread northeast, bounded by the Miami Rock Ridge and Shark River Slough. Roughly 250 km^2 of former prairie in this area is now covered by farms, residential areas, and strip malls. In all, about 30% of the original marl prairie has been lost.

The dynamic nature of sparrow habitat would have precluded the constant occupation of all of the marl prairies in southern Florida. With 30% more potential habitat, a rough extrapolation suggests that the sparrow population probably fluctuated around a lower limit of 10,000 birds over the centuries preceding the alterations of the 1900s. Apparently, a population of 10,000 sparrows is enough to ensure against extinction, at least on the temporal scale of centuries. Is a population of 6,000 enough? We may have no choice but to make sure it is. The prairies that have been lost are not likely to be recovered, and those that remain are subject to modification, not by agriculture and commercial development, but by water and fire management (or lack thereof). In the 1980s there may have been a complacent attitude about the size of the Cape Sable Seaside Sparrow population, but the population crash of the early 1990s illustrated the need for a better understanding of the sparrow's habitat, its habits, and the limits of our management options.

Chapter 2

Life History

2.1 Introduction

To provide the basis for understanding changes in sparrow numbers, which we document in later chapters, we now need to explain its life history. Information such as the length of the breeding season, the average clutch size, the vegetative composition of nests, site fidelity patterns, and breeding behavior underpin all explanations regarding population declines.

Prior to this study, life-history information came from incidental observations by early ornithologists (see Chapter 1) and from a detailed 4-year study of the Taylor Slough population by H. Werner (1975). Werner was the first to document clutch size, nest construction, nestling growth, and many other characteristics. His observations were limited, however, and he was unable to confirm many of his intuitions.

Our results build from this foundation. We have added considerably more nesting and behavior observations (e.g., Werner followed 16 nests whereas we followed 329), and we can document changes in life-history parameters across the spatial extent of the sparrow's range. The following section is organized chronologically, beginning with early breeding season observations on pair bonding, territory establishment, and nest building. After drawing heavily from Dean and Morrison's (2001) study of the nonbreeding ecology of the sparrow, we will come full circle through one year in the life of a sparrow. The appendix to this chapter briefly describes our permanent study plots.

2.2 Territories and their defense

Sparrows maintain territories within which all nesting and feeding activities occur. Territories are mutually exclusive such that no two males share a substantial proportion of their territorial space. Males establish territories beginning in late January and February. They establish and defend territories by singing, but occasionally chase males and females that violate territory boundaries. A male can increase the audibility of his song and his visibility by perching on stalks of grass that rise well above the average height of the surrounding grasses and sedges. These territorial perches are almost exclusively provided by sawgrass (*Cladium jamaicensis*) seedheads.

During timed observations of known breeding pairs in 1998–1999, we recorded the duration of male territorial behaviors; that is, vocalizing and perching in visible locations. When we compared the duration of vocalizing among stages of the nest cycle (i.e., when eggs, nestlings, or fledglings were present or when the female was laying eggs) we detected no differences (ANOVA $F = 0.56$, $p = 0.64$, D.F. = 3). We did not detect differences in the visibility of the male among nesting stages, either (ANOVA $F = 0.68$, $p = 0.57$, D.F. = 3). These results held when we referenced these territorial activities by the number of days before or after the male's nest fledged or failed (vocalizations: $r^2 = 0.015$, $p = 0.40$; visibility: $r^2 = 0.09$, $p < 0.01$). Thus, males continue to defend vigilantly the boundaries of their territories despite the added energetic burdens that tending nestlings or fledglings may impose.

Females likely choose males based on the quality of their territory. This choice is critical as sparrows have a monogamous breeding system. Thus, the female is confined to feeding herself and any young from the resources contained within that male's territorial boundaries. The size of that territory likely determines his ability to attract a mate and successfully raise young.

Territories are typically tightly packed within our study plots. From 10 to 25 males will hold territories within one 0.5-km^2 plot. Beginning in 1993 and continuing to 1996, we marked the territories of singing males by observing a singing bird and marking its perch with colored flagging tape. By advancing on the bird and marking each subsequent perch, we could establish the perimeter of its territory. In most cases, the accuracy of the territory estimates were borne out by subsequent observations of territorial disputes between neighboring birds. Occasionally adjustments were made to territories based on observed movements of resident birds. We spent the final days of the 1994, 1995, and 1996 field seasons recording marked territories with a global positioning system (GPS).

In 1993, we marked 18 territories in three sites, and in 1994 we marked 25 territories in four sites. We present a rough approximation of the extent of territories and the variation that exists in territory size among and within study sites in Table 2.1. The largest territory we marked was a sprawling 38 ha at the OIHS site (see the Appendix to this chapter for site names and descriptions). The smallest territories were less than 1 ha.

By observing marked birds, Werner (1975) detected 15 territories of singing male sparrows in his Taylor Slough study site. Werner reported average territory sizes in Taylor Slough of about 2 ha, while our average territory size is 2.36 ha. The similarity of these territory estimates is reassuring and represents the average territory size we will use throughout the remainder of this document.

Table 2.1: Mean (std. dev.) of the area of Cape Sable Seaside Sparrow territories marked on study sites during 1993 and 1994, for those sites and years in which sparrows were present.

Study site	Year	*n*	Area (ha)
Dogleg	1994	3	4.46 (2.80)
East Slough	1993	3	1.20 (0.20)
	1994	2	1.90 (0.31)
OIHN	1993	7	1.87 (0.36)
	1994	6	1.33 (0.06)
OIHS	1994	9	3.02 (0.05)
Sweetbay	1993	8	1.96 (0.35)
	1994	7	3.17 (0.66)

2.3 Courtship behavior

We have had only a few occasions to observe courtship behavior. Courtship takes place well within the grass, only a few centimeters above the soil surface. Males sing to females, although at a noticeably lower volume than when defending or marking a territory. On one occasion, we observed a male carrying nesting material in his bill, making very short hop-flights between the bases of grass tussocks, and singing. Females may respond with a “chew-chew” or “churble” call (see Werner 1975 for sound descriptions) and follow the male. Later in the nesting cycle, especially during incubation, females regularly solicit food from males just after leaving the nest. They do so by fluttering the wings and cocking the head back and down, and are very likely to make a “chew-chew” call in this situation as well. Males may or may not respond to this behavior by providing food. On rare occasions, the male will chase the female in a high-speed flight across the territory. It is possible that this is an aggressive reaction by a male that does not recognize his mate but instead reacts as if she is an intruder (McDonald and Greenberg 1991). Werner (1975) also reported females occasionally being “harassed” by a resident male. He attributed this to neighboring unmated males courting a female that had recently lost her mate.

2.4 Nest construction

Sparrows build nests near the ground with an average of 16 cm between the soil surface and the base of the nest. Nests are cup-shaped and often have a dome woven over the cup itself. Werner (1975) noted an easterly aspect for domed nests and westerly aspect to cup nests. This reflects the propensity for grasses to lean toward the west, thus making domed nests possible only if they have eastern entrances. It is unknown whether both parents contribute to nest building, or if it is solely the female’s responsibility.

Nests are woven entirely of dead grasses and sedges, all of which are readily available to the adults. We collected several nests in 1996 and found that sawgrass typically comprised better than 50% of the total volume. Muhly grass (*Muhlenbergia filipes*) or blacktop sedge (*Schoenus nigricans*), two species that are hard to distinguish once dried and dead, regularly composed 15% of the total volume. The remainder was woven from unidentifiable grass or sedge fragments. Half of the nest volume composes the nest cup, and the cup lining is made of very fine grass fragments.

We have found one nest that was clearly in the process of construction. On 4 April 1996, it was a loosely woven grass circle without any discernable sides or bottom. When next visited (18 April 1996) it held three eggs that subsequently hatched on 25 April 1996. Assuming a 12-day incubation period and 3-day laying period, this nest first held eggs 7 days after its discovery. We have found two nests that appeared complete (i.e., clearly had sides, bottom, and cup) but did not contain eggs until 5 and 8 days after discovery.

Finally, we note that of 329 nests found altogether, none were observed being re-used. It appears that new nests are constructed for every breeding attempt.

2.5 Egg laying, incubation, and brooding

We gathered information concerning incubation, egg laying, and brooding from 329 nests found and monitored from 1996 to 2000. Nests were checked every second or third day until fledging or failure. On each nest visit, we recorded the number of eggs or nestlings present and the state of the nest itself. Each visit lasted less than a minute, and neither the eggs nor nestlings were handled, decreasing the chance that monitoring efforts influenced nest success (Bibby *et al.* 1992).

Female sparrows initiate clutches (i.e., lay the first egg of a clutch) an average of 2.7 days after nest completion (S.D. $= 1.6$, $n = 14$). We recorded the timing of egg laying at seven nests. Of these, six females laid eggs every day until the clutch was complete.

Incubation lasts for 12.1 days (S.D. $= 0.5$, $n = 6$). This is the first direct observation of Cape Sable Seaside Sparrow incubation length. An incubation period of 12 days is consistent with other races of Seaside Sparrows (Post and Greenlaw 1994). Females sit on eggs for 15–30 min per incubation bout, and return to the nest after approximately the same length of time.

We followed three banded females through three nesting attempts. Over the span of all nesting attempts, these females laid 10, 8, and 7 eggs respectively. Thus, on average, these unusually successful birds laid 8.3 eggs per breeding season. The true maximum could be higher, as it is possible that one or more of these females made a fourth nesting attempt after we ceased daily searches, or that a fourth attempt failed before we found it. (As we shall show later, the chance to nest several times in one season is afforded only a small fraction of the pairs in most populations.)

Sparrows lay an average of 3.1 eggs per nest (S.D. = 0.8, $n = 160$ nests). This average did not vary between years (ANOVA $F = 2.5$, D.F. = 4, $p = 0.07$). There was also no difference in the number of eggs laid per nest across populations (ANOVA $F = 0.4$, D.F. = 2, $p = 0.64$). On average, we found 0.4 unhatched eggs per nest (S.D. = 0.7, $n = 96$). Out of the 31 nests that we followed from clutch initiation to hatching, we never observed a reduction in clutch size through the removal of an egg. Hatch rates varied from a low of 90% (1999 nests) to a high of 100% (1997 nests). Chapter 3 presents more detailed information on hatch rates.

We observed 176 nests from hatching to fledging. The average nestling period for these nests was 9.2 days (S.D. = 2.1). Cape Sable Seaside Sparrows averaged 2.7 nestlings per nest (S.D. = 1.0, $n = 254$). This varied according to year (ANOVA $F = 8.8$, D.F. = 4, $p < 0.001$). In 2000, nests held an average of 2.2 nestlings (S.D. = 1.2, $n = 75$), a value significantly lower than all other years (post-hoc comparisons). The number of nestlings per nest also varied according to population (ANOVA $F = 3.7$, D.F. = 2, $p = 0.03$). Population A nests held 3.6 (S.D. = 0.5, $n = 8$) nestlings per nest. This value was significantly higher than both population B (2.6 nestlings per nest) and population E (2.6 nestlings per nest), but we nevertheless view this result with caution given the very low sample size in population A as compared to the other populations (B, $n = 215$; E, $n = 31$).

These reproductive parameters are consistent with that of other races of Seaside Sparrow (Post and Greenlaw 1994). We will revisit these numbers when discussing the sparrow's ability to recover from adverse conditions (Chapter 3).

2.6 Nestling diet

During the 1996 and 1997 seasons, we observed daily what prey items were brought to the young, how often, and by which parent. Observations of morning and late-afternoon feedings averaged 5 hr per nest each week. We photographed adult sparrows holding prey items within 5–10 m of the nest. Comparison of these photographs to observer notes corroborated identification of prey. We were unable to classify 25% of the prey items to taxonomic order. Most unidentifiable prey items we estimated were less than half the sparrow's beak length.

In 1996 and 1997, we sampled the arthropod communities in our plots using standard sweep-net protocols (see Chapter 4 for description of methods). To measure this population's relative use of prey, we compared prey available (sweep-net samples) to prey taken (feeding observations) using the formula

$$\text{relative use} = \frac{\%\text{ taken} - \%\text{ available}}{\%\text{ available}}.$$

We divided relative use data into three periods: 25 March to 10 April, 11 April to 25 April, 26 April to 10 May 1996. By dividing the number of prey taken in one period by the total number of prey taken for all periods, we calculated the percent taken. We used the same

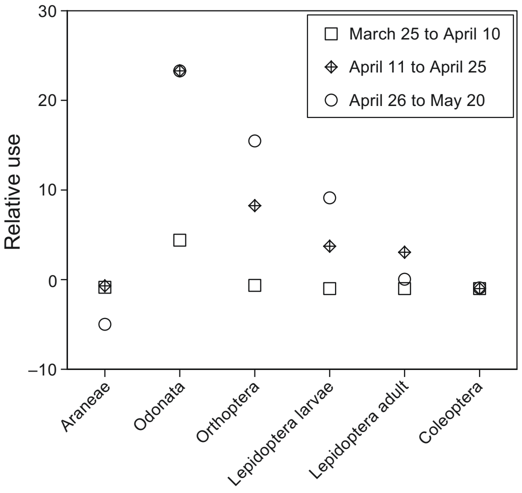

Figure 2.1: Relative use of arthropod orders by adult sparrows when feeding nestlings.

formula to calculate the percent available. We interpreted relative use as underrepresented (< 0), neutral (≈ 0), or overrepresented (> 0).

Six orders of Insecta and one order of Araneida composed the observed nestling diet. Males brought food to nestlings in 52% and females in 48% of all visits ($n = 251$). Feedings occurred approximately every 16 min ($n = 1242$) and adults commonly carried more than one arthropod per trip (mean = 1.4, S.D. = 0.6, $n = 260$). Since adults often carried only the abdomens of Odonata and Orthoptera, we suspected that they either ate or discarded all other parts before arriving at the nest. Greenlaw and Post (1985) and Greenlaw (1992) reported that adults of other Seaside Sparrow races presented macerated or mucous-bound food items to nestlings.

Nestling diet included Lepidoptera, Orthoptera, and Odonata to a greater extent than expected by their availability in 1996 (Figure 2.1). Conversely, it rarely included Coleoptera or Araneae, despite these orders comprising 88% of the available community. Relative use of prey items changed over the course of the breeding season. Early in the season (25 March to 10 April) sparrows used Odonata more frequently than would be expected based on their availability. While disproportionate use of this group persisted to the end of the season, by mid-season (11 April to 25 April) sparrows also began feeding nestlings Orthoptera and adult Lepidoptera. At the end of the season (26 April to 20 May) the sparrows switched from Lepidoptera adults to larvae but continued their disproportionate use of Orthoptera and Odonata.

Using χ^2 contingency tables, we compared proportional representation among prey taxa between years (1996, 1997) and sites (DL, OIHN, and OIHS). Our analyses included only those orders that incorporated more than 5% of the total number of individuals in either sweep-net or feeding samples. We did not include two sites for which prey observations were minimal.

Nestling diet changed between years ($\chi^2 = 59.1$, D.F. = 4, $p < 0.001$). In 1995, Odonata represented nearly 30% of the nestling diet. In 1996, this number dropped to under 10%. Conversely, Orthoptera accounted for only 15% of nestling diet in 1995 but exceeded 35% in 1996. Phasmida were absent from nestling diets in 1996 but comprised nearly 10% of it in 1995.

Nestling diet data from 1996 also evinced differences among sites ($\chi^2 = 31.5$, D.F. = 8, $p < 0.001$). Odonata were absent from nestling diets at OIHN despite their presence at all other sites. Lepidoptera were absent from DL but common at OIHN. Orthoptera had equal representation at each site, as did an unidentified (but distinct) species.

From this information, we infer that the Cape Sable Seaside Sparrow is a dietary generalist. We detected significant differences in nestling diet between years and sites. In addition, sparrows shifted the importance of prey items in their diet with their availability. This reflects the patchy distribution typical of arthropods and the opportunistic nature of Seaside Sparrow foraging (Post and Greenlaw 1994).

Sparrows rely on Orthoptera and Lepidoptera, much like all other Seaside Sparrow races (Post *et al.* 1983, Merriam 1983). The absence of Diptera and other mud-dwelling insects from the nestling diet is consistent with Scott's Seaside Sparrow (*Ammodramus maritimus peninsulae*) populations studied in northern Florida (Post and Greenlaw 1994). This behavior contrasts with that of Seaside Sparrows inhabiting saltmarshes in the northern parts of the species' range (the nominate race; Marshall and Reinert 1990). Southern races depend less on open mudflats (Post and Greenlaw 1994, Quay *et al.* 1983), and there are no mudflats within the observed range of the Cape Sable Seaside Sparrow. The sparrow appears unique among the Seaside Sparrow races in their use of Odonata. This is not surprising since they are the only extant race to inhabit freshwater marshes.

2.7 Nest losses

Of the 240 nests to which we could assign a definitive fate, 117 fledged young (49%). Of the failed nests, 61 failed during incubation and 62 failed during the brooding of nestlings. Predation accounted for the vast majority of all losses of young or eggs. Kushlan *et al.* (1982) suggested that rice rats (*Orzymus palustris*) and snakes principally threaten nests. Post (1981) indicated that rice rats, Fish Crows (*Corvus ossifragus*) and raccoons (*Procyon lotor*) threatened Seaside Sparrow populations in northern Florida. We believe several nests were depredated by rats, because they left shell pieces and their feces within the nest. No nests were excessively disheveled or destroyed, indicating that raccoons and opossums (*Didelphis virginiana*) are not particular threats to sparrow nests. Aerial predation of nests is possible, as there are often Red-winged Blackbirds (*Agelaius phoeniceus*), Northern Harri-

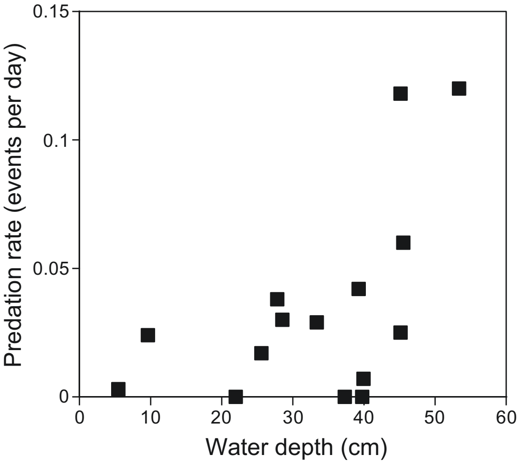

Figure 2.2: Relationship between water depth and predation rate. Information is combined from nests in population B between 1996 and 1999.

ers (*Circus cyaneus*), Red-shouldered Hawks (*Buteo lineatus*) and American Crows (*Corvus brachyrhynchos*) within our study plots. Two nests lost to apparent predation had well-defined holes within the bottom or side of the nest, perhaps indicating snake predation. The only snakes we have observed within our study plots are cottonmouths (*Agkistrodon piscivorus*). Dean and Morrison (2001) recovered a radio-tagged sparrow from within the stomach of a cottonmouth in the nonbreeding season. Given this information, and the correlation between water level and predation rate (see below, and Chapter 3), we suggest this species is a primary predator of sparrow nests and breeding adults.

Water directly influenced the success of at least four nests. Typically, eggs were lost or young drowned when water levels rose above the height of the nest after a heavy summer rainstorm. All documented nest losses due to water were recorded within population B, and all were late-season nests (i.e., had hatch dates after 1 June).

Because Lockwood *et al.* (1997) presented preliminary evidence of increased predation rates with increases in water level, we tested for a similar effect using regression techniques. We used hydrological information from an Everglades National Park monitoring station. This hydrological station (P46) is located within ~ 2 km of all population B plots. The P46 water level is the independent variable; predation rates calculated for the seven population B plots are the dependent variable. Each data point represents a particular unit of time encompassing the 1996 to 1999 breeding seasons (Fig. 2.2).

Schaub *et al.* (1992) provided the method of estimating predation rate that we employed. This method calculates predation rate by dividing the number of apparent depredations by the total number of days that nests contained eggs or young. We assumed predation when clutches disappeared between observations or when we found direct evidence, such as broken eggshells or destroyed nests. The rate calculation gives equal weight to all methods of predation detection.

Predation rates varied from 0 to 0.118 events per day with a mean of 0.034(S.D. = 0.38). The average water level at the P46 hydrological station varied from 5.5 to 53.4 cm above mean sea level (MSL) with an average of 31.8 cm MSL (S.D. = 13.5). When we plotted predation rate within the population B plots against water levels at the P46 station, most of the points in the upper right corner of Figure 2.2 (i.e., those with high predation rates and water levels) represent dates after 1 June. This substantiates our assertion that predation pressure increases after the onset of summer rains, and it indicates that this increase is in part due to the presence of water. However, not all points in the upper right corner of Figure 2.2 are late-season nests. High water levels, no matter when they occur, increase predation pressure within the population B study plots.

2.8 Fledglings and their behavior

Of all the stages of the nest cycle, the care and movement of fledglings has been the most difficult to document. For 2–3 days, fledglings remain sheltered under vegetation 5–10 m from the nest and are extremely hard to locate. We have resighted 11 banded fledglings within five different plots. Most of these resightings occurred in the 2000 breeding season. Thirty-nine nestlings were banded during the 2000 season within the Main Park Road plots. Nine of these were resighted after fledging, giving a resighting rate of 23% through the end of July. Five banded fledglings were observed on multiple occasions, giving a total of 52 resightings. Two banded fledglings were observed on 11 separate occasions, three banded individuals were observed on 6 to 8 occasions, and the remaining individuals were observed only once or twice. The average age at first resighting was 42 days since fledging. Two sets of resighted individuals were nestmates.

The youngest banded fledgling was resighted 8 days postfledging. This individual was able to make short, 1–2 m flights/hops and was observed taking food from a parent on 28 March. The adult was also banded, allowing the two individuals to be unambiguously linked. The feeding took place on the ground with the fledgling concealed within vegetation litter.

The oldest banded fledgling was resighted 93 days after it fledged. This individual was capable of flight, perched easily on top of sawgrass seedheads and other sedges and grasses, and regularly vocalized using a short “seet” or chip note. Its plumage was drab green. The white breast patch was visible; however, the characteristic spotting and streaking on the breast was absent. The yellow eyestripe could be detected, but was not as prominent as in adult plumage. This individual was three-quarters the size of adults and had noticeably shorter tail feathers. Although these, and other older fledglings, were observed in flocks with adults, they never received food from these adults. This descrip-

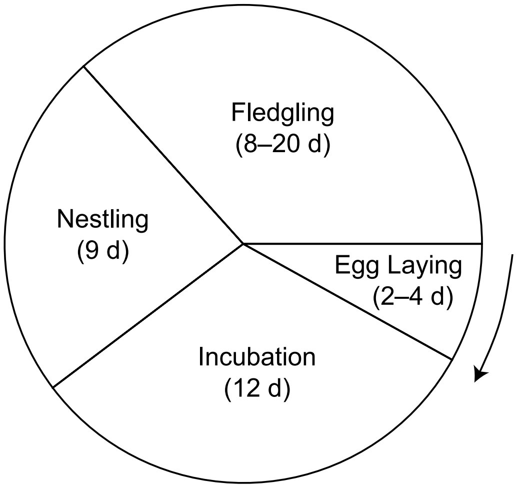

Figure 2.3: Nest cycle for Cape Sable Seaside Sparrows, showing the number of days devoted to each phase.

tion of plumage, size, vocalization, and interaction with adults is typical of the majority of resighted fledglings that were from 30 to 90 days old.

Because we did not record the location of these resighted fledglings with a GPS, we cannot precisely calculate their movements. However, we did estimate the fledglings' positions with respect to grid poles placed every 200 m. We never observed a banded fledgling more than 1 km from the nest from which it fledged; however, the fledglings regularly moved several hundred meters between sightings.

2.9 Length of breeding season

Totaling the number of days required for all the nesting stages outlined above, we estimate the nest cycle of sparrows to be 34 to 44 days. This number varies according to the number of eggs laid and the length of postfledging care (Fig. 2.3). Since nesting appears to begin in mid-March, a pair that successfully triple brooded (44 days multiplied by 3 broods) would maintain breeding activity into early August. The observations of Werner (1975) and those reported in Post and Greenlaw (1994) fall within this interval.

The earliest Cape Sable Seaside Sparrow nest was found on 20 March 1997. This nest had two eggs but was lost to predation 7 days later. Werner (1975) reported young in a nest initiated in late February. Within our records, the latest sparrow nest was found on 10 July 1999. This nest eventually fledged young on 26 July. Werner (1975) also reported observing nests with eggs as late as 26 July, and Dean and Morrison (2001) reported a nest fledging young as late as 2 August 1998, and catching recently fledged young as late as September. These reports provide information, independent from the above calculations, that Cape Sable Seaside Sparrows can nest from March until at least early August (122 to 142 days).

We observed one banded male (and his unbanded mate) through three clutches, all of which were successful. The first nest of this male was found on 16 April. The nest contained 4-day-old nestlings, indicating that the clutch was complete by 31 March (assuming 12 days of incubation). The third nest of this male fledged two young on 24 July. Thus, this male required 115 days to fledge three broods, or about 38 days per clutch. The interclutch interval (i.e., fledging to the completion of the next clutch) for these nests was 34 days between the first and second attempts and 20 days between the second and third attempts. This interval must include enough time for fledgling care, pair bonding, nest building, and egg laying. It is also possible that we missed a failed renesting attempt between clutches.

2.10 Mate choice and fidelity

We followed four banded individuals through multiple nesting attempts with other banded individuals. From this information we can document within-breeding-season mate-fidelity patterns. Two of the four banded individuals "divorced" their original mate and re-paired with neighboring individuals during the breeding season. One female attempted three clutches, the first two with the same male and the last with a different male. A male also attempted three clutches, two with one female and one with another. The two other banded individuals we followed (one male and one female) each paired with the same individual for all breeding attempts (three and two attempts respectively). We have documented too few cases to extrapolate this information to the entire population, and we cannot analyze potential reasons why pairs divorced mid-season. However, this pattern in mate fidelity is consistent with other Seaside Sparrows (Post and Greenlaw 1994).

We have observed only one pair that mated during two successive breeding seasons. This pair fledged at least two clutches in 1999 and then re-paired at the beginning of the 2000 breeding season. The pair split after their first attempt failed in 2000. Each went on to mate and renest with other individuals later in the 2000 breeding season.

We confirmed a case of polygyny in Cape Sable Seaside Sparrows during the 2000 season. A banded male fed two nestlings no more than 2 days old on 27 April 2000. The female attending this nest was unbanded. The young from this nest fledged on 7 May 2000. A second nest at which this same male fed nestlings was found 15 May with two nestlings at least five days old. The female attending this nest was also unbanded but was very likely not the same female from the first nest as the nests were $\sim$ 200 m apart. The young from this second clutch fledged on 18 May. Thus, the young from the first nest fledged approximately two days before the young from the second nest hatched. By backdating from the date of fledging, we estimated that this second clutch was complete by 28 April.

Although this male was not feeding nestlings in two nests at the same time, he paired with a different female and they had a complete second clutch 10 days before the young of the first clutch fledged. Each nest was within the male's territory. However, his territory was approximately 400 m in diameter, about twice that of other male sparrows.

We are the first to document natural polygyny in this species (Post and Greenlaw 1994). Greenlaw and Post (1985) experimentally induced polygyny among populations of Seaside Sparrows in north Florida and New York. These polygynous males, however, were never observed feeding the young of the secondary nest. Greenlaw and Post (1985) documented that territory quality (as indexed by available food, cover, and nesting sites) varied dramatically among males. This variation could induce a female to become the secondary mate of a male with an unusually "good" territory if the benefits of being on this territory outweighed the loss in fitness that may result from polygyny (Gowaty 1981). Given the work conducted by Greenlaw and Post (1985) on other Seaside Sparrows, and the fact that we do not observe skewed sex ratios in our study population, we suspect that differences in territory quality very occasionally induce polygyny in the Cape Sable Seaside Sparrow.

2.11 End-of-breeding-season behavior

Werner (1975) suggested that rising surface water ended the nesting season but provided no further information. Initially our evidence supported this hypothesis. However, we began our nesting studies in some of the wettest years on record (1995 and 1996). Thus, we may have witnessed early cessation of breeding (i.e., by July) due to higher than normal water depth in our study plots. (Water depth was so great in 1996 that we did not feel safe traveling down the Old Ingraham Highway.) Subsequent years were much drier, and it became clear sparrows could continue to breed late into the summer months. Indeed, it is clear that it requires sustained flooding of habitat for sparrows to cease breeding. In 1998, our population B study plots became inundated during a 1-week period of constant rainstorms in early June. Water depths reached 40 and 50 cm, depths at least 20 cm above the average height of nests from the ground. Despite the fact that most of the low-lying vegetation was underwater, all active nests were flooded, and it was clearly not possible to reinitiate nesting until the water receded, we still found males singing and defending their territories.

If sparrows continue to exhibit breeding behavior even when all current nests have been destroyed by high water, what then signals the end of the breeding season? From the work of Dean and Morrison (2001) we now know that it is the onset of molt. They observed the first signs of molt in July and documented that molting activity peaks in September. Molting ends by late October. Given the energetic demands of feather replacement, it is unlikely that a molting individual is capable of caring for young. (Dean and Morrison did document a few individuals feeding young while beginning to replace some feathers.)

Thus, the breeding season does not have a clear-cut end. Each individual ceases breeding activities when they begin molting, and the initiation of molt varies substantially among individuals in the population. However, we can safely say that all breeding activity likely ceases by early September, as this is the time of year when almost all adult sparrows are molting.

During the final few months of the 1999 breeding season, we consistently observed small flocks moving about the breeding areas, apparently without regard to territorial lines. In the 2000 breeding season we made a special effort to record the movements and composition of flocks. We defined a flock as two or more individuals maintaining a proximity to one another of 5 m or less and displaying synchronized behavior such as flushing in one direction. We recorded the size of the flock and distinguished between adults and juveniles using plumage characters. We recorded the identity of banded individuals and the date, plot, and duration of observation.

We classified potential perch substrates of flocks into four habitat categories: open prairie, dense sawgrass, tree island, and shrub. Open prairie was defined as continuous mixtures of grasses and sedges with stand heights of approximately 1 m or less. Dense sawgrass was defined as patches of grass or sedge dominated by sawgrass with stand heights of > 1 m. Tree islands included all bay, cypress, and willow tree associations. Tree islands did not include pine islands. Shrubs included any singular tree that was low in stature (usually < 2 m tall).

Based on the flocking information, we determined association indices for each individual resighted more than once, using the formula $A_{\mathrm{AB}} = N_{\mathrm{AB}}/(N_{\mathrm{A}} + N_{\mathrm{B}} + N_{\mathrm{AB}})$, where N_{AB} is the number of occasions when individuals A and B were observed together, N_{A} is the number of occasions when individual A was seen without B, and N_{B} is the number of occasions when individual B was seen without A (Martin and Bateson 1993). A_{AB} can vary between zero and one, with a value of one indicating complete association. Values near 0.5 indicate the two individuals were just as likely to associate as not.

On 44 occasions, we observed flocks of Cape Sable Seaside Sparrows. The first flock was observed on 2 June 2000; the last on 26 July 2000 (last day of fieldwork in the 2000 field season). Our flock information was gleaned from more than 750 min of observations. The average observation period was 20 min per flock.

The average flock size was 4.8 individuals (S.D. $= 1.9$). Maximum flock size was nine individuals and minimum flock size was set at two by definition. These flocks contained an average of 1.3 adults and 3.5 juveniles. On average, one juvenile and one adult per flock were banded.

In 71% of all flock observations, we recorded the individuals perching within dense sawgrass. In 14.5% and 11% of observations, flock members perched in open prairie and tree islands respectively. When birds were recorded in tree islands, they used only the fringing vegetation or outer tree branches. They never appeared to enter the tree islands. The remaining 4% of observations included flock members perched on shrubs or other available substrate.

Four banded juveniles were observed in flocks frequently enough to determine association indices. Three of these individuals were most often associated with each other. Banded juvenile 75288 was most often associated with banded juveniles 75291 ($A_{\mathrm{AB}} = 0.42$) and 75292 ($A_{\mathrm{AB}} = 0.33$). These latter two banded juveniles were nestmates. The nestmates were most often associated with each other ($A_{\mathrm{AB}} = 0.29$ and $A_{\mathrm{AB}} = 0.38$). The remaining banded juvenile, 75317, associated with five other banded individuals, but was never observed with the same banded bird more than once. Thus, $A_{\mathrm{AB}} = 0.125$ for each associate.

No banded adult sparrows were observed as flock members more than once. We never observed a banded juvenile with the same adult twice. None of the banded adults observed in association with banded juveniles were the parents of those juveniles. Thus, these flocks were not family groups, although nestmates may associate. Of the 28 banded adults observed in flocks, 24 (86%) were males. The males associated with observed flocks held territories in the vicinity of the observation (i.e., within $\sim$ 200 m). However, the juveniles in the flock were fledged from nests anywhere within 1 km of the observation.

Although we began observing juveniles outside of the nest by late April, observations of flocks did not occur until early June. By June, most of the banded juveniles that composed these flocks had fledged 30 or more days earlier. Once reaching this age, these juveniles were fully independent and capable of flight. Thus, it appears fledged young remain largely flightless and close to the nest for several days (up to eight by our observation). They may remain dependent on one or more of their parents for several days thereafter, even though they are becoming more mobile. By the 30th day out of the nest, juveniles begin associating with one another in loose groups with transient membership.

2.12 Life during the nonbreeding season

One of the more enigmatic portions of the sparrow's life history has been its winter, or nonbreeding season, habits. Information on the wintering habits of most Seaside Sparrows is anecdotal (Quay *et al.* 1983, Greenlaw 1992, Post and Greenlaw 1994). Northern races are sometimes migratory (Quay *et al.* 1983), and southern races are not believed to migrate at all (Post and Greenlaw 1994).

In 1997 we continued resighting efforts within our study plots throughout the nonbreeding season. Initially, we concentrated our efforts on our population B plots. Observations began immediately after the breeding season ended (mid-June 1996). We visited four of these plots from June 1996 to March 1997. Two plots (AH and DL) were visited an average of three times per week. The remaining two plots (OIHS and OIHN) were each visited once per month.

As the nonbreeding season progressed, we expanded the area of observation to include most of the southeastern portion of Everglades National Park, including Cape Sable. In order to determine if sparrows migrate out of the prairies during the nonbreeding season, we conducted point count surveys in seven different habitat types found within Everglades National Park. Habitat types selected include *marl prairie*, which is usually inundated with water during the months of June through October but is dry throughout the remainder of the year. *Mixed prairie* differs from marl prairie in its greater abundance of hardwood hammocks, small tree islands, and sawgrass. This prairie also floods during the nonbreeding season. *Dry prairie* or "finger glades" are so named because they are found between large stands of pine forests. This prairie does not flood in the nonbreeding season and is dominated by sawgrass and short grasses. *Coastal prairie* is found at the southern end of the park along shorelines. This prairie is dominated by *Batis maritimus*, *Sesuvium portulacastrum* and *Salicornia* species. Although other subspecies of Seaside Sparrows winter in coastal prairie habitats (Post and Greenlaw 1994), no Cape Sable Seaside Sparrows have been recorded in this habitat (Bass and Kushlan 1982). *Pineland* is composed of slash pine (*Pinus elliottii* var. *densa*) with heavy undergrowth of saw palmettos (*Serenoa repens*). This area does not flood. *Dwarf cypress* are forests composed of tightly clumped to well-dispersed pond cypress (*Taxodium ascendens*) interspersed with sawgrass. This area remains flooded throughout most of the year. *Mangrove* includes stands of black and white mangroves (*Avicennia germinans* and *Laguncularia racemosa*) with little or no undergrowth. This area floods in the wet season and is adjacent to brackish bodies of water.

These habitats are representative of Everglades National Park as a whole, although most censuses were conducted in readily accessible areas. At the time there were no observations of Cape Sable Seaside Sparrows during the nonbreeding season beyond that given by Stimson (1956) and Howell (1919), so we chose not to narrow the search in any manner. However, we did budget our observations according to the habitat type in which we most often found sparrows (i.e., we spent the majority of observation time within the marl prairie habitat).

Following Gutzwiller (1991), we used an unlimited-distance point count to survey each habitat type and identify all birds present. Count points were placed 200 m apart. Water measurements were taken at fixed points within two study plots (in marl prairie habitat) throughout the season. Using colored flagging tape, we followed changes in sparrow distribution by marking all locations in which we found birds. We used a GPS to record the spatial coordinates of resighted adults and calculated the distance banded individuals moved between breeding and nonbreeding locations.

We also recorded the following data for each resighted individual: any behavior observed (e.g., vocalizations, intraspecific interactions); the number of birds in the flock; status of tail and wing molt; microhabitat type in which the bird was found; and the location of the nearest resight flag.

Figure 2.4 shows the sum total of birds (total, banded, and unbanded) seen throughout the nonbreeding season per observer per day. The total number of sparrows detected showed a steady decline beginning at the end of the dry season in June. Detections reached a low of less than one bird seen per observer per day in November. Thereafter, the number of detections began to increase until an average of two birds was seen per observer per day

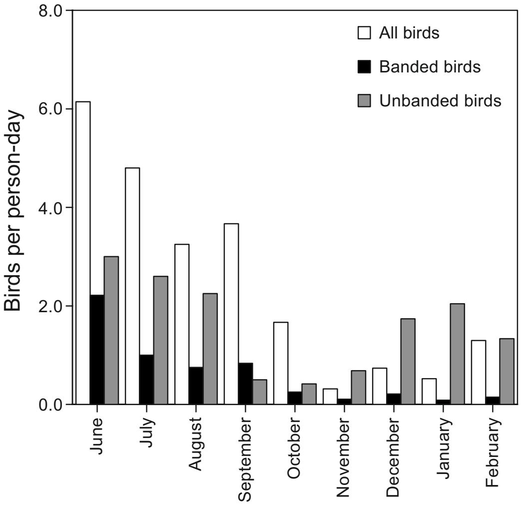

Figure 2.4: Number of birds per person-day seen throughout the wet season.

by mid-February. At this point, male sparrows were regularly observed singing from high perches within open marl prairie.

However, when banded-bird detections were separated from unbanded-bird detections, a different pattern emerged. Detections of banded birds declined steadily with no subsequent increase as the nonbreeding season progressed. Detections of unbanded birds, however, increased as the nonbreeding season ended (Fig. 2.4) and the breeding season began. Thus, the increase in total number of birds detected late in the nonbreeding season can be attributed entirely to the increase in detection of unbanded individuals.

A total of 51 hr of point count surveys conducted throughout southeastern Everglades National Park during the nonbreeding season found no Cape Sable Seaside Sparrows in habitats other than marl prairie. Simply, we did not detect sparrows outside of their breeding range, despite the fact that sparrow detections within their breeding range declined steadily throughout the wet season.

Within the marl prairies, the majority of detections throughout the wet season were of birds in dense clumps of sawgrass known as "sways" (81%). Occasionally, we found sparrows perched in small trees within hammocks (all within the plot in which they nested), saw palmettos, or roadside vegetation. Males did not sing after September, though a number of juveniles sang subsongs throughout the season. Through July, August, and September some birds showed signs of molt. Molting individuals remained within sawgrass sways, presumably for cover.

We observed little movement of sparrows. Twenty-one banded birds were resighted. Of these, 14 had all bands intact and could be positively identified. The remaining seven

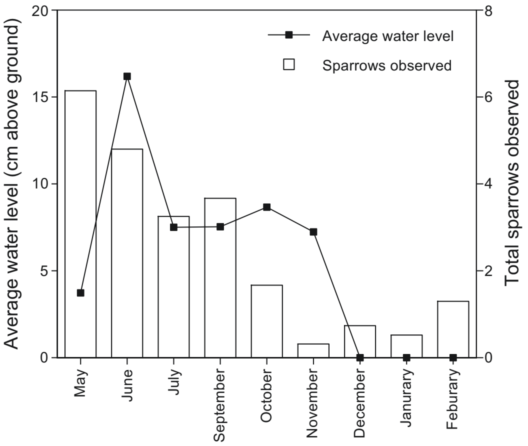

Figure 2.5: Water levels within marl prairies and the number of sparrows observed, plotted by month.

were either missing a color band (two birds) or were not seen long enough to be positively identified (five birds). The 14 banded birds positively identified were found an average of 277 m ($n = 14$, range 77 to 986 m) from the spot where they were banded in the spring of 1995 or 1996. Interestingly, the majority of all resighted birds (15 out of 21 birds) were seen only once. When locations of banded birds were revisited (at least once per month), the same individuals were not found again. The six individuals resighted more than once were usually found within a 10 to 20 m area, though two eventually moved to another study plot.

Water depth increased dramatically within marl prairies with the onset of summer rains in early June. By mid-June, however, water depth had dropped substantially, and remained constant until the marl prairies dried out in early November. For the next four months, these prairies contained no standing water except in some deeper microdepressions. The drier habitat types stayed dry throughout almost all of the wet season, and those habitats that typically remain flooded throughout the wet season experienced lower than normal water depths.

Since we found sparrows only in marl prairies we compared water levels within this habitat to sparrow detection frequency (Fig. 2.5). There appeared to be no correlation between water depth and the fall in number of birds detected, or with the onset of breeding.

Our results indicate that neither long-distance nor local migration occurs in the Cape Sable Seaside Sparrow. At least some of the sparrow population spend their nonbreeding time in the same prairies in which they breed. They do, however, show a change in microhabitat use within those prairies. The birds move out of the open prairies and into small tree hammocks and sawgrass sways. This movement to taller and denser vegetation, coupled with the birds' already secretive nature, confounds the ability of an observer to readily find these birds. However, sawgrass sways likely provide refuge and perhaps an increased food supply for the sparrows during the wet season (Post and Greenlaw 1994). In addition to food availability and protection during molt, sawgrass stands may provide an escape, in the form of higher perches, from rising waters due to spring rains (marl prairies usually stay inundated from June to March).

In the two years following this work, Dean and Morrison (2001) radio-tagged adult and juvenile sparrows and followed their movements and behavior through the nonbreeding season. Their results provide much more detail than the above but generally support our conclusions.

Dean and Morrison (2001) radio-tracked 31 individuals for 1–7 months. They found sparrows to be sedentary and to maintain a nonbreeding-season home range that is larger than the breeding territory but centered in the same general area. Occasionally individuals made long-range movements (> 500 m) from their home ranges; however they typically returned to these ranges. Dean and Morrison (2001) documented three individuals vacating their breeding territories and moving from 450 to 7000 m into a new home range. The fate of these individuals is not known. All movements of radio-collared sparrows were within marl prairie habitat. Radio-collared sparrows never entered tree hammocks, cypress forests, or other habitats. This is consistent with information we collected in 1997 and indicates that sparrows are dependent on marl prairies for the entirety of their life cycle.

Dean and Morrison (2001) radio-collared juveniles (i.e., fledglings) and followed them from June to March. As we observed at the end of the 2000 breeding season, the radio-collared fledglings ranged widely as members of small flocks. This continued until the onset of adult molt in August and September (the juveniles themselves do not molt in the year they were born). After molt, the juveniles settled into a nonbreeding-season home range. It is not clear whether this nonbreeding-season home range contained the juveniles' breeding territory for the oncoming breeding season. If so, juveniles may use the months just after fledging to explore potential breeding locations. Their association with each other may reduce predation and allow more efficient assessment of occupied versus unoccupied habitats.

Dean and Morrison (2001) were able to more accurately and completely describe the change in microhabitat use that occurs during the nonbreeding season. They developed statistical models that compared used to unused microhabitats. These models could not consistently distinguish between the two groups, as habitat selection seemed to shift with the hydrologic condition of the prairies. When water levels were low, sparrows chose sites dominated by low vegetation (which we classified as open prairie). However, when water levels rose, sparrows increased their use of dense sawgrass clumps. Combined with our observations, this suggests that such small-scale variation in habitat structure is a critical element in the nonbreeding-season ecology of the sparrow. Dean and Morrison (2001) suggested that small-scale variation in topography within marl prairies produces these mi-

Table 2.2: Return rates of banded adult Cape Sable Seaside Sparrows, listed by year banded.

Year banded	Total no. of adults banded	Returns by year 1995 *n*	%	1996 *n*	%	1997 *n*	%	1998 *n*	%	1999 *n*	%
1994	20	9	45	4	20	1	5	2	10	1	5
1995	49			20	41	22	45	13	27	7	14
1996	38					13	34	11	29	4	10
1997	80							38	48	25	31
1998	60									23	38

crohabitat features, and that these features help buffer sparrows from extreme hydrologic conditions.

2.13 Site fidelity

Finally, it would be useful to know how many individuals return to their previous territories and initiate another round of breeding. By recording the locations of banded, recaptured, and resighted individuals using a GPS we calculated return rates, breeding dispersal distances (i.e., the distance breeding individuals move from year to year), and natal dispersal distances (i.e., the distance juveniles move from their place of birth to the next breeding season).

Table 2.2 provides the proportion of adults from yearly cohorts that returned in subsequent years (data included are from 1994 to 1999). From 28% to 48% of adults returned to the same territory one year after banding; 20% to 37% returned two years postbanding, and only 5% returned four years after banding. We banded 213 juvenile sparrows (mostly in the nest) between 1997 and 1999, meaning that we can only calculate a return rate for juveniles up to two years postbanding. Return rates for juveniles ranged from 15% to 20%; nearly half that of the equivalent return rate of adults. Dividing banded individuals according to gender, males and females showed similar overall return rates. Males returned at a rate between 26% and 52%. Females returned at a rate between 25% and 45%. We do not have enough banding information from the various populations for a spatial comparison of return rates.

By following banded individuals from one breeding season to the next, we calculated breeding dispersal distances for adult sparrows. Adult Cape Sable Seaside Sparrows defend a territory an average of 212 m (S.D. $= 131$, $n = 30$) from the location of a territory established within two previous years. The distribution of these dispersal distances resembles an exponential decay with most individuals moving less than 300 m. These observations, along with those of Dean and Morrison (2001), indicate that adult Cape Sable Seaside Sparrows are quite sedentary throughout the year and thus adult immigration and emigration rates are low.

Natal dispersal is defined as the distance a juvenile moves from its place of hatching to the site in which it settles during its first breeding season. (These sites may or may not be breeding territories.) Individuals banded as nestlings were resighted or recaptured an average of 577 m (S.D. = 98, $n = 15$) from their place of hatching. This value was significantly different than that observed for equivalent time frames in adults (i.e., one and two year movements; Student's $t = -4.7$, D.F. = 42, $p < 0.001$). In contrast to the distribution of adult dispersal distances, juvenile birds moved farther, producing a more even distribution of dispersal distances. We have not yet collected enough information on juveniles to calculate longer-interval movements.

During the 2000 breeding season we documented the nesting attempts of 10 individuals banded as nestlings one or two years prior. Of these 10, four nested in the first breeding season after they fledged. The remainder were resighted or recaptured in their first breeding season, indicating that they may have bred; however, we were unable to find their nests. Of the seven individuals that were banded as nestlings in 1998 or 1997, all nested in their second breeding season. All 10 banded individuals nested within 1 km of the nest from which they fledged.

2.14 Summary

Individual sparrows do not explore much of the marl prairie habitat available to them. Their entire lives are centered around a small expanse of grassland probably no more than 3 km wide. They are born there, explore their immediate surroundings during their first few months out of the nest, and quickly settle into a breeding territory that they maintain (come hell or high water) until their death. For males, the choice of a breeding territory means the difference between high and low reproductive success. Females must choose carefully among the available males, as her mate's territory will provide the food and cover necessary for rearing young and her survival. The remainder of this document explores the consequences when marl prairies are harmed.

2.15 Appendix: The study plots

We established 12 permanent study plots between the 1993 and 2000 field seasons, distributed throughout the Cape Sable Seaside Sparrow's range. We briefly describe each below. Study plots are permanently established rectangular areas that originally spanned 36–1100 ha. All active plots were standardized in 1999 to 0.5 km^2 (50 ha). We placed them nonrandomly, with their location being determined by the nature of the question we wished to address. Nest observations, feeding observations, and survival estimates of large numbers of birds are best investigated in areas with high densities of sparrows and within easily accessible areas. For that reason we established most plots within population B along either Main Park Road (SB, DL, NM, AH; full names of plots are below) or Old Ingraham Highway (OIHN, OIHS, FE). In order to understand why sparrows avoid certain sites, and hopefully to document any population recovery, we established plots that do not contain sparrows (FG, TS). We established four plots outside of population B (TP, CP, AJ, and SV). Three of these require access via helicopter (TP, CP, SV). Each of these peripheral plots has experienced drastically different hydrologic flows. Two (AJ, CP) experienced sharp declines in sparrow numbers early on in our study. The study population at CP was extirpated in 1995. For this reason, AJ and CP were dropped from our study relatively early. In response, we established replacement peripheral plots within populations A (SV) and E (TP) in 1997 and 1998 respectively.

2.15.1 Description of study plots

All plots are 50 ha unless otherwise specified.

Taylor Slough (TS) est. 1993 This plot is 1100 × 600 m (66 ha) and lies within the plot that Harold Werner established in 1974. It runs along the east side of Taylor Slough and is bisected by the Main Park Road. The vegetation is dominated by sawgrass with some muhly grass and consists of large areas of "pinnacle rock" (exposed limestone) with infrequent patches of well-developed soil. Being at the edge of the slough, and downstream from a floodgate, this plot can become inundated early in the wet season by rain or by the opening of the floodgate. This plot is located within population D and is no longer in use.

Aerojet (AJ) est. 1993 This plot is 600 × 600 m (36 ha) and is located halfway between the two sets of buildings on the former Aerojet Corporation property (now jointly managed by the South Florida Water Management District and the Florida Game and Freshwater Fish Commission). The area predominantly has a long hydroperiod and is dominated by sawgrass; however, there are small, drier patches dominated by muhly grass. This plot is located in one such patch, which accounts for its small size. This plot is within population D and is no longer in use.

Sweetbay (SB) est. 1993 This plot is located ca. 400 m southeast of Sweetbay Pond, south of the remnants of Old Ingraham Highway, within population B. The plot is dominated by sparse to moderate muhly grass, but remnant furrows from past agricultural activity provide habitat for a wide range of other herbaceous species. This plot usually remains dry throughout April and May.

Curnutt Plot (CP) est. 1993 This plot is 800 × 800 m (64 ha) and is located on the west side of Shark Slough within population A. When originally established in 1993, the habitat was about 40% sawgrass and 60% mixed prairie. There were substantial patches of muhly grass. This plot was completely inundated throughout the 1993 field season, remained dry through most of the 1994 season, but was inundated again in 1995. The vegetation changed dramatically, and the study population was extirpated. For this reason, this plot has not been monitored since 1995.

Old Ingraham Highway North (OIHN) est. 1993 This plot is located less than 100 m north of the west end of the Old Ingraham Highway within population B. The plot is mixed prairie dominated by muhly grass and sawgrass, and remains dry throughout April and May.

Old Ingraham Highway South (OIHS) est. 1994 This plot is located south of the west end of Old Ingraham Highway within population B. The northeast corner of this plot is ca. 500 m south of Old Ingraham Highway North. Like OIHN, the plot is mixed prairie dominated by muhly grass and sawgrass, with little surface water throughout April and May. However, the grass cover at this plot is, on the whole, much more dense than at OIHN.

Dogleg (DL) est. 1994 This plot, located within population B between the Main Park Road and the remnants of the Old Ingraham Highway, is much longer than wide (hence its name) but covers 50 ha. Muhly grass and sawgrass dominate the vegetation.

Finger Glade (FG) est. 1995 This plot is located in a large finger glade west of the "Hole-in-the-Donut" and north of the (unpaved) Long Pine Key Road within population B. The vegetation is dominated by muhly grass and *Spartina* spp. Cover is very dense throughout the plot, indicating a lack of fire in recent years. Remnants of furrows indicate that much of the plot was once farmed. Sparrows have never occupied this plot, and thus we have not visited this plot since 1996.

North Mahogany (NM) est. 1996 This plot is located 0.5 mile north of the Mahogany Hammock turnoff along Main Park Road within population B. The plot originally encompassed both sides of the road but now is only east of the road. This plot is dry throughout April and May and is dominated by sawgrass and muhly grass. In the summer of 1994, the back portion of this plot burned.

Alligator Hammock (AH) est. 1996 This plot is located along Main Park Road directly across from DL and SB within population B. Despite its proximity to DL, it is more densely covered in vegetation, and sawgrass is more common than muhly grass. The area floods earlier, and stays wet longer, than the plots on the east side of Main Park Road. The road itself acts as a levee, restricting water flow and forcing water to accumulate on its "upstream" side within this plot.

Far East (FE) est. 1997 This plot is located directly east of OIHN, along the north side of the Ingraham Highway and within population B. The two plots share a border. Despite its proximity to OIHN, this plot has less cover and vegetation is much sparser. Muhly grass and sawgrass with significant amounts of *Schizachyrium rhizomatum* dominate the plot. This plot is dry throughout April and May, and usually stays drier than either OIHN or OIHS.

Shark Valley (SV) est. 1997 This plot is located in population A, about 5 miles southwest of the Shark Valley Lookout Tower. This plot lies along the western border between Everglades National Park and Big Cypress National Preserve. This plot is by far the wettest, typically containing standing water in all months except April and May. The plot is dominated by sawgrass and contains no muhly grass.

Tomato Patch (TP) est. 1998 This plot is located in population E about 1 mile north of an old tomato field and 1 mile northeast of Context Road. The plot remains dry for several months of the year; it is the last of our study plots to hold standing water during the summer storms. Sawgrass and muhly grass dominate this plot, although it contains much *Schizachyrium rhizomatum*. This plot lies adjacent to the former (pre-1980s) eastern boundary of Everglades National Park and as such contains a mosaic of burn frequencies.

Chapter 3

Demography

3.1 Introduction

Policymakers have agreed upon the need to restore Everglades hydrologic patterns (Curnutt *et al.* 2000, Lockwood and Fenn 2000). The demography of the sparrow sits squarely within this debate. Since the sparrow is listed as federally endangered, the Endangered Species Act requires that current or proposed restoration water management plans do not jeopardize the bird's future. Through a detailed look at the sparrow's demography we can better define when harm is likely to occur.

Although previous work demonstrated sharp population declines, it was not clear what part of the sparrow's life history was being compromised. Water management decisions turn on the answers to questions such as (1) How long do Cape Sable Seaside Sparrows live? (2) How many young do they produce? (3) Over what time span do they breed? (4) How spatially independent are the six sparrow populations? This chapter answers those questions.

Panglossian critics of our work speculate that were these sparrows exceptionally long lived, then short-term flooding might not affect their long-term persistence. They could live long enough to enjoy the return of good conditions (Post and Greenlaw 2000). Alternatively, if they were exceptionally fecund, they might reproduce fast enough to recover any loss in numbers (Post and Greenlaw 2000). Susceptibility and recovery are also influenced by the sparrow's ability to escape from, or recolonize, sites previously made untenable. Even a question as simple as how high sparrows place their nests from the ground have profound implications for water management, because the answer determines the depth to which sparrow habitat may be flooded before the presence of water prohibits or halts breeding. We evaluate these claims.

3.2 Methods

We used resighting and recapture information to generate a survivorship estimate for male Cape Sable Seaside Sparrows using the Cormack-Jolly-Seber statistical model from program MARK (White and Burnham 1997). We caught females less frequently than males and thus excluded them from survivorship calculations. It is not possible to age adult birds based on plumage; thus we could not calculate age-specific survival rates for adults.

We collected nesting information following the methods outlined in Chapter 2. This information allowed us to estimate nesting success according to Mayfield techniques (Mayfield 1975). The Mayfield technique calculates the daily survival probability of a nest, avoiding the assumption that all nests found were actually observed through the entirety of the nest cycle. All nests from 1996 to 2000 are included.

Because we did not band adults at all the nests we monitored, it was not always possible to unambiguously identify second and third nesting attempts. Thus, we classified all nests with a hatch date before 1 June as "early season," and all nests with a hatch date after 1 June as "late season." This allowed us to determine differences in fecundity through time without relying on banding efforts. The first of June is also the approximate beginning of the summer rains (Olmstead *et al.* 1980). We compared Mayfield nest success rates, as well as the numbers of eggs and nestlings, between early and late season nests. We measured the distance from the top of the soil to bottom of the nest structure (to the nearest 1 cm) after the young fledged, and compared the average height of nests off the ground between the early and late season.

Based on the above parameter estimates and their associated variability, we performed simple demographic calculations. Our purpose was not to produce a detailed viability assessment (see Pimm and Bass 2001), but to understand which parameters most restrict population growth. We began by exploring a best-case scenario that uses our highest recorded demographic values. We then sequentially decreased each parameter to its lowest recorded value or to the mean minus one standard error. By comparing decreases in projected one-year population growth between scenarios, we identified which demographic trait produces the largest impacts on population growth. Since we cannot estimate juvenile survivorship from our records, we based our estimate on values of other small passerines (Ricklefs 1973).

Our calculations are as follows: We obtained the number of young produced per nesting attempt by multiplying the proportion of adults that bred by average clutch size discounted by the daily probability that the young will survive to fledging across the time taken to fledge (Mayfield score). We then divided this value by 2, to express productivity per individual. (A nest is the product of a pair of birds, obviously.) To obtain one-year population growth (X_1) we incorporated juvenile ($\mathrm{Juv_s}$) and adult survival ($\mathrm{Adult_s}$) rates in the following way:

$$X_{t+1} = (\mathrm{Adult_s} \times X_t) + (\mathrm{Juv_s} \times \text{individual productivity}).$$

Annual population growth is then expressed as

$$\text{Population growth} = X_{t+1} X_t.$$

$$\text{Population growth per individual} = (X_{t+1} X_t)/X_t.$$

3.3 Results

We banded 247 adult Cape Sable Seaside Sparrows from 1994 to 1998 inclusive, of which 188 (76%) were males. We recaptured or resighted 82 adults just once in subsequent years and 36 adults in two or more years following banding. One male, banded as an adult in 1994, was resighted in all following years, making it at least 6 years old. A female, banded in 1995 as an adult, was at least five years old. Of the 118 resighted adults, 93 (79%) were males.

A Cormack-Jolly-Seber model that assumes constant survivorship and recapture probability provided the best fit to our adult-male recapture data. This model estimated survival and recapture rates as 0.66 (S.E. = 0.06) and 0.65 (S.E. = 0.08), respectively. Thus, 66% of all adult males in our sampled population survive from one year to the next.

We found 329 Cape Sable Seaside Sparrow nests between 1996 and 2000. After 4 years of searching, we found 10 nests in population A. After 6 years of searching, we found 278 nests in population B; and after 3 years of searching, we found 39 nests in population E. Most nests (205) were early season. We found 89 late-season nests, and 34 could not be classified. Among the 10 nests in population A, only one (10%) was late season. Of the 264 classifiable nests in population B, 91 were late season (34%). Of the 35 nests in population E that could be classified, 7 were late season (20%).

Information from Chapter 2 yielded a per-annum clutch production of 2–4 under optimal conditions and under the assumption that a pair of birds is physiologically capable of this continued effort. Sparrows laid an average of 3.1 eggs per nest (S.D. = 0.7, $n = 160$). Clutch size did not vary between early and late season nests ($t = -0.7$, D.F. = 146, $p = 0.46$). Sparrows averaged 2.7 nestlings per nest (S.D. = 1.0, $n = 254$). This value did not vary between early and late season nests ($t = 1.7$, D.F. = 222, $p = 0.08$).

Mayfield nest success rates varied considerably from year to year. Nests found in 1998 showed the highest overall success rate, at 0.60. Nests found in 1999 showed the lowest success rate at 0.12. Comparing Mayfield nest success rates across populations showed that E had the highest success rate, at 0.46, whereas nest success in population A was only 0.13. Population B was the only group with enough information to divide these probabilities according to early versus late season. Early season population B nests had a success rate of 0.28, whereas late-season nests had a success rate of 0.11.

The average height of the nests (i.e., from soil surface to bottom of the nest structure) increased after the onset of summer rains in early June ($t = -4.516$, D.F. = 259, $p < 0.001$). Nests that hatched young before 1 June sat an average of 16 cm off the ground (S.D. = 6,

$n = 184$) whereas nests that hatched young after 1 June sat 20 cm off the ground (S.D. $= 7$, $n = 77$). Similarly, average nest height varied from year to year (ANOVA $F = 12.6$, D.F. $= 4$, $p < 0.001$). During the 1996 and 1997 breeding seasons, Cape Sable Seaside Sparrows built nests lower to the ground (16 and 15 cm, respectively) than during the 1998 and 1999 breeding seasons (21 and 19 cm, respectively). Sparrows placed their nests an average of 13 cm from the ground during the 2000 breeding season.

3.3.1 Demographic model

Any demographic model has to address two questions. The first is what fraction of the population is breeding. Previous work (Lockwood *et al.* 1997, Curnutt *et al.* 1998, Nott *et al.* 1998) showed that large fractions of some populations cannot breed each year because high water or other factors prevent them. The second question is how successful are the birds that do breed. It is this we now address, and we begin by exploring the best-case scenario.

We assumed all breeding individuals produce large clutches (3.8, the mean plus one standard deviation) and these clutches fledge equal to the maximum observed success rate, discounted over the length of time eggs and nestlings are in the nest (0.60). Further, we assumed late breeding attempts have the same clutch size and success rate as early attempts and that all breeding individuals that produce an early nest also produce a late nest. Finally, we assumed that adults have a high survival rate (0.72, the mean plus standard error) and that juveniles survive nearly as well as adults (0.50).

When we employed these parameters, we estimated a per-capita annual increase of 1.86; an 86% annual growth rate. (Table 3.1; second column from the left.) This is clearly unreasonably optimistic. It is unlikely that all individuals in every segment of the sparrow population would enjoy the conditions that would produce this annual rate of increase. Even under this wildly optimistic scenario, however, the sparrow population will not double in one year.

Next, we changed each variable in turn to its lowest recorded value and recalculated annual growth rate. When we changed adult survivorship to the mean minus one standard error, per-capita annual increase was 1.74, 12% below the unreasonably optimistic scenario of 1.86. Changing clutch size to its lowest recorded level resulted in per-capita annual increase of 1.44, a 42% decline in annual growth rate from the optimistic scenario. Reducing juvenile annual survivorship rates to a value more typical of small landbirds (30%; Ricklefs 1973) resulted in a per-capita annual increase of 1.47; a 39% decline in annual population growth as compared to the optimistic scenario.

Changing the frequency of late-season nesting attempts to their lowest observed value (9% in population A) resulted in a per-capita annual increase of 1.34; a value that is nearly a third of the growth rate under the optimistic scenario.

Table 3.1: (a) Estimates of Cape Sable Seaside Sparrow population growth derived from demographic modeling of six scenarios. All population parameters derive from field observations except juvenile survivorship, which follows Ricklefs (1973). (b) Actual population growth observed in three populations. Cells in boldface indicate the demographic attribute altered under each scenario.

Scenario	Popn. growth per individual	Clutch size	Adult survival	Juvenile survival	Nest success	Late breeders (% of popn.)
(a)						
Optimistic	1.86	3.80	0.72	0.50	0.60	100
Low adult survival	1.74	3.80	**0.60**	0.50	0.60	100
Low juvenile survival	1.47	3.80	0.72	**0.33**	0.60	100
Low clutch size	1.44	**2.40**	0.72	0.50	0.60	100
Few late breeders	1.34	3.80	0.72	0.50	0.60	**9**
Low nest success	0.97	3.80	0.72	0.50	**0.13**	100
(b)						
Population A	0.77	3.10	0.66	0.50	**0.13**	**10**
Population B	0.95	3.10	0.66	0.50	**0.28**	**33**
Population E	1.11	3.10	0.66	0.50	**0.46**	**27**

Negative annual growth rates only occurred when nest success rates were set to levels observed in population A. This change, from 0.60 to 0.13, resulted in a per-capita annual increase of 0.97. This is equivalent to a 3% decline in numbers of sparrows each year.

Obviously annual growth rates will become more realistic (and less optimistic) as we incorporate observed demographic parameters. If our model is robust, when we insert the observed values for each population, we should obtain annual growth rates that broadly match the observed population trajectories (see Chapter 5). Encouragingly, they did. When we used the demographic parameters described here for population B, we estimated an annual growth rate of -0.05%, essentially zero. This is consistent with annual population estimates showing static numbers in population B since 1981. Population E has increased in individuals since 1997, and accordingly we predicted an annual growth rate of 11% using demographic data collected since 1998. Population A declined by more than 90% between 1992 and 1993 and has not recovered since. Using demographic data collected since 1997, we obtained an annual growth rate of -23%, suggesting this population may continue to decline.

3.4 Discussion

Cape Sable Seaside Sparrows appear sedentary and are extremely faithful to particular breeding locations. Sparrows do not regularly move more than 1 km (see Chapter 2). Thus, the various populations likely do not "trade" immigrants such that one could be the source for another in decline (i.e., a sink; Pulliam 1998) as has been suggested by Post and Greenlaw (2000). This does not rule out the possibility of occasional long-range movements as observed by Dean and Morrison (1998). We currently have no comparable radio-telemetry information on juveniles, and none from populations that have experienced unusually high water events (such as population A) or recent fires. These conditions may increase the likelihood of long-range dispersal if the resident population has not already established breeding territories. The results of Werner (1975) and Lockwood *et al.* (1997) indicate that after territories are established, adult sparrows do not leave their territories, even if their nests are flooded or habitat is burned. Thus, we suggest the future of the sparrow will play out in several smaller arenas — the populations — with the fate of each determined largely independently of the others. Also, we cannot safely assume that sparrows will escape temporarily adverse conditions through immigration until evidence linking unusual events (i.e., fire or flood) to long-range movement is produced.

Very few sparrows live past 3 years of age and, based on survival estimates, about 40% of the population dies each year. These estimates are typical of small landbirds (Ricklefs 1973, Perrins and Birkhead 1983) and other races of Seaside Sparrows (Post and Greenlaw 1994). We were restricted to calculating survivorship for adult males only. Adult males typically show higher survival rates than females and juveniles (Bulmer and Perrins 1973, Ricklefs 1973), and thus this estimate can tentatively be considered a maximum rate among all population segments. It is still desirable to estimate juvenile and female survival rates, as their chances of mortality may be considerably higher than adult males and represent a particularly vulnerable segment of the sparrow's life history. Furthermore, continuing with mark-recapture studies within populations such as A may reveal spatial differences in survival rate related to water flows. Such detailed information could inform refined population viability analyses and efforts to model the fate of the sparrow under various restoration options (Curnutt *et al.* 2000).

Although survivorship, dispersal, and low clutch sizes clearly influence the future of the sparrow, impacts on nesting success seem to drive population declines. Cape Sable Seaside Sparrow fecundity reached its maximum potential early in the breeding season (March to June). Some sparrows can breed well into the wet season, allowing recovery from population declines. However, in order to realize this potential, most pairs of sparrows in the population must breed at least twice, and most nests must be successful, including the late-season nests. Sparrows produce only 2–3 young per nesting attempt. If most annual nesting attempts fail (e.g., within population A) or only early season nests are successful (e.g., within population B), any young produced will replace breeding adults but population levels will not rise. In practice, population levels may decline due to the low survivorship of juveniles. Under the best conditions we have observed (i.e., population E growing at a rate of 21% annually), it would take more than four years for population size to double.

The above discussion outlines the more subtle effects of altered water flow on sparrow fecundity. All races of Seaside Sparrow incur the blunt effects of periodic high water. Unusually high tides cause mass loss of active nests in other races of Seaside Sparrows (Marshall and Reinert 1990). Since Cape Sable Seaside Sparrows exist within a nontidal ecosystem, nesting success is influenced by annual variation in the summer rains and management decisions regarding water releases (Nott *et al.* 1998).

The height of nests from the ground varies through the breeding season and from year to year. This variation blurs exact predictions of whether water levels will cause the widespread loss of active nests. However, we can make general predictions. The highest recorded average height of nests off the ground was 21 cm (late season nest average). If we add one standard deviation to this value, we can estimate that at locations where water levels rise above 29 cm during the nesting season, nearly 70% of all active Cape Sable Seaside Sparrow nests will flood and fail. The fate of the other nests not completely inundated is hardly likely to be favorable.

Together, these demographic traits make the Cape Sable Seaside Sparrow extremely dependent on the hydrologic patterns of marl prairies. Relatively short-term excesses of water can have long-lasting impacts, especially if impacts are experienced within two or more successive breeding seasons. Most resident sparrows will have died after three years of initial impact, and if there are very few or no successful nesting attempts during this period, the affected population will inevitably decline sharply. Once sparrow numbers are driven low, recovery is relatively slow. At the very best, a population can be expected to double in four years. Further, managers cannot rely on emigration from adjacent populations to rescue the affected population. If proposed restoration schemes are to truly benefit the ecosystem, they must abide by the demographic constraints constituent species such as the Cape Sable Seaside Sparrow impose.

Chapter 4

Habitat Selection

4.1 Introduction

Determining habitat use and selection in birds has a long tradition, beginning with the seminal studies of Grinnell (1917). Habitat can be thought of as "a distinctive set of physical environmental factors that a species uses for its survival and reproduction" (Jones 2001). The topic is central to understanding the ecological and evolutionary forces that determine how species are distributed across a landscape. Habitat selection studies took on an entirely new emphasis with the passing of the Endangered Species Act of 1973, and especially after the U.S. Supreme Court decision in *Sweet Home vs. Babbitt*. These decisions transformed habitat selection studies from a purely intellectual pursuit to a fundamental step in preserving biological diversity. In essence, the destruction of habitat is now equivalent to taking individuals of federally protected species, an act that is expressly forbidden by law. Because of this, it is paramount that investigations into the habitat selections of such species be carefully documented and interpreted. With this in mind, we review what is known about Cape Sable Seaside Sparrow habitat selection. We then present results from our investigations into how sparrows select habitat within population B. We conclude by discussing how this information informs management decisions.

It is important to better define habitat selection, especially as it compares to habitat use. Habitat use refers to how an individual uses environmental factors to meet its basic reproductive and maintenance needs (Jones 2001). Habitat selection refers to a hierarchical process by which an individual chooses habitats that maximize its survival and reproduction (Johnson 1980). These differences in fitness consequences cause certain habitats to be used disproportionate to their availability (i.e., they are selected). In a legal sense, the phenomenon of habitat selection implies that some habitat types are better than others at sustaining populations, and if recovery goals are to be met, these "good" habitats require strong protection.

There are at least four spatial scales at which birds may select habitat (*sensu* Johnson 1980). The decisions made by individuals at one spatial scale constrain the set of decisions they can make at a lower scale. For example, an individual's choice of a territory constrains the space within which it may place its nest. Johnson (1980) defined first-order selection as the physical or geographical range of a species. Understanding first-order habitat selection of endangered species is the basis for delineating critical habitat under the Endangered Species Act. Critical habitat has already been determined for the Cape Sable Seaside Sparrow, although it is in need of update (USFWS 1998). Chapters 6 and 7 update the present extent of critical habitat and document detrimental changes to it. The remaining selection scales thus far have not entered into interpretation of the Endangered Species Act, despite their relevance to assuring population persistence. Second-order selection criteria determine the breeding territory (or nonbreeding-season home range) of an individual. Third-order selection involves decisions made within the territory, such as selection of the nest or foraging site. The following results and discussion pertain to second- and third-order selections.

4.2 What habitat is available to Cape Sable Seaside Sparrows?

When looking for habitat selection criteria among birds, comparison between used and available habitats is a more powerful analysis than describing used habitat alone (Jones 2001). Available habitat includes all habitat types within a defined area, including habitats currently in use (Jones 2001). The initial difficulty in such studies is determining the habitat types and areas that are accessible and procurable to focal individuals. Defining available habitat as simply the proportional representation of various habitat types makes the assumption that all such areas are equally available (Wiens 1973, Martin and Roper 1988). As Johnson (1980) described, there is also a concern over the spatial scale within which to define available habitat. If individuals do not regularly explore large areas in their lifetime, measuring available habitat at landscape scales can tell us nothing of interest about habitat selection. Without attention to the life history of the species, it is possible to define habitat as "available" when it is actually unavailable to any one individual and thus can play no role in maximizing their demographic rates.

In what follows, we review existing literature to better define the spatial scale within which sparrows choose breeding habitat. We also narrow the range of habitats that sparrows can reasonably procure and use. In so doing, it becomes clear where habitat selection studies should begin and how the Cape Sable Seaside Sparrow's habitat options compare to other Seaside Sparrow races.

Cape Sable Seaside Sparrows do not explore much of the area surrounding their place of hatching. Adults, once settled, tend to stay within the same area for the duration of their lives (Dean and Morrison 2001, Lockwood *et al.* 2001). Breeding-season territories average

2 ha in extent. During the nonbreeding season, adults explore from 5–50 ha (mean 17 ha; Dean and Morrison 2001). Juveniles may explore more area than adults (Lockwood *et al.* 2001). However, evidence collected thus far indicates they settle within 3 km of their natal site. Thus, the area over which the average Cape Sable Seaside Sparrow travels in its lifetime is well under 50 ha. It is within this 50-ha area that an individual must make decisions that influence its survival and its probability of reproducing. Thus, it is within this area that we should concentrate our efforts at defining habitat selection criteria.

Not only are individual Cape Sable Seaside Sparrows limited in the spatial extent over which they can select habitat, the range of habitat options appears small as well. Sparrows remain exclusively within marl prairies for the entirety of their life cycle (Werner and Woolfenden 1983, Lockwood *et al.* 1997, Dean and Morrison 2001). They do not cross forested areas and they do not venture into the interiors of tree islands. This is true despite the fact that each of these habitat types typically lie adjacent to, or imbedded within, marl prairies. Tree islands clearly could be used during any period of the sparrow's life cycle, as they are scattered liberally within the 50 ha an individual sparrow may explore in its lifetime. Instead, sparrows base their existence on the habitat provided by grasses, sedges, and small shrubs typical of marl prairies. Sparrows only nest within the grass layer of these prairies (Werner 1975, Lockwood *et al.* 2001) and generally avoid placing their nests near bushes (Chapter 7).

The range of habitat options within marl prairies appears smaller than for other races of Seaside Sparrows. The other extant races are restricted to intertidal fringe marshes along the Atlantic Ocean and eastern Gulf of Mexico (Post and Greenlaw 1994). These marshes are characterized by a mosaic of mudflats, tidal creeks, and patches of marsh vegetation. These vegetation patches differ from one another in species composition. For example, in Massachusetts and New York, Seaside Sparrows have the option of establishing territories (and thus nesting) within relatively extensive (> 10 m) stands of *Juncus gerardi*, *Spartina patens*, or *S. alterniflora* (Greenlaw and Post 1985, Marshall and Reinert 1990). These individuals often select suitable foraging substrate within the tidal creeks that bisect these vegetation patches (Marshall and Reinert 1990).

There are no such vegetation patches, nor are there tidal creeks or mudflats, within Everglades marl prairies. Marl prairies are characterized by their plant species diversity rather than the dominance of a few species typical of tidally influenced marshes. Researchers often find more than 10 plant species per m^2 (Olmstead and Armentano 1997, Ross *et al.* 2001) in marl prairies. The majority of plant species are short (< 1 m tall) and sparsely distributed. This configuration creates open space near the base of the vegetation, especially around plant species that grow in bunches. Instead of mudflats, this is the space Cape Sable Seaside Sparrows use for foraging.

Although sawgrass (*Cladium jamaicense*) is numerically the most common plant species within marl prairies, dense stands of sawgrass only occur in small (< 5 m^2) clusters (Dean and Morrison 2001). These sawgrass clusters are produced by fine-scale topographic relief. Sawgrass grows taller and denser than other plants only within relatively deep topographic pockets typically created through the differential erosion of exposed limestone bedrock (i.e., solution holes). These dense clusters of sawgrass occasionally support a sparrow nest, but they are never large enough to encompass more than 5–10% of an individual's territory.

All remaining differences in habitat are due to the presence of tree islands and pine forests, habitat types that are unavailable to sparrows (Werner 1975, Kushlan and Bass 1983, Dean and Morrison 2001, Chapter 7). Thus, individual sparrows must decide where to place their breeding territory, and subsequently their nests and foraging locations, within this relatively homogeneous landscape.

In sum, individual Cape Sable Seaside Sparrows make decisions based on the limited habitat that is available to them. These limits are naturally imposed by the evolutionary history of the subspecies, and thus we should expect a range of behavioral responses that reflect these restrictions. Modification of habitat selection options, and fundamental alteration in available habitat, represent significant threats to the subspecies' continued survival. These alterations may be manifest at larger scales ($>$ 10 km; e.g., Chapters 6, 7 and 8); however they are mechanistically driven by changes at this small spatial scale ($<$ 50 ha).

4.3 Determining criteria for occupancy

Individual Cape Sable Seaside Sparrows appear to decide where to settle within their first 6 months out of the nest (Dean and Morrison 2001; Chapter 2). These young sparrows move over several kilometers as members of small flocks (Chapter 2). Their initial challenge is to locate habitat that is suitable for occupancy. What cues do sparrows use in making this decision? Habitat characteristics, such as plant biomass and floristic composition, often play a role in such decisions (Morrison *et al.* 1998). Thus, our first investigation into habitat selection endeavored to identify differences in habitat variables between occupied and unoccupied sites.

4.3.1 Plants

In 1995 we conducted plant surveys in two unoccupied sites, Taylor Slough (TS) and Finger Glade (FG), and in three occupied sites, Old Ingraham Highway South (OIHS), Dogleg (DL), and Sweetbay (SB). In each occupied site, eight quadrats were randomly set in the vicinity of a territory-holding male. Within unoccupied sites, eight quadrats were randomly placed.

The percent coverage of the dominant plant species was determined, and five soil samples were taken (one at each corner of the 1-m^2 quadrat and one from the middle). All live and aboveground vegetation, as well as all dead material above the periphyton mat, was removed. All live material was sorted to species, and the stem density (number of stems or bundles per quadrat) of each species was counted. We also measured the maximum and average height of all graminoids. Finally, we dried and weighed all species

Table 4.1: Summary of 1995 plant survey results. [a]Total dry biomass of live and dead plant material. [b]Percentages of live and dead material relative to total material. [c]Percentages of live muhly grass, live sawgrass, and all other live plant species, relative to total material.

	Unoccupied		Occupied		
	FG	TS	OIHS	DL	SB
Total material (g)[a]	445	260	798	696	679
Live (%)[b]	25	45	23	26	26
Muhly grass (%)[c]	9	14	14	13	10
Sawgrass (%)[c]	14	31	2	7	6
Other (%)[c]	2	0	7	6	10
Dead (%)[b]	75	55	77	74	74

bundles and dead biomass to the nearest tenth of a gram. All species were identified using sources from the Everglades National Park museum.

We tested for differences among the floral composition of each of the sites by ranking each species by its frequency of occurrence in the combined eight sample quadrats. We then compared the ranks from all sites with each other using Hoefding's nonparametric rank correlation. This method results in a D-statistic, ranging from -1.0 to 1.0; as values approach 1.0 the data are more related and vice versa.

Sites occupied by birds were not different from each other in the frequency dominance of plant species. Conversely, TS (an unoccupied plot) exhibited a significantly different pattern from each of the occupied sites. FG, the other unoccupied plot, was similar in frequency dominance to two of the occupied sites (DL and OIHS) but was different from SB (occupied) and TS (unoccupied).

Finally, we examined the relative contribution of muhly grass (*Muhlenbergia filipes*), sawgrass, and other plant species (combined) to overall biomass and compared occupied and unoccupied sites (Table 4.1). The proportions of muhly grass and sawgrass differed considerably (two tailed t-test, $p < 0.05$). In the occupied sites, muhly grass was the dominant species in terms of biomass, and sawgrass was the second most dominant. For unoccupied sites (TS and FG), this relationship was reversed.

In 1996, we resampled these same sites. In addition to TS, we included a portion of the North Mahogany plot (NM) that burned in 1994 to represent an unoccupied plot and a separate, unburned portion as an occupied plot. We did not resample FG. We added OIHN and Alligator Hammock (AH) to our survey as occupied sites.

A summary of results is presented in Table 4.2. Unburned NM and TS had equal proportions of sawgrass, both of which were much higher than in the other sites. The Old Ingraham sites had the highest plant species richness and also had the highest proportion of "other" species biomass.

Table 4.2: Summary of 1996 plant survey results. [a]Total dry biomass of live and dead plant material. [b]Percentages of live and dead material relative to total material. [c]Percentages of live muhly grass, live sawgrass, and all other live plant species, relative to total material.

	Unoccupied		Occupied					
	NM (burned)	TS	NM (unburned)	OIHS	OIHN	DL	SB	AH
Total material (g)[a]	123	202	144	251	154	236	147	236
Live (%)[b]	43	42	56	70	69	41	37	43
Muhly grass (%)[c]	14	9	5	9	17	8	16	7
Sawgrass (%)[c]	7	24	33	12	11	10	13	9
Other (%)[c]	22	9	18	49	41	23	8	27
Dead (%)[b]	57	58	44	30	31	59	63	57
No. of species	3	5	5	11	7	5	3	6

Taylor (1983) found that dead biomass and total biomass has an effect on sparrow presence. His results suggest that areas with 550 g/m^2 of dead biomass and 700 g/m^2 total biomass or higher are not occupied by sparrows. We found no such effect in our results, although our sampling methods were identical. TS and NM (burned), both unoccupied, did not significantly differ from occupied sites in either total biomass, dead biomass, or proportion of dead biomass. In fact, among the 1996 comparisons, few vegetation characteristics of the sites seemed correlated with sparrow occupation. Only one variable was at least marginally correlated with sparrow occupancy. Higher plant species richness occurred in the occupied sites. Both unoccupied sites (TS and burned NM) had low plant species richness and plant species diversity. However, no other microhabitat variable (such as soil depth or proportion of dead biomass) demonstrated a correlation with sparrow presence.

We found little change in most vegetation characteristics between 1995 and 1996. However, we did detect a change in proportion of live biomass within TS. This site had a large reduction in the proportion of live plant biomass (from 45% in 1995 to 26% in 1996).

4.3.2 Arthropods

In 1996, we used sweep nets to collect arthropods (primarily insects and spiders) from transects in the same set of occupied and unoccupied sites. We started sampling early in the mornings, immediately after dew had evaporated from the vegetation. Four 150-m transects were established in TS, DL, SB, AH, and OIHS and OIHN. On alternate weeks, an area of approximately 40 m^2 was sampled. Two sweep transects totaling 250 sweeps were conducted. One transect was oriented north-south comprising 60 sweeps north, 5 sweeps

Table 4.3: Ranked proportions of biomass of arthropod orders collected by sweep netting at six sites. Taylor Slough (TS) was unoccupied; all other sites were occupied by sparrows.

Arthropod order	OIHS	DL	AH	OIHN	SB	TS
Araneae	1	1	1	1	1	2
Orthoptera	2	2	5	3	3	1
Diptera	3	3	2	2	2	3
Coleoptera	4	5	3	4	5	4
Lepidoptera	5	6	4	6	4	6
Homoptera	6	4	6	5	6	5
Hymenoptera	7	7	7	7	7	7

east, and 60 sweeps south. An east-west transect was performed in a similar manner. For occupied sites (all but TS), we placed our transects near known territories.

We kept all samples separated in plastic bags in an iced cooler until they were sorted. We sorted the samples within 4 hr after collection. First, we separated the invertebrates from the frass. We then killed and fixed all arthropods in formalin vapor. The samples were sorted by order, counted, and weighed (wet biomass). We stored the samples in 70% alcohol for future reference. Our arthropod collection is stored in the Everglades National Park museum.

We present relative biomass for each order by plot in Table 4.3. This table shows the average proportional biomass of the seven most common orders, averaged over March through July 1996 sweep samples. Clearly, spiders, crickets and grasshoppers, and flies constituted most of the arthropod biomass. Beetles also contributed substantially. Arthropod abundances were highly variable over time for all orders.

Most sites had a high proportion of spiders (Order Araneae) and orthopterans (crickets and grasshoppers). All sites occupied by sparrows (OIHS, DL, AH, OIHN, and SB) had similar arthropod order compositions. However, data from the unoccupied plot (TS) demonstrated a paucity of Araneae (spiders), which were a relatively common food item for the sparrow (see Chapter 2). Instead, Orthoptera and Diptera dominated the arthropods collected from TS. Similarly, arthropod diversity appeared unrelated to occupancy by sparrows. Old Ingraham Highway South ($D = 3.85$) supported many breeding territories, while Taylor Slough supported none ($D = 4.37$). We express these results with several caveats:

- Large but rare orders of arthropods can bias the trends in proportional biomass.

- Highly aggregated orders of arthropods, whether due to social behavior or hatching young in large numbers, can bias both abundance and proportional biomass trends.

- Highly mobile orders, such as adult Lepidoptera and Odonata, can be underrepresented due to our sampling techniques (which may not be fast enough to catch them).

- Ground- and soil-dwelling arthropods can be underrepresented, as our sampling technique sweeps only aboveground vegetation.

4.3.3 Summary

In summary, there are few floristic differences between sites that are occupied by sparrows versus those that are not. Instead, the differences relate to the relative dominance of muhly grass versus sawgrass and overall species richness. Sites that are not occupied by sparrows tend to be dominated by sawgrass and be species poor, whereas sites that are occupied tend to be dominated by muhly grass and species rich. There is some evidence to suggest these two factors are related, such that sawgrass dominance precludes the establishment of a variety of other plant species (Olmstead and Armentano 1997, Ross *et al.* 2001).

This shift in dominance does not appear to translate into differences in total biomass or to live-to-dead biomass ratios. This latter result contradicts the work of Taylor (1983) and suggests his results may only apply to circumstances within the Taylor Slough plot before water flows were altered there by the addition of a pumping station (see Chapter 6 for more details on this transition).

Finally, the differences we detected in plant dominance between occupied versus unoccupied sites do not appear to translate into a difference in the arthropod fauna. The possible exception is the reduction in spider abundance at the Taylor Slough plot. However, our efforts at determining differences in arthropod fauna between sites are rudimentary. Given the nature of arthropod sampling, and of arthropod populations, a much broader effort will be required if such information is deemed noteworthy.

4.4 Determining criteria for territory placement

Once sparrows determine the suitability of a habitat for breeding, they must decide the location of their territory. This decision is of considerable importance to a male's survival and reproductive success. His territory must be of high enough quality to attract a mate. This territory will also hold the nest and provide all food resources for himself, his mate, and their young. To investigate the role that habitat may play in territory placement, we compared plant data collected inside and outside active sparrow territories in 1996. Our plant sampling methods were identical to those from above.

We found no differences in any of the variables examined. We compared the total dead and live plant material biomass, the proportion of live biomass, and the proportion of the biomass represented by muhly grass, sawgrass, and all other species. All were the

Table 4.4: Plant biomass percentage comparisons for four 1-m^2 quadrats inside and four quadrats outside territories of Cape Sable Seaside Sparrows. [a]Total dry biomass of live and dead plant material. [b]Percentages of live and dead material relative to total material. [c]Percentages of live muhly grass, live sawgrass, and all other live plant species, relative to total material.

	OIHS		DL		SB		Mean	
	In	Out	In	Out	In	Out	In	Out
Total material (g)[a]	288	496	385	311	347	331	366	379
Live (%)[b]	28	21	27	26	26	27	27	25
Muhly grass (%)[c]	17	13	15	12	10	9	14	12
Sawgrass (%)[c]	3	2	6	8	8	6	6	5
Other (%)[c]	8	6	6	6	8	12	7	8
Dead (%)[b]	72	79	73	74	74	73	73	75

same for quadrats inside and quadrats outside territories in OIHS, DL, and SB sites. These data are shown in Table 4.4.

In the process of collecting this information it became obvious that our distinction between "inside" and "outside" a territory was arbitrary from the sparrow's perspective. Adult male sparrows will pack any suitable habitat such that there are very few spaces that are not claimed by some individual. Thus, the plant information collected outside of one individual's territory was very likely inside an adjacent territory. Given this situation, it is not surprising that we could not detect differences within our data.

The sites included in this analysis were chosen for general study precisely because they held high numbers of individuals. Assuming sparrows distribute themselves according to habitat quality, these sites represent the best locations for breeding and survival. Sites that are less dense, and thus we assume of lower quality, may contain spaces that are clearly not desirable. It is within these lower density sites that we may learn more about how individual sparrows select sites for their territories from the array of available habitats.

It is also possible that sparrows select territory locations based on factors other than habitat characteristics. For example, sparrows staunchly defend their territories throughout the breeding season (Chapter 2). One sparrow's choice of territorial boundaries is likely constrained by interactions with its neighbor. This competition for space may override any relationship between territorial boundaries and vegetation components.

4.5 Determining criteria for nest placement

In contrast to the difficulty in determining territory placement criteria, determining what cues sparrows use in placing their nest is a more manageable endeavor. Once the territory is established, any location within that territory is available to the pair for nest construction. (Territories very rarely contain any habitat other than marl prairie grasses and sedges.) Given the prevalence of nest loss due to predators and seasonal flooding (see Chapters 2 and 3), nest placement should play a large role in the chances the pair will fledge young. In order to document these nest placement criteria, we collected microhabitat variables around 74 sparrow nests and compared them to random points within their associated territories. All nests included in this analysis were located within population B.

Between 1997 and 1999, we measured vegetation characteristics within 1-m^2 quadrats placed at two locations. Several days after fledging or failure, we took measurements at five 1-m^2 quadrats placed around the nest site. As an indication of available, but unused, habitat, we took measurements at random sites located from 5 to 50 m from each nest. We selected a cardinal direction and three numbers between 5 and 50 from a random number table. We used these numbers to guide us to a point within 50 m of each nest site.

Within each quadrat, we identified and recorded percent cover of all live vegetation following the Braun-Blanquet scale (Bullock 1996). We recorded the percent cover of litter using the same scale. We also recorded structural microhabitat variables. Effective cover and maximum vegetation height were measured to the nearest cm. The former we estimated by placing a PVC pole upright from the ground and through the vegetation layer. The upper limit of effective cover was measured as the maximum height at which 5% of the pole was visible. This crudely estimates the degree of camouflage and shelter a habitat provides (Wiens 1973).

Since O'Meara and Marion (1985) suggest that the presence of vegetative clumps characterize Cape Sable Seaside Sparrow nesting habitat, we included a measure of the degree of vegetative clumping. This was done by creating an ordinal scale based on the O'Meara and Marion (1985) definition of clumps (i.e., bunchgrass-type growth form with a basal diameter of > 5 cm). This scale included four categories: (1) vegetation present as all single stems, with no clumps; (2) vegetation present with mostly single stems, and a few clumps; (3) vegetation present as mostly clumps, with few single stems; (4) vegetation present as all clumps, with no single stems.

We found 7–10 plant species per nest-site quadrat. A list of all species found appears in Table 4.5. We identified four dominant species (i.e., species that consistently ranked highest in cover class), and only these comprise the following statistical comparisons. These species were sawgrass, muhly grass, *Rhynchospora* spp., and *Schizachyrium rhizomatum*.

We used logistic regression to determine the principal habitat differences between nests and random sites. We began by fitting an equation for the full model (i.e., one including all independent variables). The variable that had the lowest χ^2 value according to the

Table 4.5: Plant species found at 74 sparrow nest sites found within population B.

Agalinis purpurea	*Muhlenbergia filipes*
Aster tenuifolius	*Oxypolis filiformis*
Calopogon tuberosus	*Panicum* spp. (*tenerum* or *virgatum*)
Centella asiatica	*Persea borbonia*
Cladium jamaicense	*Piriqueta caroliniana*
Crinum americanum	*Pluchea rosea*
Cuscuta campestris	*Polygala grandiflora*
Dichromena colorata	*Rhynchospora tracyi*
Eleocharis cellulosa	*Rhynchospora microcarpa*
Helenium pinnatifidum	*Sabatia grandiflora*
Hymenocallis palmeri	*Sagittaria lancifolia*
Ipomoea sagittata	*Schizachyrium rhizomatum*
Iva microcephala	*Schoenus nigricans*
Linum spp.	*Setaria geniculata*
Magnolia virginiana	*Solidago stricta*
Mikania scandens	*Taxodium distichum*

logistic likelihood-ratio test was deleted, and a new equation was fitted (Zar 1999). This backward elimination of variables proceeded until only significant variables remained. We choose to set $\alpha = 0.10$ in order to avoid removing variables that contributed to the explanatory power of the final model (Hosmer and Lemeshow 2000). Whole-model fit was evaluated using a maximum likelihood ratio test (SAS 1998). The ability of the model to discriminate between the two outcomes was judged using a logistic classification table. This procedure utilized the final model to back-classify each quadrat as located at a random site or at a nest site. If the model is accurate, it should categorize nests correctly at a suitably high rate ($\sim$ 70% or more).

The final model included six habitat variables, thus indicating that sparrows place their nests in very specific locations within a territory (Table 4.6). Three of these variables relate to habitat structure. Maximum vegetation height, effective vegetation height, and percent litter cover were all higher at the nest site than at the random sites. The remaining three significant variables relate to floristic features. The percent cover of muhly grass, *Rhynchospora* spp., and *Schizachyrium rhizomatum* were higher at nest sites than at random sites. The final model correctly classified 69% of the quadrats. The model was equally successful at classifying random sites (68%) and nest sites (70%). None of these variables showed colinearity (defined as correlation coefficients > 0.80, SAS 1998).

In sum, the Cape Sable Seaside Sparrow shows a preference for nest sites that provide specific vegetative characteristics. Nests are selectively placed where effective cover

Table 4.6: Mean values (std. dev.) for habitat variables that differed between nest and random sites, as identified by logistic regression.

Variable	Nest	Random
Maximum vegetation height (cm)	11.2 (2.8)	10.6 (2.6)
Effective vegetation height (cm)	20.7 (1.4)	22.0 (1.5)
Coverage litter (%)	25–50	10–25
Coverage muhly grass (%)	10–25	5–10
Coverage *Rhynchospora* spp. (%)	5–10	1–5
Coverage *Schizachyrium rhizomatum* (%)	10–25	5–10

is twice as high and perches are 3 to 4 cm higher than elsewhere in the territory. Nests are built where litter cover is moderately high (25–50%). The presence of particular grasses such as muhly, *Rhynchospora* spp., and *S. rhizomatum* also appear to be cues for nest placement.

4.6 Consequences of habitat selection

It is important to take the second step in this research and attach meaning to the differences observed in the above analyses. After all, the relevance of these selected habitat characteristics lies in their ability to determine population fluctuations. If the differences we have observed have little effect on sparrow survival or reproduction, then they are not relevant to managers or to the realization of recovery goals. A standard procedure for determining the consequences of selecting habitat variables is to regress them against indices such as nest success rates, adult density, and nest fate (Morrison *et al.* 1998, Jones 2001).

The above analyses suggest that maximum and effective vegetation heights, and the percent coverage of muhly grass, sawgrass, litter, *Rhynchospora* spp., and *S. rhizomatum* all play a role in a sparrow's habitat selection. Our first analyses sought to explain between-plot differences in nest success rates and density using these habitat variables.

Our early habitat sampling methods did not adequately sample each plot, and they did not coincide with the vast majority of information on density and nest success rates. Thus, we used the information collected from all quadrats in the nest selection study as plot-level habitat quality information. A visual inspection of the location of these quadrats confirms that they systematically and completely cover each study plot (see Table 4.7 for sample sizes).

We averaged maximum and effective heights across all quadrats within a plot to produce one value for each plot. Similarly, we averaged the percent cover scores for muhly grass, sawgrass, and litter to produce one value for each plot. The percent coverage of *Rhynchospora* spp. and *S. rhizomatum* was too sparse across the entire plot to be informa-

Table 4.7: Per-plot values of fitness and habitat variables entered into multiple regression equations. Also shown are the number of sample quadrats used to derive per-plot habitat variable means. [a]Variables that entered significantly into explanatory model for sparrow density.

Variable	DL	FE	OIHN	OIHS	NM	SB
Mayfield success (1996–99)	0.33	0.23	0.34	0.20	0.54	0.36
Average adults per plot (1996–99)	9.0	11.0	11.3	11.0	7.3	7.0
Mean maximum vegetation height (cm)[a]	11.2	10.4	11.7	11.3	10.9	10.4
Mean effective vegetation height (cm)	2.3	2.3	2.7	2.7	1.5	2.2
Mean % coverage of sawgrass	2.0	1.5	2.1	1.7	2.4	1.8
Mean % coverage of muhly grass[a]	1.6	1.7	1.8	2.3	1.8	2.3
Mean % coverage of litter[a]	3.0	2.7	3.2	3.4	3.4	3.7
Number of sample quadrats	125	155	150	120	40	75

tive. Because all sites within population B are near one another, they have experienced approximately the same flooding and fire patterns, which are potential confounding effects on nest success and density (see Chapter 3).

We calculated nest success rates per plot using the Mayfield method (for details, see Chapter 3). For this analysis, Mayfield scores were computed using all nests found before 1 June (i.e., early season) during the 1996 to 1999 breeding seasons. We estimated adult density for each plot using banding and resighting information spanning this same period. Because the Alligator Hammock plot varied in its dimensions between years, making density estimates difficult, we excluded this plot from the following analyses. We chose the time span over which to calculate nest success and adult density to match the period over which we measured the habitat variables.

We performed two multiple regressions with male density and Mayfield nest success scores as the dependent variables and the per-plot habitat variables as independent variables. Following the recommendations of Zar (1999), model selection proceeded in a backward stepwise manner. A multiple regression equation was fitted to the full model (i.e., a model with all independent variables included). Using t-tests for each partial regression coefficient, we examined whether each variable had a slope that was significantly different from zero. The habitat variable showing the lowest absolute value of t was then removed, and a new multiple regression equation was fitted. This procedure was repeated until all included variables showed statistical significance at the $\alpha = 0.10$ level.

None of the independent variables successfully explained Mayfield success scores. However, percentage cover of muhly grass and litter and maximum vegetation height were included in the final explanatory model for male sparrow density (ANOVA $F = 21$, D.F. $=$ 5, $p = 0.04$). The model explained almost all the variance in density between sites ($r^2 =$

0.97). Sparrow density increased with an increase in percent coverage of muhly grass and an increase in maximum vegetation height. Sparrow density decreased with an increase in percent litter coverage.

In our second analysis, we used habitat variables quantified at the nest sites as potential explanatory agents for nest fate. The fate of an individual's nest reflects the fitness consequences of nest site selection (Jones 2001). Because nest fate is a binary variable (i.e., either successful or failed), we used a logistic regression in this analysis. We collated the fate of early-season nests monitored between 1996 and 1999. As above, we only used nests found within population B; however in this analysis we included Alligator Hammock nests. We included as independent variables percent coverage of muhly grass, sawgrass, litter, *Rhynchospora* spp., and *S. rhizomatum*; and maximum and effective vegetation heights. Each of these variables entered significantly into the nest site selection model derived above. We only included habitat values from the quadrats placed at nest sites. We followed the same backward stepwise procedure in this analysis as we did when determining nest site selection criteria above.

The final model included percent cover of muhly grass and maximum vegetation as significant explanatory variables for nest fate (whole-model maximum likelihood ratio $\chi^2 = 7.45$, D.F. $= 2$, $p = 0.024$). Larger values for each of these variables were most often associated with successful nests. As a test of the model's ability to discriminate between the two nest outcomes (success versus failure), we built a logistic classification table. The table correctly classified 68% of nests. Most correct classifications were for successful nests (86% correct). The model performed less well in correctly classifying failed nests (38% correct).

4.7 Summary

Our results suggest that Cape Sable Seaside Sparrows select habitats on a scale of < 50 ha and base these decisions on the inherently limited habitat variation in Everglades marl prairies . They show distinct habitat preferences at two spatial scales. The first is occupying habitat that is dominated by muhly grass and is relatively species rich, and not occupying habitat that is dominated by sawgrass and is species poor. Once this decision is made, individuals must defend a territory and select a nest site within it. Our results are inconclusive about the role of habitat variables in territory selection. However, we demonstrated that individuals select nest sites that have high muhly grass, litter, *Rhynchospora* spp., and *S. rhizomatum* coverage, as well as high effective and maximum vegetation heights. This result is relative to habitat available within the territory.

Several of these habitat variables have measurable consequences for sparrow populations. Higher sparrow densities are associated with high coverage of muhly grass and litter as well as high vegetation heights. Successful nests are more often associated with high muhly grass coverage and high vegetation heights. Thus, the habitat components we identified as important selection cues translate into higher sparrow numbers and higher fecundity of breeding individuals.

The role these habitat characteristics play in selection varies according to scale. For example, individuals select against sawgrass dominance when making an initial decision concerning settlement site. Large areas of dense sawgrass provide little open space for foraging near the ground. These areas typically support fewer other plant species, including the smaller-stature sedges within which sparrows typically place their nests (see Chapter 2). They may also provide fewer food resources, such as odonates.

However, the presence of some sawgrass is desirable when a sparrow chooses a site within which to establish a territory. In fact, the more sawgrass the better, relative to other suitable locations for territory establishment. The presence of sawgrass does not directly enter into decisions concerning nest placement, but, in almost all cases, the tallest vegetation within a territory is the collection of sawgrass seedheads. Individuals clearly select for nest sites that coincide with these, and this choice appears to increase the probability of a successful nesting attempt. Nesting sparrows use seedheads to defend and delineate their territorial boundaries. They use seedheads around nests as perches to scan the nest site for predators and, if located, deter that predator. Thus, an individual that chooses a site with more coverage of mature sawgrass will enjoy more options in terms of territory establishment and nest placement and will be better equipped to ward off nest predators.

In contrast to the varied role of sawgrass in habitat selection, muhly grass always seems to be selected. Higher percent cover of muhly grass is associated with site occupancy, higher sparrow density, and successful nests. The importance of muhly grass may lie in its use as nesting substrate and in its extensive use within the nest structure itself (Chapter 2).

There is some evidence to suggest that muhly grass depends on fire to set seed (Gunderson and Snyder 1994) and certainly it will not grow in areas that are wet for long periods (Olmstead and Armentano 1997). Nest predators are more active at higher water levels (Chapter 4), and high water and frequent fires have been implicated as driving forces in recent population declines. Maintaining appropriate ecosystem-wide disturbance regimes appear to be principal mechanisms to ensure the recovery of the sparrow. These disturbance regimes may act upon populations, in part, through their effects on the vegetative composition of marl prairies; including favoring the establishment and persistence of muhly grass.

Our results are echoed by results from Dean and Morrison (2001) concerning the nonbreeding season. Using a very similar study design and similar statistics, they showed that sparrows favor particular habitat characteristics during periods of high water inundation and other characteristics during low-water periods. When the water was low, nonbreeding sparrows preferred sites with higher effective vegetation heights, lower litter coverage, and higher coverage of *S. rhizomatum*. When water was high, they selected sites with lower litter coverage, lower *S. rhizomatum*, higher sawgrass coverage, and higher litter coverage (Dean and Morrison 2001). They suggested sparrows respond to the sometimes extreme changes in water heights during the nonbreeding season by shifting their habitat preferences. During high water, only sawgrass provides the suitable structure for sparrows to perch above the water level. Lower lying vegetation is simply not available, and sparrows do not consider tree islands and forests as useable habitat. Dean and Morrison (2001) did not demonstrate consequences for these choices; however they are not hard to deduce. If sparrows are unwilling to move into tree islands and forests, sawgrass is their only remaining refuge during high water. During periods of low water, individuals are not so constrained and likely choose sites that afford high levels of predator protection and high concentrations of food.

Our results, combined with those of Dean and Morrison (2001), provide strong evidence that certain habitat characteristics should be considered a guide to the type of habitat sparrows require for population increases. Thus, having the right level of sawgrass, with its attendant effects on available perches, and having muhly grass present, seem to encourage more sparrows to settle and may allow these individuals to breed successfully. Management options should then be directed towards maintaining the ecosystem processes that support this type of habitat, including the natural variability of these habitat features. The chapters that follow deal with these issues.

Chapter 5

Numbers

5.1 Introduction

The first chapter documented the history of our knowledge of the Cape Sable Seaside Sparrow up to the first range-wide helicopter survey in 1981. All those who had seen the bird realized that its distribution was patchy and temporally dynamic. This realization, and the rapid extinction of the Dusky Seaside Sparrow (*Ammodramus maritimus nigrescens*) in northern Florida, prompted the rangewide survey of 1981 and the annual surveys from 1992 to the present.

This chapter provides the details of these surveys and the results we have obtained. We first explain how we collect these data. We then discuss the issues of calibrating the survey and those who perform it. We postpone some statistical issues to the appendix. Next, we present the sparrow numbers in summary tabular form and then the complete survey results as maps. Finally, we discuss the changes in numbers and the inferences we have drawn from them.

5.2 Methods: The helicopter survey

5.2.1 Basic method

Bass and Kushlan (1982) conducted the first extensive Cape Sable Seaside Sparrow survey in 1981. Bass repeated the survey in 1992 and, as part of this study, annually through 2001. Pimm accompanied Bass on one day of the 1992 survey. He and a small number of other highly trained observers (principally Mario Alvarado, Jason Osborne and Lori Oberhoffer) have played an increasingly important role in later years. The survey uses a helicopter to drop observers at sites along a 1-km grid that covers all sparrow habitat. Observers record the number of sparrows seen or heard within a 7-min interval for up to 3 hr each morning.

We take particular care to visit all sites that we consider to have even a remote chance of holding sparrows. We show later that we do not observe birds at most of the sites we survey.

Initially, the survey had just one observer — a second passenger was a tight squeeze into the Bell 47 helicopter. The helicopter landed and switched off its engine, the observer counted the birds (if present), then boarded the helicopter and moved on. In 1995, changes in equipment forced a change to a different craft and so a different scheme. Each of three observers were dropped off in turn, the helicopter flew out of earshot, landed for a few minutes (but did not turn off its engine), then returned to pick up the three observers in turn.

On a perfect day in a perfect world, three observers can cover about 10 sites each per morning. In practice, observers are sometimes sick or have other duties, pilots oversleep, helicopters break down, fog sometimes prevents operations, winds pick up earlier than expected (and so birds become quiet). Even with four observers to cover the observer positions, practice is less than perfect, and some years' surveys are incomplete. In 1999 we completed two surveys, though the second one was late in the season and did not, in our opinion, provide a suitable replicate. In 2000 we completed two independent surveys more or less across the same time span (and at the same time as surveys in other years).

5.2.2 Observer differences

Over the duration of the survey we have used about a dozen observers, though Bass, Pimm, and two assistants (Mario Alvarado and Jason Osborne) have done most of the surveying in the last five years. In some cases, we dropped two observers at one site and compared their observations. From the small number of sites for which this was possible we could not detect any differences between observers. Logistical problems prevented us from doing this for all observers, so we resorted to an alternative calibration. For the data up to 1996, Curnutt *et al.* (1998) compared survey results at adjacent survey sites at the same time on the same day taken by different observers. There were no significant differences between observations made by different observers (one-way ANOVA: $F = 0.74$; D.F. $= 470$; $p = 0.61$).

In 1999, we undertook two surveys with separate survey teams, one after the other. The counts obtained were not consistent, but we conclude that this reflected a genuine increase in sparrow numbers in two populations late in the breeding season in the second survey. We also undertook two nearly simultaneous surveys in 2000 with separate teams and did not find sufficient differences to conclude that observer skill was a factor in detecting sparrows.

5.2.3 Correcting counts to obtain absolute numbers

To estimate the actual numbers of sparrows from the number we observed on our survey, we need a correction factor. Bass and Kushlan (1982) used a value of 15.87 (rounding it to 16) based on the range at which they could detect the sparrow's distinctive song, and on the assumption that each singing male was accompanied by one female.

We found support for this value by comparing the maximum densities we observed in our study plots with those calculated from the survey. The highest number of sparrows observed at a survey site is typically five. Applying the correction factor produces a maximum density of 80 birds/km^2. Similarly, the highest densities of sparrows on our plots were 22 birds/25 ha (at Dogleg and Alligator Hammock), a density equivalent to 88 birds/km^2.

We further investigated the soundness of the correction factor by comparing our study site densities with the concurrent survey data. This allowed us to calibrate the number of birds recorded during the helicopter survey with the numbers known on the ground. Our intensive plots range in size between 0.25 and 0.6 km^2; large enough that we averaged the four nearest helicopter survey points for our calibration.

The data in Table 5.1 suggest a correction factor of $559/22.5 \approx 25$. This may seem at odds with the value of 16 proposed by Bass and Kushlan (1982). The formality of the calculation, however, overlooks an important source of error. Some of the study plots (the Old Ingraham Highway ones, for example) we established without respect to the known densities of sparrows at those sites; other plots (Dogleg and Alligator Hammock, for example) were established because of known concentrations of birds. This bias towards high density sites drives the correction factor higher than if our sites were more randomly distributed with respect to sparrow numbers. In short, we can and do get zero values during the survey, but we do not get them at most of our study sites. Thus, we feel that the correction factor of 16 must be close to the correct value.

5.2.4 The Appendix and its implications

The Appendix to this report presents an exhaustive analysis of the survey, its statistical properties, questions raised by the American Ornithologists' Union panel that reviewed our work (Walters *et al.* 2000), and our responses to them.

In what follows, we assert that while these properties (and so the accuracy of the survey) are interesting in themselves, they are peripheral to the main issues. At issue is not whether sparrow numbers change, for all populations fluctuate, some wildly, from year to year (see Pimm 1991 for a review). Simply, a *statistically* significant change in sparrow numbers is not sufficient to demonstrate an *ecologically* significant change, let alone a change driven by human actions. Conversely, even apparently statistically nonsignificant changes can be of major concern when other evidence is brought into play. Trivially, when one expects a direction for change in numbers, statistical tests should be one-tailed,

Table 5.1: The average number of sparrows recorded at the four nearest helicopter sites to the intensive survey plots, the number of territories on each plot, and the estimates of the numbers of birds per square kilometer assuming two birds per territory.

Study Site	Year	Area (km^2)	No. of territories	No. of sparrows	No. of sparrows per km^2	Mean no. of sparrows observed on survey
Old Ingraham Highway North	1993	0.60	7	14	23	2.75
	1994	0.60	6	12	20	1.50
	1995	0.60	8	16	27	0.50
	1996	0.60	15	30	50	0.50
Old Ingraham Highway South	1994	0.60	9	18	30	3.50
	1995	0.60	9	18	30	0.25
	1996	0.60	10	20	33	2.75
Dogleg	1995	0.25	3	6	24	2.50
	1996	0.25	11	22	88	1.25
Sweetbay	1993	0.60	8	16	27	2.50
	1994	0.60	7	14	23	1.25
	1995	0.60	6	12	20	1.25
	1996	0.60	6	12	20	1.50
Alligator Hammock	1995	0.25	11	22	88	0.25
	1996	0.25	7	14	56	0.25
Total					559	22.5

not two-tailed. Less obviously, there can be other sources of information that support and extend what would otherwise be a nonsignificant result. In what follows, we shall first present the numbers, and then draw conclusions from them. It is these inferences that matter, and we discuss the evidence to support them.

Figure 5.1 shows the areas where we have seen the great majority of the sparrows. For convenience, we divide the sparrows into six populations, A through F. Natural barriers of unsuitable habitat divide these populations. They include the long hydroperiod marshes of Shark River Slough and areas with too many bushes. The populations have different fates and factors that determine them.

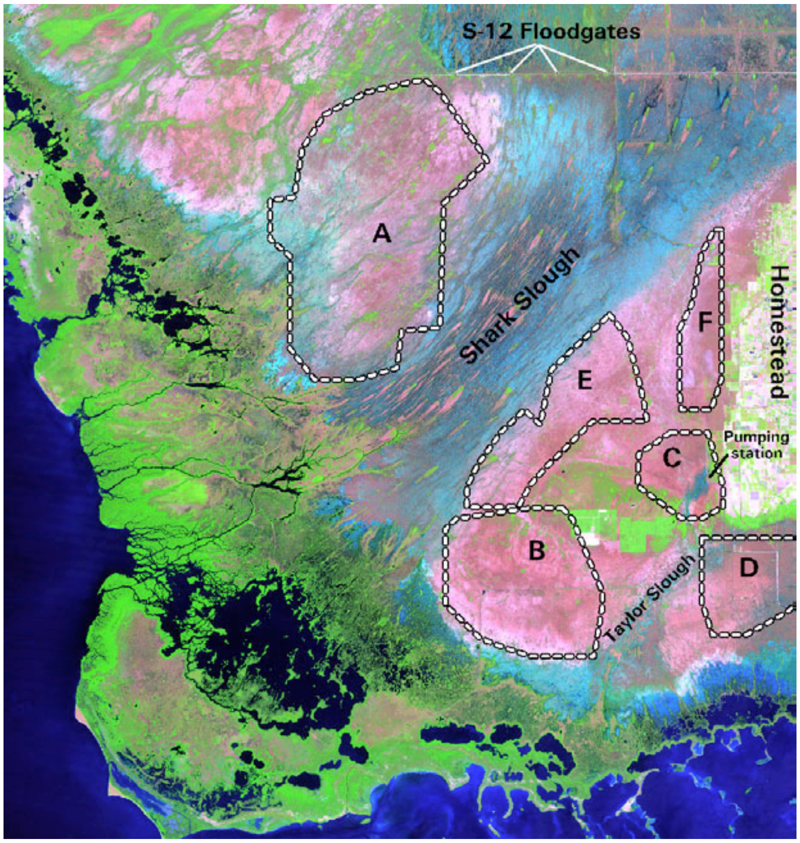

Figure 5.1: Location of sparrow populations (A–F) in Everglades National Park and Big Cypress National Preserve. Water enters the park from two sources, the S-12 floodgates and a pumping station north of Taylor Slough. From there, the water flows south-west. The pink, teardrop-shaped features in Shark Slough are tree islands; they align to the Slough's natural flow path, which enters at the northeast of this image. The S-12 floodgates are west of this natural entry point.

5.3 Results of the extensive survey

We present the results of the extensive survey in two ways. In Tables 5.2 and 5.3, we show the number of birds we counted, and estimated population sizes, respectively. We used the correction factor of 16 to convert counts to population estimates. Figures 5.2–5.13 show the locations of these counts.

Table 5.2: Actual counts of sparrows in each year in each population. NS means not surveyed. [a]survey incomplete.

	Year												
	1981	1992	1993	1994	1995	1996	1997	1998	1999	2000a	2000b	2001	2002
A	168	163	27	5[a]	15	24	17	12	25	28	25	8	6
B	147	199	154	139	133	118	177	113	128	114	153	133	119
C	27	3	0	NS	0	3	3	5	9	7	4	6	7
D	25	7	6	NS	0	5	3	3	11	4	1	2	0
E	42	37	20	7[a]	22	13	52	57	48	65	44	53	36
F	7	2	0	NS	0	1[a]	1	1	1	0	7	2	1
Total	416	411	207	151	170	164	253	191	222	218	234	204	169

Table 5.3: Estimated numbers of sparrows in each year in each population. NE means not estimated because the population was not surveyed, or the survey was incomplete. [a]minimum estimate.

	Year												
	1981	1992	1993	1994	1995	1996	1997	1998	1999	2000a	2000b	2001	2002
A	2688	2608	432	80[a]	240	384	272	192	400	448	400	128	96
B	2352	3184	2464	2224	2128	1888	2832	1808	2048	1824	2448	2128	1904
C	432	48	0	NE	0	48	48	80	144	112	64	96	112
D	400	112	96	NE	0	80	48	48	176	64	16	32	0
E	672	592	320	NE	352	208	832	912	768	1040	704	848	576
F	112	32	0	NE	0	NE	16	16	16	0	112	32	16
Total	6656	6576	3312	2416[a]	2720	2624	4048	3056	3552	3488	3744	3264	2704

5.4 Conclusions: the changes in sparrow numbers over time

We surveyed the sparrow in 1981, every year since 1992, and twice in 2000. There were substantial changes in many of the six populations. As a means to introduce these changes, we start with the first survey in 1981 and compare the numbers in each population to it.

In 1981, population A inhabited the marl prairies west of Shark River Slough, interlaced between drier shrub-dominated areas and wetter sawgrass-dominated areas. It extended into Big Cypress National Preserve and held an estimated 2688 individuals. (Henceforth, we drop the word "estimated" and take it to be read.) Population B held 2352 individuals near the center of Everglades National Park. Population E, just north of B, held 672 sparrows, while C and D, located along the Park's eastern boundary, held about 400 individuals each. F was the smallest population, at 112 individuals.

The subsequent changes are many and they are complex. For simplicity, we draw some key inferences and number them for convenience.

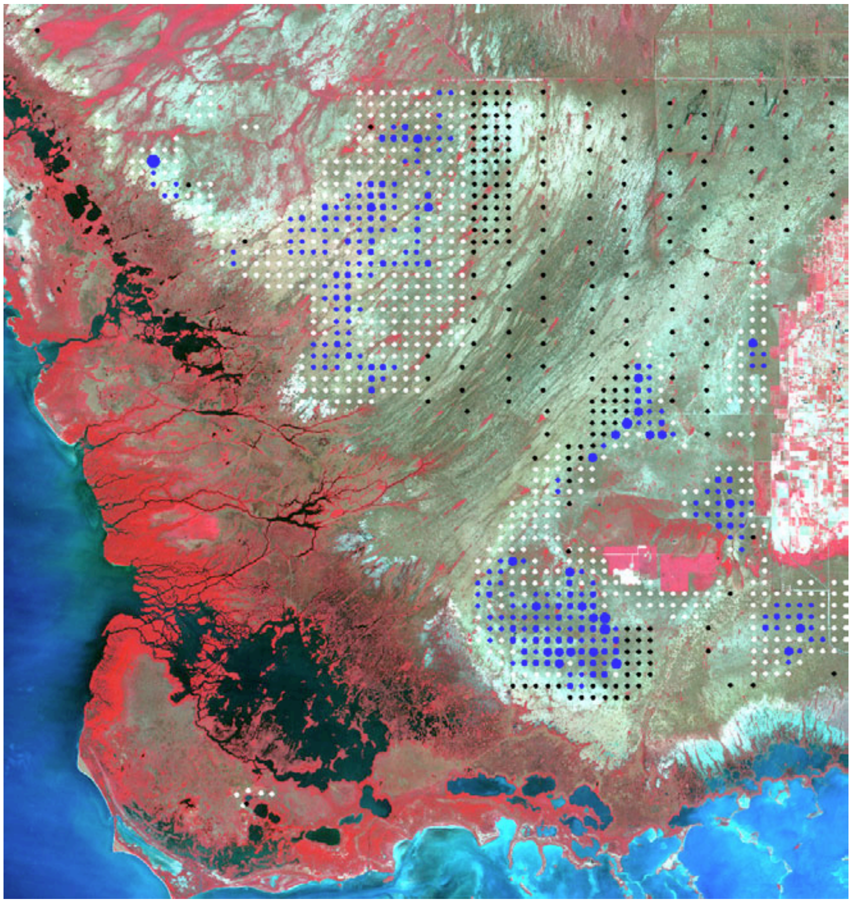

Figure 5.2: Sparrow numbers for 1981. Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

5.4.1 Population A, inference 1

This population suffered the most dramatic sparrow population event we observed. The population decreased by 84% from 1992 to 1993, a decline from over 2600 birds to just over 400 birds. In 1994, we visited only about 25% of population A's sites and found 80 sparrows. When it was apparent that we would not be able to complete the survey in that year, we made sure to revisit sites that held birds in 1993 so that we could make a partial comparison between surveys. The sites surveyed in 1994 also held 80 birds in 1993, limiting the conclusions we can draw about population A in 1994.

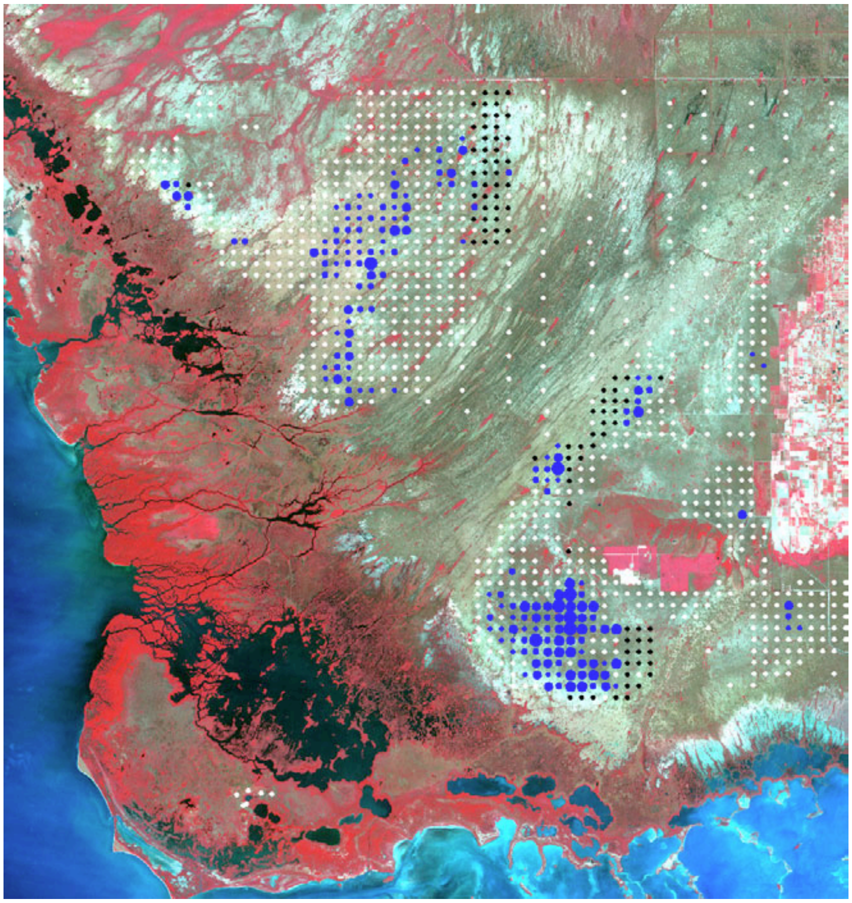

Figure 5.3: Sparrow numbers for 1992. Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

In 1995, the population had decreased to just over half of the 1993 abundance. It has remained low ever since. The difference between the 1981 and 1992 numbers and the 1993 and subsequent numbers is significant as a two-tailed test (t-test, $p < 0.005$). This corresponds to a pre- and post-flood comparison. The more appropriate one-tailed test — we expect that flooding would cause a decline — shows this decline to be even more remarkable statistically ($p < 0.003$).

The important *ecological* question is whether a decline of this size is remarkable given the normal year-to-year variation in population densities found in comparable species. In

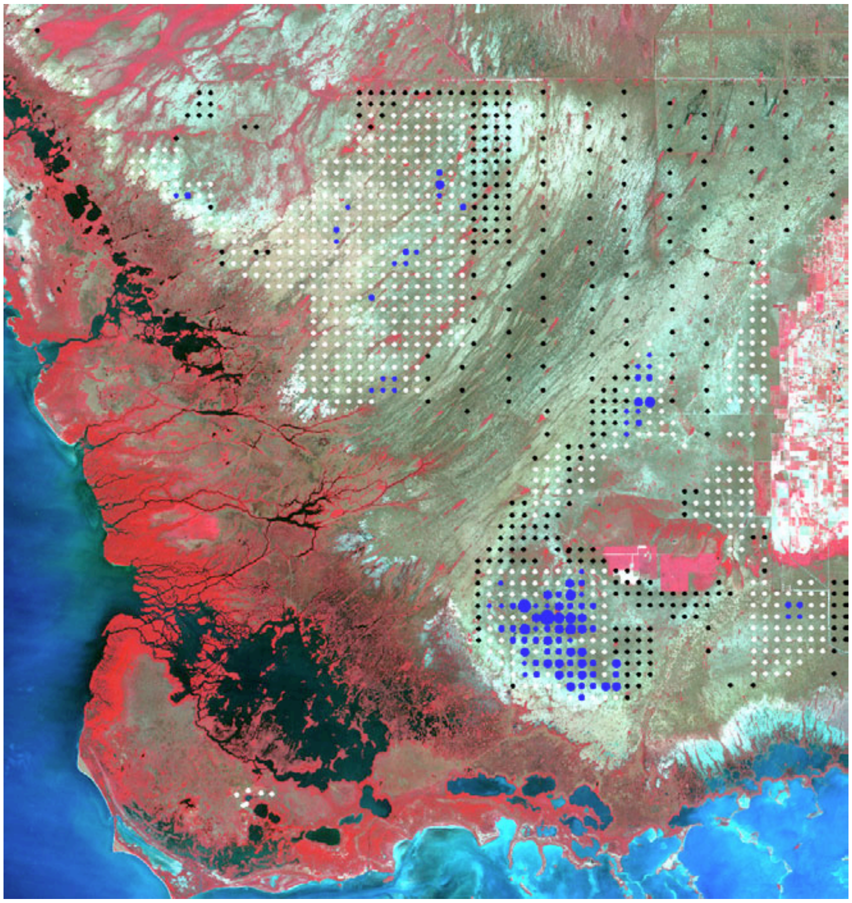

Figure 5.4: Sparrow numbers for 1993. Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

fact, it is not only remarkable but unprecedented (Pimm 1991). We discuss the causes of this and the other changes in later chapters.

5.4.2 Population A, inference 2

Population A made some modest gains after the floods of 1993 to 1995, but the 2001 and 2002 counts (eight and six singing males respectively, for estimated populations of 128 and 96) is clearly cause for concern. Is this also an ecologically significant event? Other

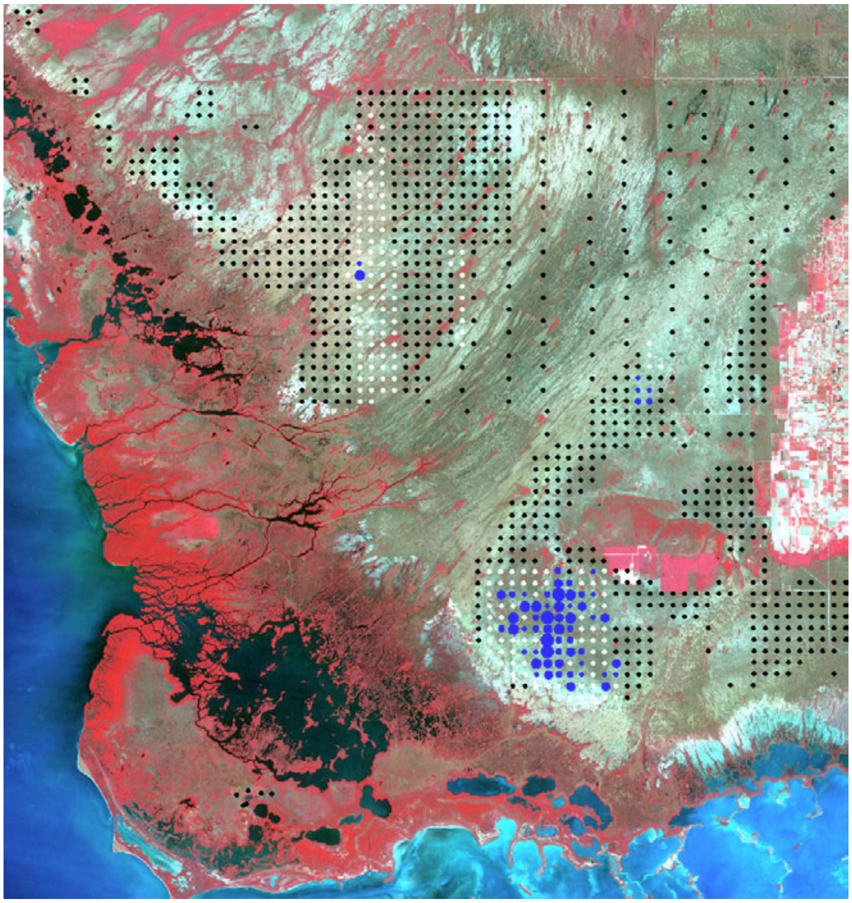

Figure 5.5: Sparrow numbers for 1994. Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

evidence suggests that it likely is. During the winter of 1999–2000, water levels were very high until just prior to the 2000 breeding season. We noticed a precipitous decline in the numbers of sparrows breeding on the intensive survey plot located in the northeast of this population. Numbers on the plot were also low in 2001. That the decline was not obvious in the 2000 count is likely a consequence of the birds being present and attempting to nest during the brief dry spell but failing to produce sufficient young.

Chapter 3 shows than unless *all* the pairs in a population can breed successfully at least once in a year, the population will decline. Only when *all* the pairs can complete

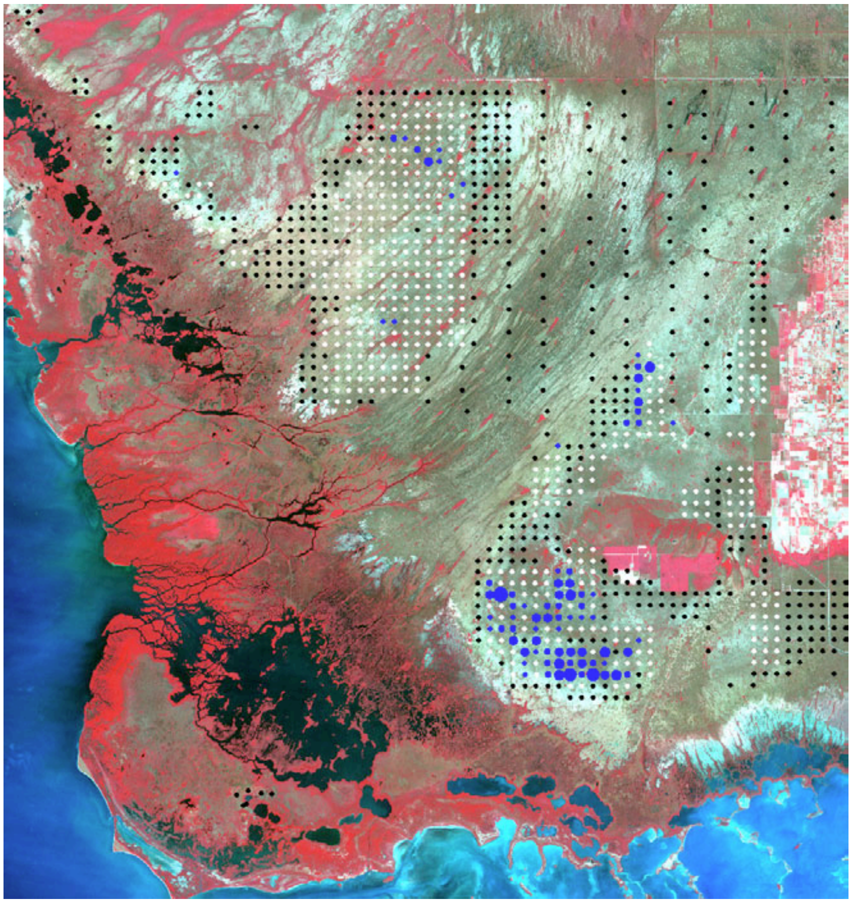

Figure 5.6: Sparrow numbers for 1995. Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

two successful clutches can the population increase. (There are year-to-year changes and population-to-population differences in breeding success across the intensive study plots, but this variation is small compared to the huge variation in the fraction of pairs that are able to breed.)

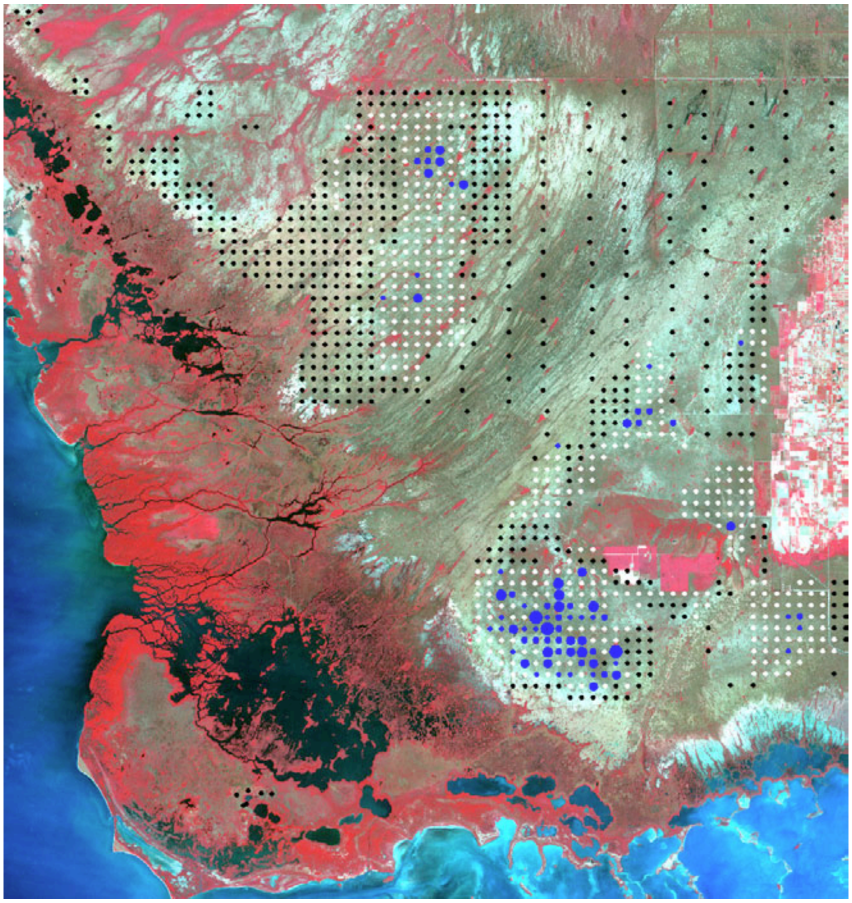

Figure 5.7: Sparrow numbers for 1996. Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

5.4.3 Population B, inference 3

Population B has remained more or less constant, the range in numbers being encompassed by the two surveys in 2000.

5.4.4 Populations C and F, inference 4

The two northeastern populations, C and F, held an estimated 544 sparrows in 1981; since 1992, the estimate has never reached 200. The difference between the 1981 and 1992 surveys

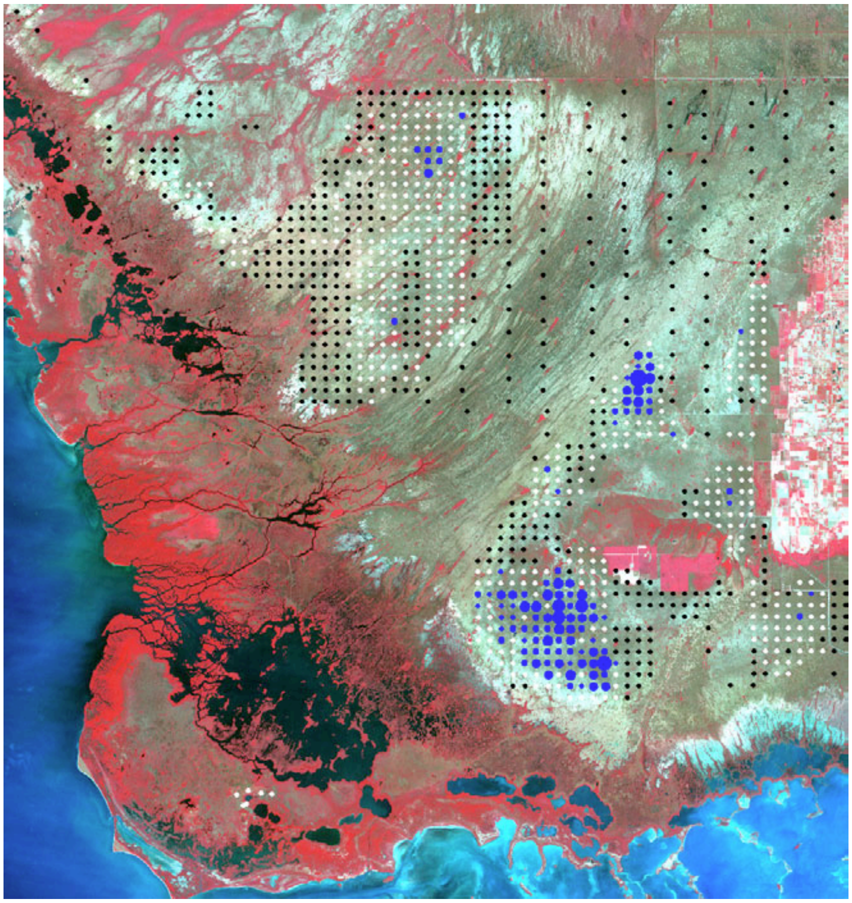

Figure 5.8: Sparrow numbers for 1997. Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

and the combined estimates of subsequent years is significant ($p < 0.001$). Once again, we ask: what is the ecological significance of this difference, based as it is on comparing one count in 1981 with counts starting a decade later? We believe that the underlying mechanism is fire (Chapter 6). (With one caveat: a small area in C, south of pumping station S-332 and downstream of Taylor Slough bridge, has changed from muhly grass-dominated prairie to sawgrass marsh as a consequence of higher water levels. Though a small area, it is very well studied and Nott *et al.* [1998] discuss it in detail.)

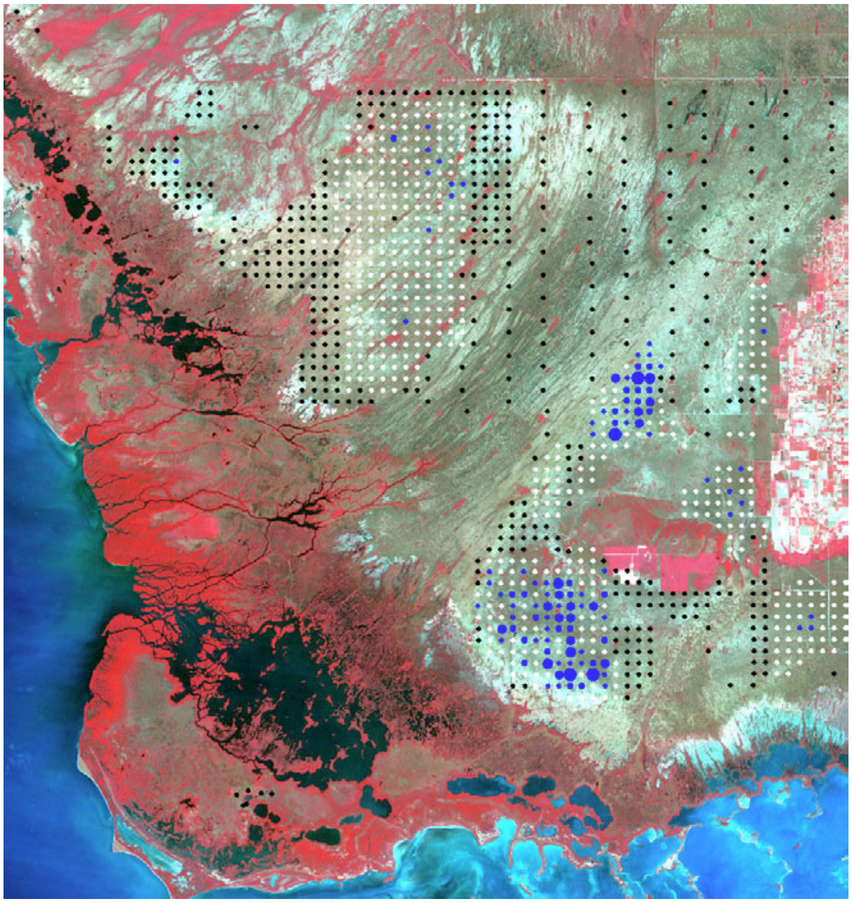

Figure 5.9: Sparrow numbers for 1998. Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

5.4.5 Population D, inference 5

Population D held 400 birds in 1981, numbers that it has not seen since. Again, simple statistics suggest a highly significant decline ($p < 0.001$), raising the question of whether this decline is ecologically significant. It is. This area too has suffered high water levels that have precluded birds from nesting there successfully.

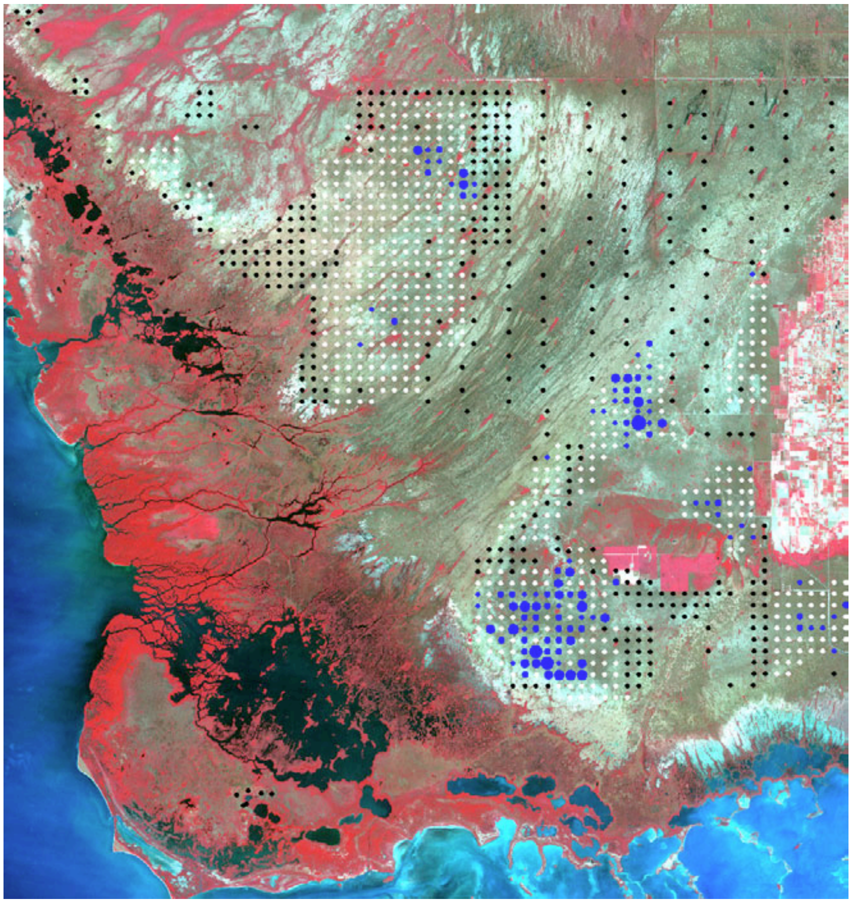

Figure 5.10: Sparrow numbers for 1999 (first survey). Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

5.4.6 Population E, inference 6

This population has a particularly complex history. It may be best understood by splitting the population into two pieces, E (North) and E (South). This division is readily understood by looking at the maps. Although the numbers are small, it appears that E (South) held roughly 300 birds in 1992, but after that there were only sporadic sightings until 2000 and 2001, when the area may have held > 100 birds. These numbers, though too small for confident statistical analysis, add to the evidence that flooding harms the birds. This is not surprising given its location adjacent to Shark River Slough.

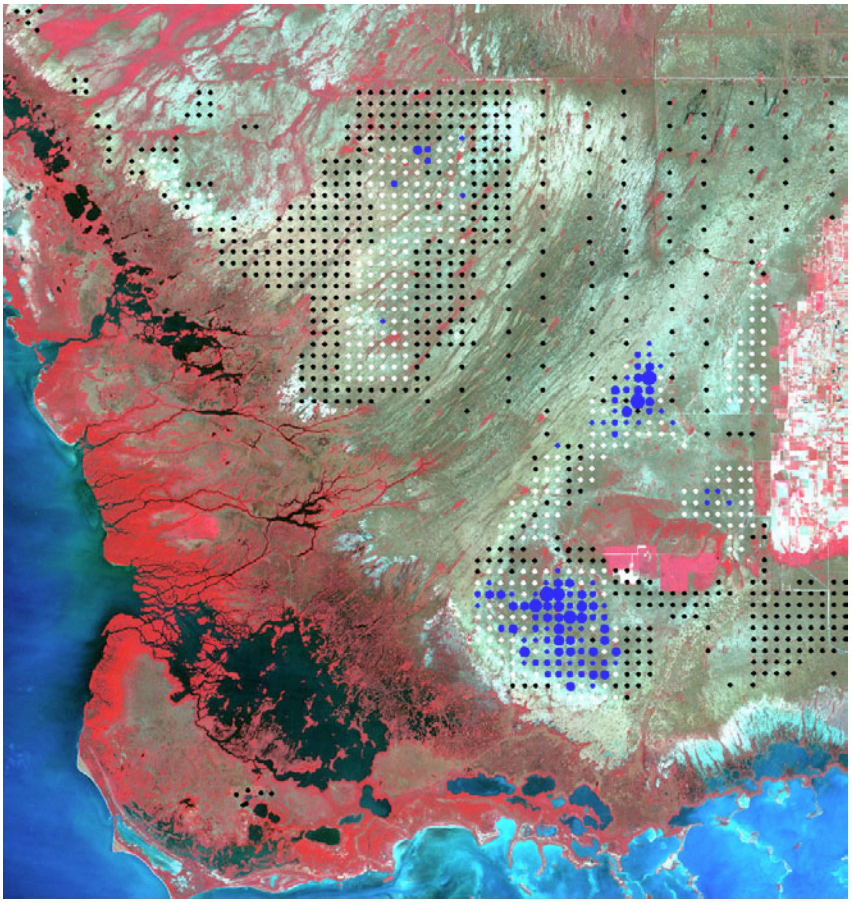

Figure 5.11: Sparrow numbers for 1999 (second survey). Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

5.4.7 Population E, inference 7

Population E (North) had relatively low numbers in 1992 through 1996, but since 1997 has held at least 600 birds. It is possible that this increase is a recovery from the 1989 Ingraham fire that burned across this area.

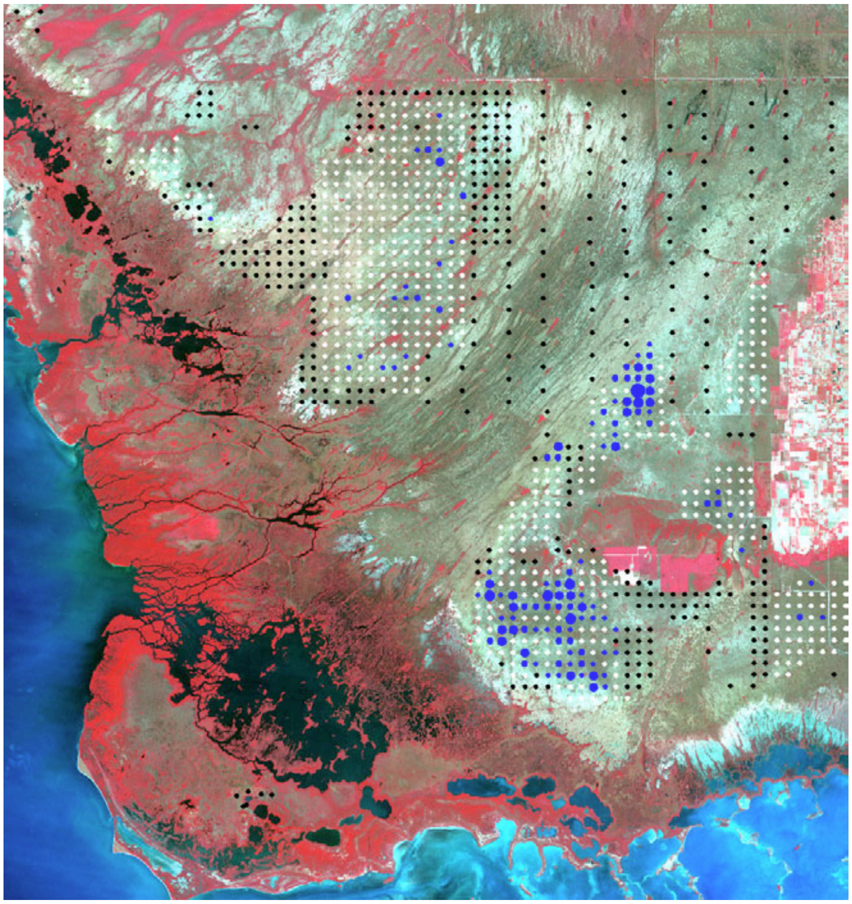

Figure 5.12: Sparrow numbers for 2000 (first survey). Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

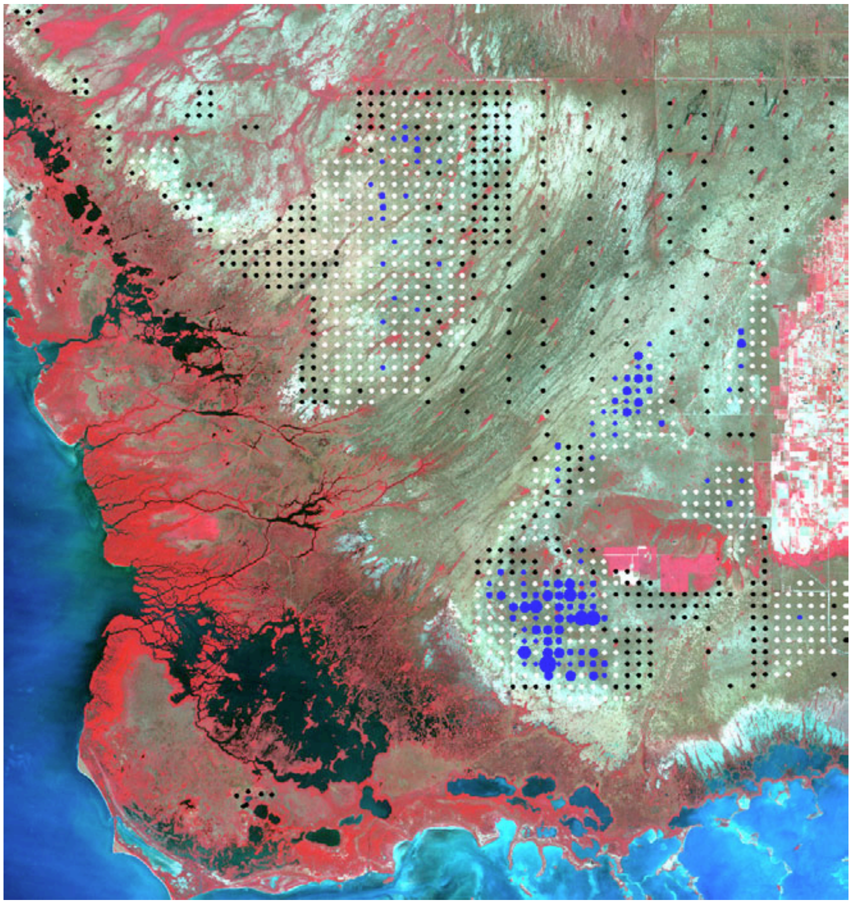

Figure 5.13: Sparrow numbers for 2000 (second survey). Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

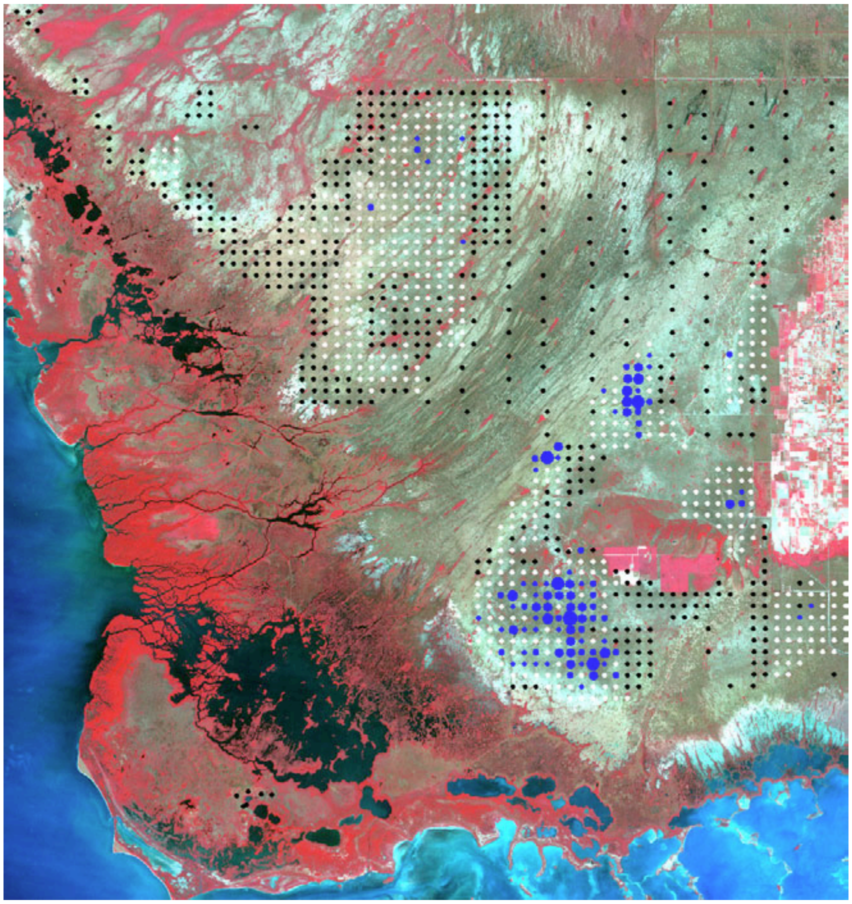

Figure 5.14: Sparrow numbers for 2001. Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

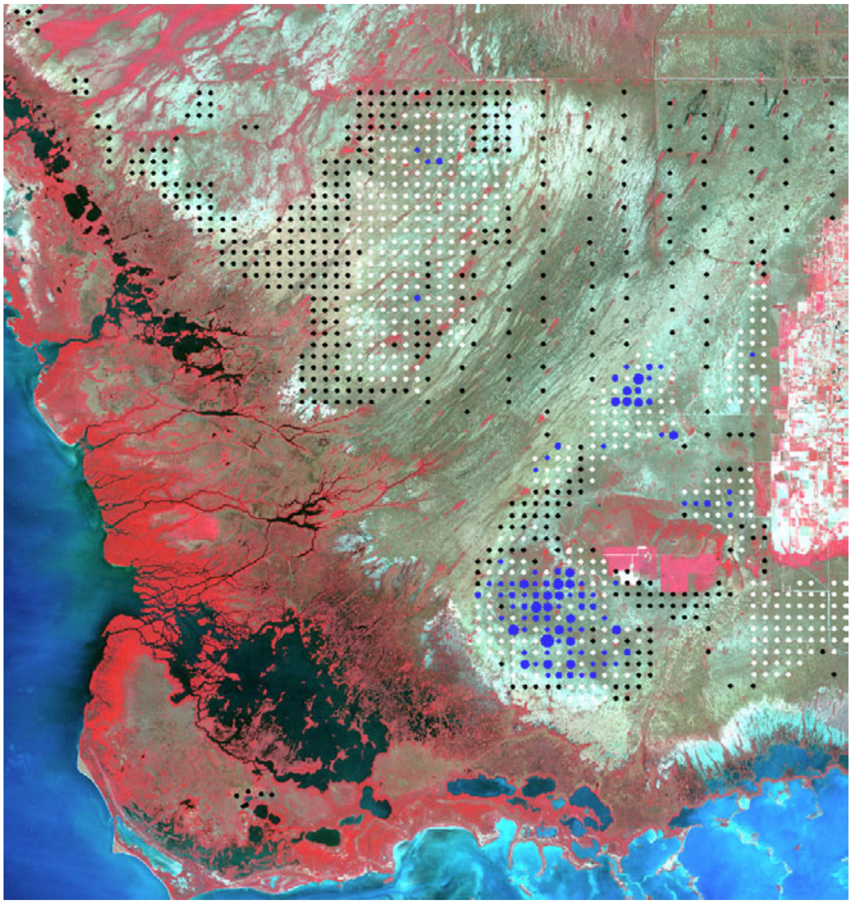

Figure 5.15: Sparrow numbers for 2002. Purple dots indicate number of birds counted in the year depicted, ranging from 1 (smallest dots) to 6 (largest dots). White dots indicate points without birds in the year depicted. Black dots indicate points surveyed in one or more years but not surveyed in the year depicted.

Chapter 6

Causes of Population Changes

6.1 Proposed explanations

The previous chapter summarized the key changes to Cape Sable Seaside Sparrow populations that we have observed. With so many events occurring in more or less the same time frame, we must be careful in assigning cause and effect. Sorting through various hypotheses requires a disciplined approach. Following are some of the hypotheses that have been suggested from time to time:

- *The sparrows did not disappear; we just haven't been looking for them in the right places.*
- *Population fluctuations are a normal part of the ecology of all small birds, especially those with small, restricted populations.*
- *Flooding is a natural part of Everglades hydrology. We have always had wet years and dry years.*
- *Flooding causes only temporary damage to the habitat on which the sparrows critically depend.*
- *Colonists from the healthy eastern populations will quickly restore the western population.*
- *The eastern areas suffer from a much higher frequency of fires, mostly anthropogenic, accounting for repeated extirpations in population F and the northern part of population C.*
- *Habitat in populations C and D has been permanently altered by the change in water regimes due to pumping of water into Everglades National Park, just north of Taylor Slough Bridge.*
- *Three years of almost continual flooding caused significant damage to sparrow habitat that is only now, six years later, regaining its former extent.*
- *Sparrow numbers are recovering slowly as their breeding ecology suggests they should.*

In this chapter, we will examine each of these hypotheses in turn, subjecting each of them to objective scrutiny in order to build a comprehensive explanation for the dramatic decline in sparrow numbers. Once we understand how this disaster occurred, we will be in a position to suggest policies to prevent its recurrence.

Some of these hypotheses are sensible ones, proposed in the peer-reviewed literature, and they require serious analysis. We treat these first. Others have have not been deemed credible by the peer-reviewed literature, but we will discuss them briefly.

6.2 Chance fluctuations in numbers

All populations fluctuate from year to year (Pimm 1991). Grassland sparrow populations fluctuate considerably, and populations at the edge of a species' range are the most variable (Curnutt *et al.* 1996). Before we point the accusatory finger at some specific explanation, we should be sure that this sparrow's declines and local extinctions are sufficiently unusual events.

The one-year decline in population A to 16% of its 1992 level is not merely statistically significant, it is ecologically atypical. For instance, in extensive, long-term population monitoring of British birds, it is unprecedented (Pimm 1991). (These data constitute the largest long-term study of bird population dynamics.) The most severe natural event to affect these species was the exceptionally cold winter of 1962–1963. By 1993, the most severely affected species, small-bodied insectivores, declined to $\sim 50\%$ of their 1962 levels.

More problematic are populations C, D, and F, which have gone extinct locally in some years (2, 1, and 2 years respectively.) These zero counts could be sampling error: the range of birds counted in population F, for instance, is 0 to 7, exactly the two counts obtained in the repeated survey in 2000 (see Table 5.2). Combined, the numbers in the two northeastern populations, C and F, are significantly lower in the years from 1992 onward than they were in 1981. But is this event *ecologically* significant — specifically, how long should populations be absent locally before we express concern? We addressed this question by referring to another long-term dataset on bird numbers, the North American Breeding Bird Survey (BBS).

6.2.1 Methods

Curnutt *et al.* (1996) used BBS (Robbins *et al.* 1986) data to analyze the spatial and temporal population variability of 10 species of grassland sparrows. Their distributions typically consist of one or more areas of high density and relatively low variability, surrounded by low-density populations that are highly variable. The Cape Sable Seaside Sparrow population appears to behave in much the same way. With two assumptions, we could apply these analyzes to the Cape Sable Seaside Sparrow. We wish to estimate the probability that the sparrow will be absent from an area for a specified period. The first assumption is that its dynamics are typical of other, nonendangered grassland sparrows. There was little variation among the 10 species of sparrows Curnutt *et al.* (1996) analyzed and it seemed reasonable to assume that this sparrow's dynamics were comparable.

The second assumption rested in the correspondence of BBS data and the extensive sparrow survey (Bass and Kushlan 1982). Each BBS route consists of 50 observation points at least 0.8 km apart, where participants recorded all birds heard or seen. Observations for the Cape Sable Seaside Sparrow survey were similar, though the distance between sites was exactly 1 km. As in the BBS, no observations did not necessarily mean an actual local extinction. But if not, then the apparent absence represented a fall in the numbers to some small and comparable level. (Recognizing this possibility we will, for simplicity's sake, not preface each use of the word "absent" by "apparently.")

We determined the probabilities of sparrows being continuously absent from a BBS route for 1–12 years (the maximum possible length of an absence in our Cape Sable Seaside Sparrow data). We combined the data for all 10 grassland species and selected all BBS routes that had continuous data from 1970 to 1989. We only used routes where birds were present in the first and last years of record ($n = 284$) to exclude areas where the species might be lost from long-term habitat changes. For each route, we calculated the mean abundance over 20 years and tallied the number of times that a species was absent one year, two consecutive years, three consecutive years, etc. We grouped routes by their mean abundances (in increments of 10) and determined the proportion of occurrences for each length of absence. We expressed these rates as proportions to determine probabilities (Fig. 6.1).

6.2.2 Results

Populations A, B, and E have consistently held sparrows over all survey years (1981 and 1992–1996). In contrast, populations D, C, and F have apparently dropped to zero on one or more occasions during the years up to and including 1996 (Table 5.2). For these areas we can compare the survey results with our probability model to determine whether we would expect these absences to be due to chance. In typical years, there are 70 survey sites within the area of population D, 43 sites in C, and 38 in F. We assume that these numbers are close enough to the 50 sites of a BBS route that we can compare them directly. That is, a zero count from one of these areas is equivalent to a zero value in the BBS data set. Survey data for both populations C and D are incomplete for 1994. We counted 25 birds in population D in 1981; birds were absent for one year (1995) and could also have been missing in 1994. For BBS routes with between 20 and 30 birds counted on average, the probability of a single-year absence is 0.15 (Fig. 6.1). On its own, we should not consider this one-year absence to be unusual. If there were no birds in D in 1994, then a two-year absence would have been highly unusual (Fig. 6.1). Population C occupies the upper reaches of Taylor Slough, formerly prime sparrow habitat, where Werner (1975) conducted much of his work. Here, as late as 1981, sparrows were relatively plentiful (27 birds). This population was absent for either three consecutive years (1993–1995) or twice for one year,

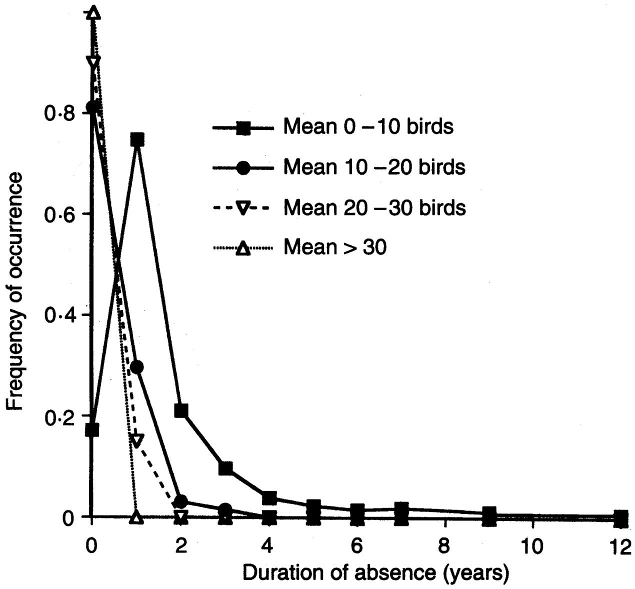

Figure 6.1: The frequency of occurrence of consecutive zero counts of 10 species of grassland sparrows on BBS routes for different overall mean abundances.

depending on the unknown value for 1994. In the BBS data, three-year absences are unknown for populations that average more than 20 birds. They occur less than 5% of the time for those that average more than 10 birds.

The area of population F holds only 38 sites, so we should be cautious in applying the BBS-derived model to these survey data. The area is bounded to the east by agricultural fields and is surrounded by habitat unsuitable for sparrows, primarily due to high densities of native and exotic shrubs. We can assume, therefore, that the survey results represent the entire population of the area and that zero values are comparable to BBS zeros. We counted seven birds in 1981, two in 1992, and no more until we saw one in 1996. The sparrows could have been absent for a maximum of three consecutive survey years. The probability of a population averaging seven birds being absent for this length of time is 9%, a low but not statistically significant probability.

6.2.3 Summary

First, in the west, the drop in population A from 1992 to 1993 is highly unusual and requires explanation. Second, the sporadic absences of sparrows in the small eastern and peripheral populations do not appear to be consistent with the normal fluctuations of small, peripheral grassland sparrow populations.

If 1981 represented an average year for the populations, then the likely three-year absence of the birds from population C, and the possible two-year absence from population D, are unusual. Population F is so small that such absences might occur in roughly one in 10 comparable data series. Taken together, the declines in these three peripheral eastern populations are sufficiently unlikely to require our searching for specific causes.

6.3 Hurricanes

In the 20th century, 80 hurricanes and other tropical storms passed close enough to south Florida to affect the Everglades (Duever *et al.* 1994). The official hurricane season lasts from June to November, and hurricanes are most frequent in September. Hurricanes could have a variety of effects on sparrows. They normally fall outside of the main sparrow breeding season (March to early June, Lockwood *et al.* 1997) and thus are unlikely to kill nesting birds. When hurricanes do strike, the high winds could kill birds directly. Hurricanes and tropical storms can drop up to 25 cm of rain. Thus, a storm early in the storm season could result in flooding and the termination of nesting, since most nests are within 25 cm of the ground. Wet storms that occur as late as October or November could prolong a high wet-season water table (Duever *et al.* 1994). In turn, this could delay the return of low water the following spring and so delay nesting.

We know of two hurricanes that have affected the sparrow. In 1935, a hurricane temporarily flooded Cape Sable with saltwater causing subsequent changes in vegetation that made Cape Sable unsuitable for the sparrow (Chapter 1).

In August 1992, Hurricane Andrew scored a direct hit on the Cape Sable Seaside Sparrow, its eye and eyewall encompassing almost the bird's entire range (Fig. 6.2; Armentano *et al.* 1995). The strongest winds, those trailing the eye itself, passed over the southern part of populations A and E (Pimm *et al.* 1994). Population B lay to the south of the storm's eye, while populations C, D, and F held few birds in 1992 in any case.

Hurricane Andrew's effect was most obvious in the hardwood hammocks and pines within its path. Changes to the prairies were less obvious (Pimm *et al.* 1994). There is no evidence that hurricanes kill sparrows directly, although surely Hurricane Andrew's sustained winds of 242 km/hr were lethal to some of them. We did not count the birds immediately after the storm, nor indeed, can we count them outside of any breeding season.

Despite the overall declines in populations A and E from 1992 to 1993, the details suggest that Andrew was not their major cause. In population A, the numbers outside the eye but within the northern eyewall declined dramatically. The numbers in population B, in the southern eyewall, did not. Only the southern part of population E declined; numbers in the northern part of population E, though also within the storm's eye, actually increased.

We might expect population A to recover from a short, sharp mortality were habitat conditions suitable. In fact, it declined further and has remained at low levels since, suggesting that other influences are also at work.

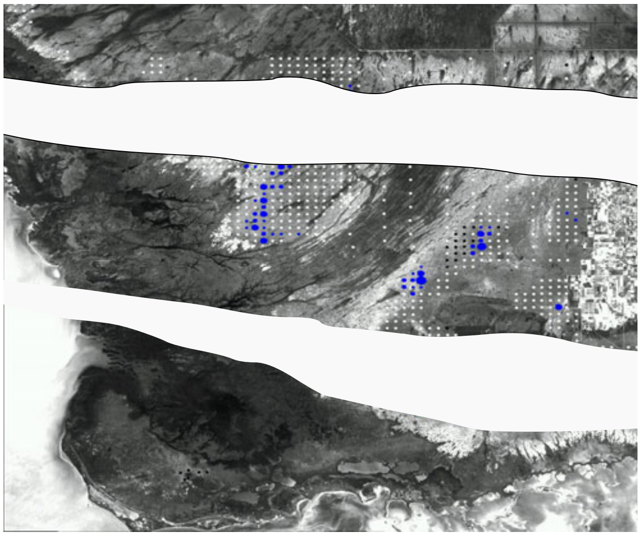

Figure 6.2: The path of the eyewall of Hurricane Andrew in 1992 (stippled) superimposed upon the sparrow survey results from 1992. The area between the two eyewalls was the path of the eye itself. All known sparrows were encompassed by either the eye or its wall.

6.4 Fire

Between 1948 and 1992 the wetland areas of Everglades National Park caught fire 752 times for an average of 17 fires per year (Gunderson and Snyder 1994). Fire is a natural component of the Everglades. It likely maintains a habitat mosaic and prevents hardwood shrubs from invading the characteristically open Everglades marshes (Egler 1952, Robertson 1953, Taylor 1983). The sparrow relies on marl prairies that are influenced by fire regimes (Werner 1975). There are three sources of fire in Everglades National Park: lightning strikes, unplanned human ignition (and arson), and prescribed management. Prescribed burns occur throughout the year, with a slightly higher proportion occurring from November to March (Herndan and Taylor 1986). These fires are usually small and account for a small proportion of the fire activity in the park. Unplanned human-caused fires have been the most numerous and have burned the most area. Most occur around the perimeter of the park, especially in the northeast corner near urban areas. The timing and frequency of lightning- and human-caused fires are highly divergent (Gunderson and Snyder 1994). Lightning-strike fires are most numerous from March to September with a peak in July. Human-induced fires (nonprescribed) occur mostly in the dry season from December to May with a peak in April and May: the birds' breeding season. For sparrows, a key aspect of this seasonal distinction lies in the differential effects of wet and dry season fires on the availability of breeding areas. Prairie fires in wet months tend to leave behind a mosaic of burned and unburned patches, while in the dry season burning is still patchy but much more complete (Taylor 1983).

Currently, Everglades National Park manages fires through prescribed burning and strategic control of natural fires. Of central concern is the development of a fire management protocol that promotes U.S. Fish and Wildlife Service recovery goals for the sparrow. The conception of this fire management plan is profoundly inhibited by the lack of knowledge surrounding the sparrow's response to, and recovery from, fire. We first review previous work, making explicit the proposed mechanistic links between fire, sparrow density, vegetation, and soil depth. We then test whether sparrows were harmed by a 1994 fire that burned through the core of their population, and if so to what degree and how long this impact was apparent. In so doing, we also evaluate proposed benefits of fire to sparrow numbers.

6.4.1 The history of sparrows and fire (with a critique)

The first accounts of fire's effect on sparrows portrayed it as a threat. Stimson (1956; see also Bent 1968) recorded the loss of isolated populations of sparrows due to fires damaging grassy marshes. Fires move through Everglades marshes fueled almost exclusively by grass (Gunderson and Snyder 1994). Given that sparrows place their nests near the ground and well within the grass layer, a fire that burns during the breeding season (the driest time of the year) will almost certainly destroy active nests. It is not as clear whether fire kills adults, since they can fly away.

Werner and Taylor countered this view by suggesting that (1) fire does not impose long-term negative impacts on sparrow numbers and (2) fire maintains vegetation in a state that is suitable for sparrow breeding (Werner 1975, Taylor 1983, Werner and Woolfenden 1983). Werner and Taylor observed individuals recolonizing a burned site one-year postfire, thus documenting that the direct negative effects of fire may not persist. Using existing spatial patterns in time since fire, Werner (1975) also recorded that sparrow density declined within sites that did not burn for four or more years. Taylor (1983) documented that the rate at which vegetation recovers postfire is the principal determinant of how quickly sparrows return to a site and how long they occupy it. Werner and Woolfenden (1983) speculated that fires prevent shrub invasion and decrease the accumulation of dead vegetation. They suggested that preventing these processes is key to maintaining the suitability of habitat for sparrows. Combined, these studies led to recommendations that frequent (e.g., four-year interval) prescribed fires be considered a necessary component to the maintenance of sparrow populations (Kushlan and Bass 1983, Taylor 1983, Werner and Woolfenden 1983).

Figure 6.3 illustrates how the proposed benefits of fire for sparrow numbers are supposed to operate under normal hydrologic conditions. The principal factors are considered to be soil depth and vegetation growth rates. Sites are ill-suited for sparrow occupancy immediately following a burn, because they lack any vegetation cover. Some cover is re-

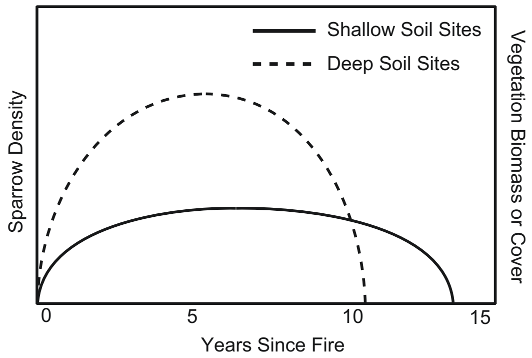

Figure 6.3: The hypothesized relationship between fire, vegetation, soil depth, and sparrow density. Based on Werner (1975), Taylor (1983) and Werner and Woolfenden (1983).

quired for the placement of nests, as substrate for arthropod prey, and as cover for recently fledged young (Werner 1975, Dean and Morrison 1998). Sites that have deep soils will begin to resprout vegetation almost immediately. Sawgrass (*Cladium jamaicense*), the principal graminoid of Everglades marshes, can reach heights of 20 to 40 cm within 2 weeks postfire, as its terminal bud lies underneath the soil and does not burn (Miao *et al.* 1998). The rapid regrowth of sawgrass, and supposedly other marl prairie vegetation, often produces enough cover for sparrows to use by the next breeding season (Werner 1975, Taylor 1983). This rapid regrowth may be confined, however, to sites with deeper soils, which provide the necessary nutrient and water reserves. The same cannot be said of vegetation overlying shallow soils. Regrowth there is much slower, and thus it takes far longer to accumulate enough cover to attract sparrows.

The second component of this mechanism, and the one that implies that occasional burning is necessary, is fire's effect on the accumulation of dead vegetation (i.e., litter) and the effect that too much litter has on sparrow occupancy (Werner and Woolfenden 1983, Taylor 1983). Taylor (1983) showed that sites gradually accumulate biomass, some live and some dead, in the years postfire. The ratio of live to dead biomass is initially weighted heavily toward live growth, but as time passes, the ratio tends in the other direction (Taylor 1983). Dead vegetation tends to lie horizontal to the soil surface, creating impenetrable mats (Werner 1975). These mats are thought to prohibit sparrow movement on the ground, a characteristic behavior of this subspecies that allows it to forage, enter the nest undetected, and hide from predators (Werner 1975, Lockwood *et al.* 1997). Thus, the initial removal of this mat due to fire was thought to increase the suitability of the vegetation for sparrows, and the eventual reburning of the vegetation was necessary to keep the litter layer from accumulating to the point where sparrows were excluded.

Although not often made explicit, this mechanism predicts that over deep soils this transition into an unsuitable state will occur much sooner than over shallow soils. So, while sparrows may occupy a burned site sooner if the soil is deeper, they may also find themselves in suboptimal habitat more quickly. Conversely, burned sites with shallow soils will not support sparrows for several years, but sparrows that occupy these sites will enjoy prime conditions for longer periods.

Curnutt *et al.* (1998), using a greatly expanded spatial scale compared to either Werner or Taylor, countered the argument that long periods without fire drive sparrow numbers down. Using density estimates combined with maps of fire extent within Everglades National Park, Curnutt *et al.* (1998) found no decrease in sparrow density for up to 10 years postfire. Countering the argument that sparrows can recover quickly from all fires, Curnutt *et al.* (1998) found that sparrow densities responded to season of fire, and fire frequency, such that dry-season fires that recur often (sometimes once or more per year) significantly decrease sparrow densities. They suggest that very short-interval, dry-season, human-ignited fires may have driven northeastern sparrow populations toward extinction (Curnutt *et al.* 1998).

Clearly, the role of fire in sustaining populations of the Cape Sable Seaside Sparrow is a complicated one. Given the natural prevalence of fire in the Everglades ecosystem and the results of Werner and Taylor, it seems certain that sparrow populations are not permanently harmed by natural fire events. However, there is little that is natural about the current fire regime, and Curnutt *et al.* (1998) show that human-induced changes to this regime could pose a serious risk to sparrow recovery. Furthermore, it is not at all clear whether fires benefit sparrows through occasional thinning of the litter layer within their habitat. If we are to effectively manage sparrow populations we must be able to distinguish between fires, and fire regimes, that harm sparrow numbers versus those that do not. We must also determine if sparrows require occasional fires for their long-term persistence. The studies outlined above have important limitations that preclude our making such distinctions.

By necessity and circumstance, previous research relied heavily on point-in-time observations and study designs that severely limit making broader inferences. Stimson's conclusions were based on exemplary natural history observations but no quantitative analysis. Werner (1975) and Curnutt *et al.* (1998) relied on synchronic study designs, where existing spatial patterns in time since fire were assumed to mimic patterns we would observe by following several populations through fires. Although this is the dominant method for studying the effects of fire on vertebrate populations (e.g., Breininger and Schmalzer 1989, Pylypec 1991, Davis *et al.* 2000, Dees *et al.* 2001), this approach confounds the effects of fire with unrelated differences between sites (Whelan 1995). Thus, observed differences in sparrow density between sites could reflect unaccounted-for variance in soil depth, hydrologic flow, or elevation as easily as they could reflect varying time since fire (Tyre *et al.* 2000).

Some of Werner's and Taylor's analyses avoided such problems by documenting sparrow densities just before a prescribed fire and again just afterward (i.e., they were diachronic or longitudinal study designs). However, these studies suffered from problems in inference because (1) they often did not compare sparrow densities within the burned plots to unburned "control" plots, and (2) observations did not extend long enough before or after fire to account for natural variations in the sparrow's annual population size (Whelan 1995). Thus, it is difficult to affirm that changes in sparrow density after burning were due to the fire's effects and not to unaccounted-for variables that also determine fluctuations in sparrow densities, such as food supplies, predator densities, or overwintering survival rates.

An effect that is seen consistently in replicates of a well-designed experiment can only reasonably be explained by the manipulation of experimental variables (Manly 2001). Thus, Whelan (1995) suggests that studies of the effects of fire on vertebrate populations should use experimental study designs whenever possible. Fire is the manipulated experimental variable, and thus fire is introduced to several replicate study plots. Some replicate plots are not subjected to fires, thus serving as controls. The effects of fire (e.g., changes in sparrow density) are monitored before and after the experimental manipulation across all plots, including the controls. This study design effectively distinguishes between natural variation in the effect variable (sparrow density) and variation caused by the experimental manipulation (fire).

This approach would solve problems associated with previous research. However, fully implementing an experimental design here is impossible, principally because the manipulated variable (fire) has a direct effect on the survival of sparrow populations. It is possible (maybe even probable) that fire will have a benign or positive effect on sparrow populations. However, we cannot discount the possibility that the experimental manipulation will harm the sparrow. Given that the sparrow is listed as federally endangered, subjecting populations to harm is against federal law.

When replication is not feasible, as is the case here, the same basic study design is still desirable (Stewart-Oaten *et al.* 1986, Whelan 1995, Manly 2001). It is possible to draw robust inferences from such quasi-experimental designs (Whelan 1995, Manly 2001). A quasi-experimental design employs a two-group comparison without randomization (Manly 2001). The manipulation (fire) is introduced into one plot, while another is left unaffected. The effect variable of interest (sparrow density) is monitored before and after the manipulation. In order to account for underlying annual variations in the effect variables, Whelan (1995) suggests monitoring the plots for equal periods before and after the manipulation. For vertebrate populations, this typically requires two or more years of information collected before fire is introduced, followed by a further two or more years of postfire information (Whelan 1995).

The assumption in such designs is that any natural (i.e., unaccounted for) changes in density will be nearly the same in the control and burned plots. Any extreme changes in density within the burned plot can then be attributed to the fire (Manly 2001). Evidence for an effect of fire on sparrow populations is provided by a statistically significant change in the difference between the control and burned plot before and after burning. On the other hand, if the difference between the two plots remains exactly the same before and after fire, then there is no evidence of an effect on sparrow population dynamics. This study design also allows us to determine the nature of any lasting effects of fire on sparrow populations. A principal factor in determining how often sparrow habitat may burn is determining how quickly their numbers return to pre-burn levels. By comparing sparrow density between the control and burned plots, we can accurately calculate this return time.

We are able to use such a design to preliminarily investigate the impact of fire because an unplanned fire burned through sections of occupied sparrow habitat in late May 1994. This fire impacted several point-count stations where sparrow numbers had been recorded since 1992, thus providing three years of pre-burn information. Since that time, these same points have been surveyed annually (up to 2001), providing seven years of postfire information. These pre- and post-fire time frames are long enough to capture background variability in sparrow numbers and detect the length of time sparrow numbers may have been depressed as compared to their pre-burn levels. Importantly, we also have information on sparrow numbers over this same time span in adjacent areas that did not burn in 1994. These areas can serve as controls.

Ideally we would have several such burns to evaluate. However, the 1994 fire is the only one for which we have highly accurate maps of fire extent. It is possible that further work with satellite imagery will prove useful in delineating other fires, so that we can replicate the analyses below and thus test some suggestions covered in the Discussion.

6.4.2 The 1994 burn analyses

Using an aerial photograph produced by the U.S. Geologic Survey in 1994, we identified a fire scar produced by a May 1994 fire. By overlaying the extensive survey results (see Chapter 5), we identified locations that consistently held sparrows over the period of record and were either burned in this fire or lay adjacent to the fire but were left unburned. Some points lay at the edge of the fire scar. Because the radius within which birds are counted in the extensive survey is 200 m, it is possible for the survey to record birds in these edge sites even though they show up as burned on the aerial photo. Because of this, we separated these sites into a third burn category, “edge.” The appendix to this chapter provides the points we located and the number of sparrows counted at each site between 1992 and 2001.

Our initial concern was whether the sites that burned in 1994 held similar numbers of sparrows pre-burn as sites that did not burn in 1994. Here, we asked if the sites are intrinsically similar in their ability to support sparrows. If they are not similar, we must be careful in attributing differences in postfire densities to the effects of fire. To do this we considered each point count an independent observation and tested for differences between the mean number of birds across the three burn categories (burned, control, edge) using only pre-burn density records. Because adults are extremely philopatric, it is unlikely adults counted at one survey location were the same as those counted at another either

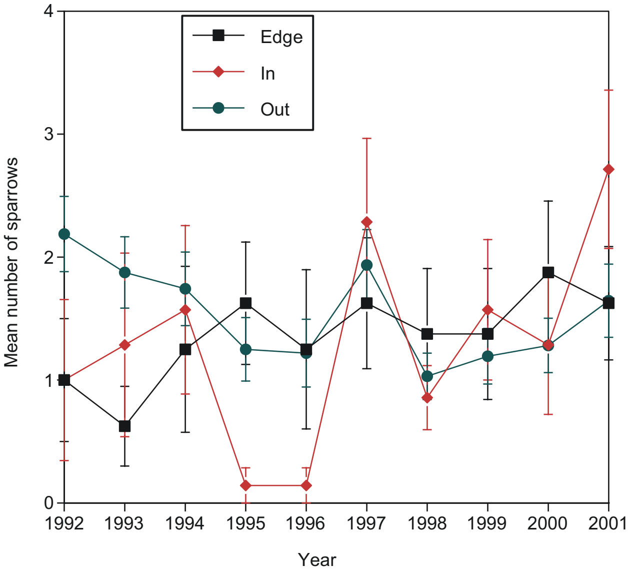

Figure 6.4: Sparrow numbers (mean ± S.E.) before and after the 1994 fire, at survey points inside, outside, or on the edge of the burn. For procedures in classifying points see text.

within or between years (see Chapter 2). For this reason we felt comfortable considering each surveyed density as an independent source of information on the effects of fire.

Because the same sites were resampled through time, and thus the annual density estimates for each survey location are not independent from each other, we used a repeated measures ANOVA. The results indicated that there was no difference between burn categories ($F = 2.0$, D.F. $= 2$, $p = 0.15$). There was also no evidence for an effect of time ($F = 0.4$, D.F. $= 2$, $p = 0.69$) or an interaction effect between burn category and time ($F = 1.2$, D.F. $= 4$, $p = 0.33$). Thus, we considered the burned sites as representing the same intrinsic quality of sparrow habitat as the unburned and edge sites.

Our next concern was whether sparrow numbers were lower in the years after the fire within the burned sites as compared to unburned or edge sites. Following the advice of Manly (2001), we included all years (i.e., before and after the burn) in a repeated measures ANOVA. The results indicated no difference between sparrow densities based on burn category alone ($F = 0.4$, D.F. $= 2$, $p = 0.64$). However, there was a significant effect of time ($F = 2.2$, D.F. $= 9$, $p = 0.02$) and more importantly, an interaction effect of burn category and time ($F = 2.5$, D.F. $= 18$, $p = 0.01$). This indicates that through time, the different sites reacted very differently to the fire.

Figure 6.4 illustrates this result. In the years prior to the 1994 fire, all sites had roughly the same sparrow densities. After the 1994 fire, the burned sites showed roughly one-third as many sparrows as the unburned and edge sites. This effect lasted for 2 years, after which the burned sites were indistinguishable from unburned or edge sites. The statistical significance of time, and especially the interaction effect between time and burn category, reflects this dip in sparrow density within the burned sites in 1995 and 1996. The recovery of sparrow densities in later years to pre-burn densities likely accounts for the nonsignificant difference in mean sparrow density among burn categories alone.

We can learn two more things from Figure 6.4. First, sparrow density appears the same for the entire five years after recovery from fire (i.e., post-1996). We tested this using the same methods as above, but including only sparrow density information post-1997. The results indicated no differences among burn categories ($F = 0.1$, D.F. $= 2$, $p = 0.89$). There was an effect of time alone ($F = 2.7$, D.F. $= 4$, $p = 0.03$) likely reflecting the decrease in numbers across all burn categories in 1998. Importantly, there was no interaction effect between time and burn category ($F = 0.7$, D.F. $= 8$, $p = 0.79$). Thus, we have no evidence that the 1994 burn increased the density of sparrows within the burned sites in post-recovery years, as has been presumed to be due to the removal of built-up litter (see Fig. 6.3). Second, this same analysis indicated that the sites that did not burn in 1994 did not appreciably change in sparrow density after 1992, a time span of nearly 10 years. The mechanism outlined by Werner, Taylor, and others predicted we should have seen such a decline (Fig. 6.3).

6.4.3 Discussion

Our results alternately support and refute the predictions stemming from the combined work of Stimson (1956), Werner (1975), and Taylor (1983). We clearly support the contention that sparrow populations are not permanently damaged by the effects of fire under some conditions. Sparrow populations in sites that burned in 1994 suffered significant impact but recovered to pre-burn densities after two years.

Of considerable importance when translating this result into management actions is the location of these sites in relation to areas that have been impacted by either altered hydrologic flows or unnaturally frequent fires. Figure 6.5 shows the number of sparrows counted at each survey location scaled by the total number of sparrows ever counted between 1992 and 2001. The sites included in these analyses are enclosed in a black box. They are embedded within the largest and most stable sparrow population (population B). This population has been largely spared from the detrimental impacts of altered hydrologic flows that are apparent within all other sparrow populations (Chapter 5). Thus, annually, sparrow densities are high in the survey points we included in these analyses, and all available adjacent habitat appears filled. This likely translates into a faster recovery time, as there are plenty of potential breeders nearby capable of immigrating into the burned area once the habitat recovers.

This is not likely true for fires that burn through other populations. We observed a severe impact on sparrow density due to fire as sparrow density decreased to essentially

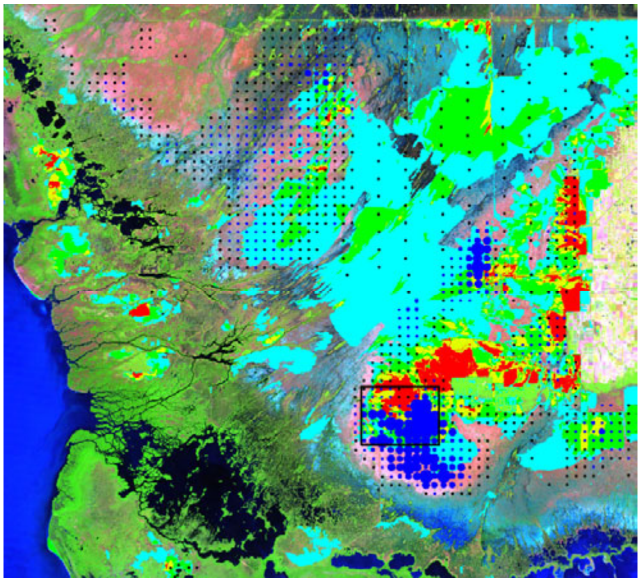

Figure 6.5: Fire frequencies in Everglades National Park, sparrow survey points (black), and the scaled combined sparrow numbers from 1992 to 2001 (dark blue dots). Color indicates number of fires over the interval 1980 to 2001: pale blue, green, yellow, and red indicate areas that have burned one, two, three, or ≥ 4 times since 1980, respectively.

zero postfire. Very isolated pockets of sparrows may not be capable of recovering from these low densities simply because there are no unaffected sites from which new immigrants can be drawn. This isolation effect may be the same one noticed by Stimson in 1956, which accounts for his differing opinion of fire as compared to Werner (1975). Today, the lack of unaffected sites may be due to fire itself (e.g., in an extensive fire, or very common fires), or because all other areas have been negatively affected by altered hydrologic flows.

The possibility that other fires limit the recovery potential of sparrows postfire is of particular relevance when formulating fire management plans. Figure 6.5 also shows the frequency with which fires have burned across Everglades National Park since 1980. Red indicates areas that have burned four or more times since 1980, yellow indicates areas that have burned three times, dark blue indicates areas that have burned twice and light blue indicates areas that have burned only once since 1980. According to Gunderson and Snyder (1994), large fires naturally occur only every 10 years (small fires are more common but burn very small proportions of the park annually). If we use this as a rough guide as to how often marl prairies should have burned since 1980, the blue areas, and possibly the yellow areas, should be considered within the natural regime. Red areas, however, have burned too often. These areas are not randomly placed within the park boundaries, providing further evidence that such a fire frequency is unnatural. All red areas are located either directly adjacent to the current park boundary or adjacent to the former park boundary. Several coincide with sparrow populations indicating that frequent fires may preclude sparrow occupancy. These spatial effects are independent of any natural variation in sparrow recovery due to differences in soil depth or unnatural variability due to alteration of hydrologic flows. We are largely ignorant of the combined effect these spatial differences have on sparrow populations.

In sum, we should expect considerable spatial variability in the way current sparrow populations respond to fire. Thus, we should be very cautious in assuming that all segments of the sparrow population will return to prefire densities within 2–3 years, and instead view this recovery potential as a best-case scenario. There is much yet to learn about the demographic response of sparrows to fire, especially as it relates to the natural and human-induced spatial heterogeneity of the ecosystem.

Our results do not support the assertion that burning marl prairies benefits sparrows either by increasing the suitability of prairies immediately postfire or by preventing a decrease in suitability through time. This is in direct contrast to the recommendations of Werner (1975) and thus questions the need to prescribe fire within marl prairies every four years in order to maintain sparrow populations. Further, we find no evidence to suggest prescribing fires at any other time interval will be beneficial.

There are two caveats to these findings. First, marl prairies may require fire for reasons other than the preservation of Cape Sable Seaside Sparrow populations (for example, fire is believed to inhibit the growth of shrubs and other woody vegetation). Sparrows are capable, under maximally favorable conditions, of enduring the effects of fire without long-term damage to their numbers. This indicates that fire was a regular part of their evolutionary history and is consistent with what we know of the natural fire regime in the Everglades. Nevertheless, given the current threatened status of the sparrow and the current unnatural fire regime, we suggest that strong evidence proving a non-sparrow-related need to burn marl prairies must be presented before Everglades National Park management reinstates prescribed fires within sparrow habitat.

Second, our record of sparrow density encompasses only 10 years of postfire information. Although this time span is remarkably long for any conservation study, it may not capture the variability associated with the natural Everglades fire regime. If the fire frequency of Gunderson and Snyder (1994) is correct, and these are the types of fires to which sparrows (and marl prairies) are adapted, we should not expect to see declines in sparrow density until well after 10 years postfire. Currently our records are incapable of detecting such an effect. However, we are presently on the cusp of this time frame. Continued monitoring of fire and rangewide sparrow density should shed light on this possibility.

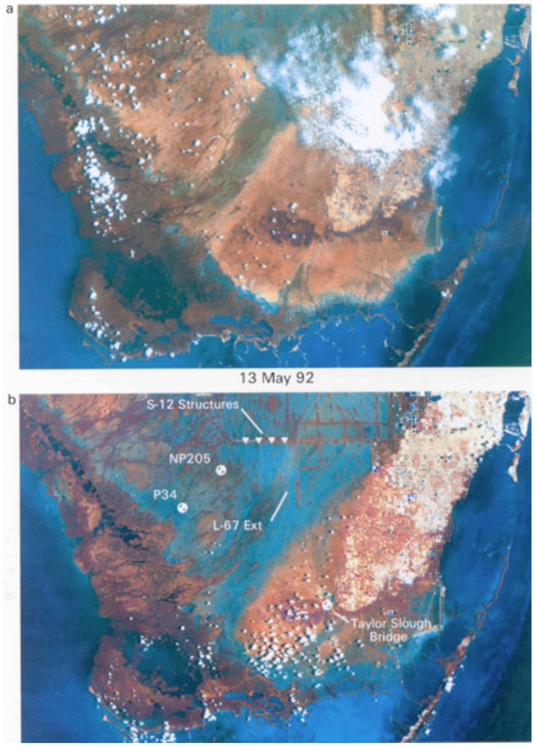

Figure 6.6: Satellite images of Everglades National Park and surrounding areas, taken in the dry seasons of 1992 (upper) and 1995 (lower). Flooded areas are blue; dry areas, including marl prairie, are pink. Clouds are white.

6.5 Flooding

In this section, we ask two questions about the effect of water levels on population changes. In the first of two main parts, we ask whether there is a tight connection between water levels and sparrow breeding. We then consider the immediate and direct consequences of high water during the breeding season. In the second section, we examine the bird's habitat. The sparrow occupies prairies with plants characteristic of short periods of flooding (hydroperiods). It avoids vegetation characteristic of long hydroperiods. Might prolonged flooding alter the bird's habitat?

6.5.1 The area and its hydrology

The area's main features are obvious in the satellite images that constitute Figure 6.6. Shark River Slough is the central flow-way through the southern Everglades and is flooded most of the year; it is blue in the image. Marl prairies, in pink, are flooded for 3–7 months each year. They flank the eastern and western edges of the slough and are the sparrow's preferred habitat.

Historically, water flowed across the entire width of Shark River Slough. The construction of a system of levees created the Water Conservation Area 3A (WCA3A) impoundment in the mid 1960s. This is the area immediately to the north of Everglades National Park. The boundary is obvious as a pink line in the satellite image for 1995 and as a sharp boundary between blue (water) and pink (dry prairie) obscured by clouds in the 1992 image. Four gated spillways (S12A–S12D) control the release of water from WCA3A into Shark River Slough. These structures constrict the flow primarily to the western portion of the slough.

Another levee (L67-extension) prevents water from these spillways from flowing to the east (see also Fig. 5.1). The resulting redistribution of flows causes deeper water levels within the western portion of Shark River Slough than occurred historically. It also extends the period these western prairies are flooded (Van Lent 1996).

Taylor Slough, to the east, is a much smaller drainage of marl prairies that flows roughly southward to Florida Bay. The agricultural and urban areas to its east are drained by an extensive network of canals. Toward the southern end of these areas, a pumping station started operation in 1980 with important consequences for the sparrow and its habitat.

6.5.2 Water levels and breeding

The sparrow's breeding season peaks during the dry period (normally, mid-March through mid-June) when the water table can be as low as 1 m below the surface. They breed until the onset of molt and may nest into August (Werner 1975, Lockwood *et al.* 1997). We have established a tight empirical connection between dry conditions and breeding (Chapter 2).

On our extensive surveys in 1981 and 1992, we rarely heard singing birds when water levels exceeded 10 cm. It is reasonable to assume that even if birds were present, they were not singing because they had not been able to establish territories.

Detailed studies of the birds' breeding success shows the number of nests lost to predators increases dramatically as water levels rise above 10 cm (Fig. 2.2). In any case, nests are built 10–20 cm above the base of the grass tussocks (Chapter 4). Water levels above these heights flood the nests and so restrict the breeding habitat.

6.5.3 The immediate consequences of high water levels

The differences in water levels between 1992 and 1995 are self-evident in the satellite images of the area, taken during the birds' peak breeding season of April and May (Fig. 6.6). In 1992, large areas of dry prairie are visible as pink regions on either side of Shark River Slough. In 1995, in contrast, the area west of the slough is blue, indicating it was covered in water. The years 1993 and 1995 were broadly similar, while 1994 and 1996 were only slightly drier.

Within these images lies the essence of our story: one year of high water (1993) was responsible for greatly reducing the sparrow's numbers west of Shark River Slough. Three more wet years kept the numbers low. There may have been sparrows in the area in 1993, but unless they sing we cannot find them. We do know, however, that the annual survival of territory-holding males is about 65%, and likely less for females and young males (Chapter 3). We would expect few individuals to live through four years without breeding to see the relatively dry year of 1997.

Although the overall story is obvious from Fig. 6.6, there are details. It is on these details of the sparrow population to the west of Shark River Slough that we focus in this section. We first document the detailed temporal changes at two water level monitoring stations, then spatially extend the information from these two points. As a final step, we ask what factors drive the water levels.

6.5.4 Temporal changes

The South Florida Natural Resources Center provides us three sources of information about water. First, there is a rainfall monitoring station situated close to the S12A spillway at the northeastern corner of the survey area. Second, there are daily water release data for the S12A structure. Finally there are two hydrological monitoring index stations, NP205 and P34, at the northeast and southwest edges of the bird's western population (population A) respectively (Fig. 5.1). The NP205 station lies on the ridge that separates Shark River Slough from the western prairies. This gauge is $\sim$ 7.5 km south and downstream of S12A. The ground elevation of NP205 is $\sim$ 180 cm above mean sea level (MSL). The P34 station is $\sim$ 60 cm above MSL.

There are several gaps in these data. The NP205 data contain periods with no records. We estimated data points for gaps of less than 10 days using linear interpolation. For a 76-day period covering April, May, and some of June 1992, and for predictive purposes only, we estimated missing values by adding 120 cm (the difference between NP205 and P34 elevations) to P34 levels for the same period. We used the same technique to cover a large gap during spring 1989. Finally, rainfall figures were not available for January–July 1993; we inserted the 20-year mean breeding season rainfall.

The temporal trends in mean breeding season water levels at NP205 and P34 over the period 1976–1996 are very tightly correlated. The exceptions are the dry years 1977, 1989, 1990, and 1991, when the water levels in P34 remained relatively high. P34's much lower elevation means that it cannot dry down to the levels seen at NP205. (P34 levels cannot drop below sea level [-60 cm MSL]). With this caveat, we find the water levels to be so similar that we conclude that the water levels are even across the survey area. Henceforth, we will consider the levels at NP205 to adequately represent water levels for the entire study area.

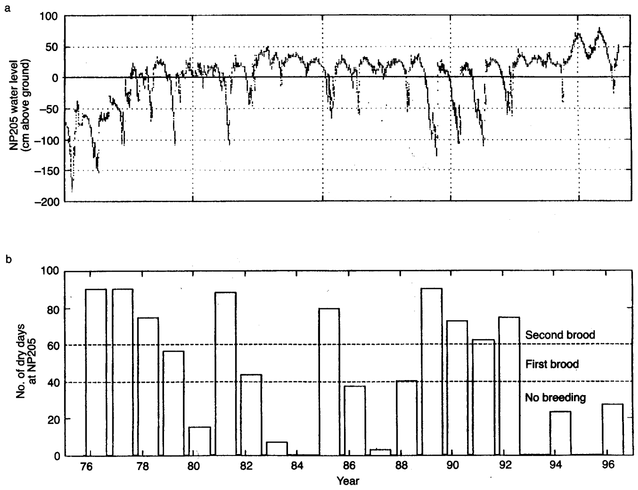

Figure 6.7: (a) Water levels at the NP205 gauge. (b) The number of dry days during the breeding season at NP205. Values > 40 days would permit sparrows to complete one brood; values > 60 would allow them to begin a second brood. Missing bars indicate zero dry days.

Between 1975 and 1978, the water table was permanently 50–200 cm below ground level (Fig. 6.7a). The 1980s were generally much wetter. From 1989 to 1992, the dry period lasted two months during the first half of the year. Since 1993, NP205 water levels have remained above ground level for most of the time. There were two short dry periods during 1994 and 1996. The four wettest breeding seasons were 1984, 1987, 1993, and 1995. Other than these, only two years (1980, 1983) were wetter than 1994 and 1996. The period from 1988 until 1992 was a dry one, comparable to the four years ending in 1979.

We calculated how many days would be dry during each breeding season, defined as 15 March and 90 days thereafter (Fig. 6.7b). Figure 2.3 suggests $\sim$ 40 days as the dry period within which one breeding cycle can occur. Sixty days allows for the initiation of second clutches, and 80 days allows for the fledglings of the second clutch to leave the nest.

Interpreting these numbers as sparrow breeding opportunities, we see that from 1993 to 1996 high water left little opportunity for sparrows to breed at the elevation of NP205 (Fig. 6.7b). The window of breeding opportunity also lasted less than 40 days in 1980, 1983, 1984, 1986, and 1987. In all but two of the remaining years (1982 and 1988), the breeding opportunity lasted more than 60 days allowing for the potential of second clutches.

In the years of the extensive sparrow survey (Chapter 5), 1981 and 1992 were dry years and sparrows were abundant. The survey years 1993 to 1996 were initially wet and remained too wet to allow breeding. The sharp decline in sparrow numbers from 1992 to

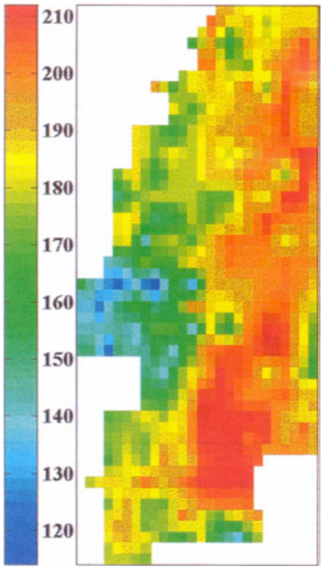

Figure 6.8: Map of elevation in the area west of Shark River Slough, estimated from water depths relative to the depth at the NP205 gauge. Scale at left is cm above mean sea level.

1993 corresponded to a change from four drier than average years to four unusually wet ones.

6.5.5 Spatial patterns

Is NP205 typical of the several hundred square kilometers over which the sparrow occurs? Everglades National Park scientists endeavor to pick monitoring stations that are typical of the surrounding region. Nonetheless, we will now try to answer the question. The answer, obviously, depends on the topography of the area.

No detailed data on the area's topography exist. Consequently, during the 1995 sparrow survey, we measured the water depth at 284 census sites within the western survey area. That we could do this across the entire area is itself testimony to that year's high water levels. For each site we calculated the mean water depth from measurements taken at six random points. We expressed these as elevations relative to the NP205 water level for the survey date. Finally, we constructed a sparse landscape matrix at a 500 × 500 m resolution.

Alternate cells contained no data, but we estimated their values by taking the average value of neighboring cells. Figure 6.8 shows the results. The sites span about 1 m in elevation, and a higher ridge runs north to south along the eastern edge of the area.

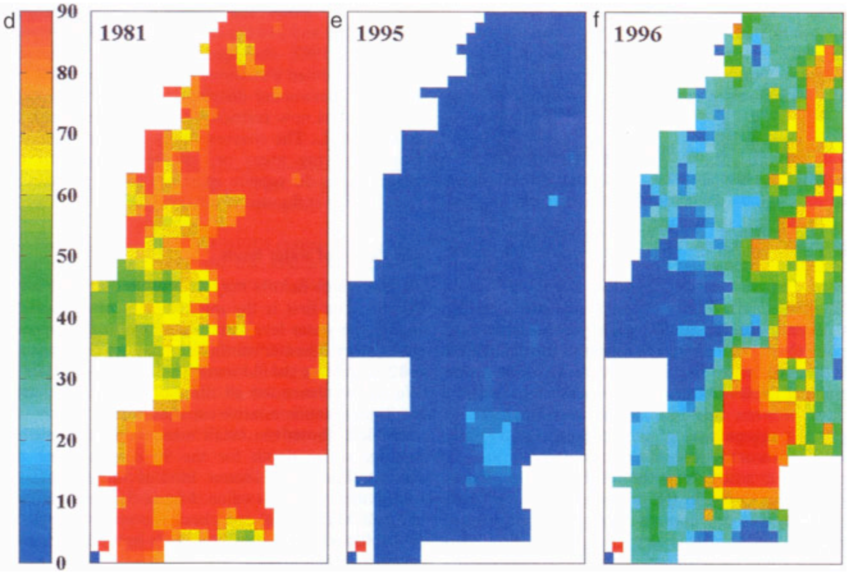

Figure 6.9: Number of dry days in sparrow habitat west of Shark River Slough (scale, at left, is in days).

We predicted the hydrological history of each cell by comparing daily NP205 levels with the elevation of that cell. For each year since 1976, we counted the number of dry days in each cell for each year. These data allowed us to map the annual duration of the dry period across the extent of the survey. We calculated the percentage of the census sites that were dry for > 40 and > 80 days between mid-March and mid-June. These represent the percentages of the landscape potentially available for one or two broods, respectively.

Figure 6.9 shows the results of this process for three sample years. In the dry year of 1981, 56% of the total area was dry enough to support one brood, and a further 39% of the area was dry enough to allow two breeding attempts. In contrast, in 1995, no part of this area was dry long enough to allow the birds to attempt even one brood.

Table 6.1 summarizes the predictions of available habitat for the 20 years for which we have hydrological data. The years 1993 and 1995 were the worst years on record in terms of the available breeding habitat for the sparrow. Only 1983 and 1984 were worse than 1994 and 1996. The four years from 1993 were exceptionally poor in terms of the area of available breeding habitat. These spatial results exactly match those based on the point record of NP205 (Fig. 6.7).

Figure 6.8 shows that most of the landscape lies between 180 and 210 cm above MSL. In the dry years of 1981 and 1992, the sparrows were widespread but mainly inhabited elevations of 170 to 210 cm. Since 1993, the elevational distribution of sparrows has narrowed

Table 6.1: Breeding season water levels (cm above mean sea level) at the NP205 gauge and associated statistics for 1977 to 1996. [a]As explained in the text, no rainfall data were available for the breeding season in 1993, so the long-term average has been substituted.

Year	Mean breeding-season water level	Mid-March water level	Water level change during breeding season (cm)	S12A water release (cm-acre /day)	Breeding-season rainfall (cm)	Habitat available for one brood (%)	Habitat available for two broods (%)
1977	−59.96	−81.25	21.29	0.00	6.32	100	89
1978	−27.55	10.20	−37.75	0.00	8.98	94	59
1979	−35.05	−48.94	13.89	0.00	10.33	88	55
1980	9.44	19.95	−10.51	0.00	15.39	42	23
1981	−51.77	−1.69	−50.08	0.00	3.63	100	74
1982	−3.27	−22.33	19.06	0.00	16.95	72	18
1983	20.71	37.63	−16.92	767.05	4.56	15	0
1984	17.68	24.83	−7.15	745.00	12.84	27	11
1985	−27.64	−32.78	5.14	55.16	6.95	93	63
1986	−8.42	3.79	−12.21	213.07	5.64	56	35
1987	13.71	19.64	−5.93	248.75	12.72	33	23
1988	−7.15	11.72	−18.87	14.88	13.13	63	37
1989				0.00	4.11	100	100
1990	−61.77	−69.97	8.20	0.59	9.53	100	35
1991	−42.77	−72.10	29.33	18.79	15.51	99	20
1992				0.00	5.75	95	56
1993	29.56	27.56	2.00	2063.64	8.00[a]	4	0
1994	8.55	21.17	−12.62	143.72	5.89	27	18
1995	38.32	52.26	−13.94	1121.48	10.31	0	0
1996	9.46	27.87	−18.41	0.00	12.94	33	9

and is now restricted to elevations above 200 cm. The sparrows may have been eliminated from low-lying areas or, sensibly, moved to higher ground, as do Seaside Sparrows in flooded saltmarshes (Post 1974).

6.5.6 The causes of water levels

At least three factors may determine the water levels at NP205. The first is the initial height of the water: the higher the water level, the faster one might expect it to drain away. The second, rainfall, and the third, flows across the S12 structures, should also affect the average water level. We found evidence for all three of these effects; what is important is their relative contributions.

Table 6.1 shows the mean breeding-season water level: the average water depth for the 90 days starting on 15 March. The change in water level is this average value minus the 15 March value. Nott *et al.* (1998) analyzed this change in water level and found that at the highest water levels (in mid-March), the decline in level is the greatest ($p < 0.01$).

They then took the residuals about this relationship, and found that water levels fall less than expected when there is more rain ($p < 0.02$, one-tailed test). Interestingly, the regression coefficient is 1.8, meaning that 1 cm of rain creates 1.8 cm of flooding. This suggests that the water at NP205 is driven partly by water flows from elsewhere. The coefficient also suggests that the roughly 10-cm range in rainfall over the 20 years of the study would contribute a $\sim$ 18-cm range in water levels at NP205, other things being equal.

Finally, Nott *et al.* (1998) examined the residual fall in water levels given both the mid-March level and the rainfall in relation to the managed flow over the S12 gates. Positive residuals characterized all but the two smallest flows of the 11 years in which such flows occurred. Conservatively, they restricted the analysis to these 11 years. Water levels dropped least during the highest flows ($p < 0.01$).

These analyses recreate a forward selection process in a stepwise multiple regression. The procedure discriminates against the last variable to be entered, because its predictive power is stripped by any correlation it may have with the independent variables already in the model. In this case, they entered this variable last to make the results as conservative as possible.

Stated simply, this analysis shows that the managed flows over the S12 gates contributed to the inundation of the sparrow's nesting habitat. The largest residual water level coincides with the largest release over the S12 gates in 1993 and the year when the sparrow population in this area plummeted. In 1993, the flows added over 22 cm to the water level. Had the water levels been 22 cm lower, roughly half the area would have been dry enough, long enough, to allow nesting pairs to complete one brood.

No reader should miss the significance of this: this is "take" under the definition within the Endangered Species Act. Poor water management eliminated almost half of the population of this endangered species.

6.5.7 The effects of water levels on vegetation type

The results of our extensive surveys show that the sparrow is found almost exclusively in marl prairies. These prairies are either dominated by muhly grass (*Muhlenbergia filipes*)

Table 6.2: A comparison of the vegetation of Taylor Slough between 1975 (from Werner 1975), and 1995–1996. We determined species dominance for the 1995 and 1996 data by scaling percent coverage measurements per m^2 to percent coverage of all live plants, after Werner's method.

Year	1975	1995–1996
Mean number of plant species/m^2	9.9	4.1
Muhly grass dominance (% cover)	82	21
Sawgrass dominance (% cover)	14	77

or are mixed prairies with no dominant grass species. Mixed prairies are often diverse and include muhly grass, sawgrass, and black-top sedge (*Schoenus nigricans*). The sparrow avoids prairies dominated by sawgrass and spikerush (*Eleocharis* spp.) that have longer hydroperiods. We now show that prolonged flooding altered the vegetation and prevented sparrows from breeding in two areas. These changes were quite rapid, but they had longer term consequences to the sparrow than the ephemeral flooding.

6.5.8 The history of Taylor Slough

After the western population, the largest decline of the sparrow has been in the Taylor Slough drainage (Chapter 5, inference 3). In Taylor Slough, in addition to the extensive sparrow survey, we have long-term data on both bird and plant community composition. Werner established a study plot in 1974 on the east side of Taylor Slough (Werner 1975). The site was a north to south oriented 150-ha rectangle. In 1992, Curnutt established a permanent study plot in the southwest corner of Werner's site measuring 66 ha. The population of sparrows increased from 11 singing males in 1974 to 21 in 1975 (Werner 1975). In 1981, the extensive survey heard three males singing at three points, suggesting a density of 8 territories per 100 ha (1 km^2). In 1993, Curnutt found no sparrows in Taylor Slough.

We compared the floral composition of Taylor Slough in 1995 and 1996 to that of Werner's study in 1975 (Table 6.2). Just as Werner recorded, we found muhly grass and sawgrass to be the dominant species in this area. However, in the 21 years between the surveys, the relative dominance of these two species had switched. The area changed from a diverse, muhly grass-dominated prairie to a less diverse, sawgrass-dominated one.

Further support for these changes comes from a detailed vegetation study of Taylor Slough by Armentano *et al.* (1997 **[or is it 1995?]**). Across 10 plots in a transect just north of Werner and Curnutt's plots, muhly grass cover averaged 61% in 1980 but only 9% in 1995. Armentano *et al.* (1997) suggested that the changes did not happen gradually. In a transect placed within both Werner's and Curnutt's study plots, muhly grass increased in

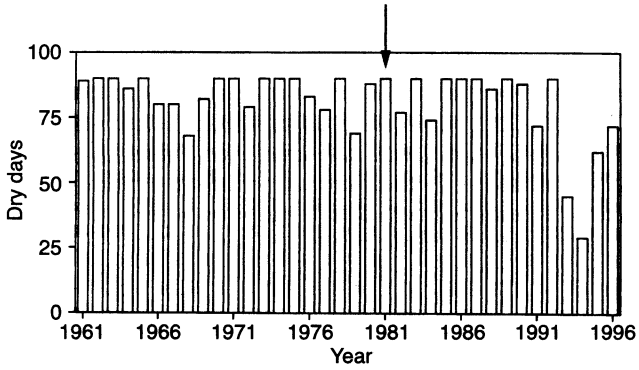

Figure 6.10: The number of dry days at Taylor Slough bridge during the first 90 days of the breeding season; the arrow indicates the date of increased pumping.

abundance from 35% cover in 1980 to 54% in the dry year of 1992. By 1995, its cover had declined to only 25%.

The conversion of this area from a muhly grass-dominated to a sawgrass-dominated prairie indicates a lengthening of the hydroperiod. The placement of a pumping station (S332) at the boundary of Everglades National Park and Taylor Slough in July 1980 altered the hydrology of the downstream drainage of the slough. Interestingly, Kushlan *et al.* (1982) correctly predicted a change from muhly grass to sawgrass dominance in the plant community directly downstream of the station. Figure 6.10 shows the number of days the water level at the monitoring station at Taylor Slough bridge was above ground level for the 90 days following 15 March. The area was typically dry for most breeding seasons up until 1992. Almost certainly as a consequence of increased pumping from S332, the area since 1993 has been much wetter than the 20 years prior to the pump's operation.

This is not the whole story, however. The sparrow population has also declined dramatically in areas upstream of S332. Earlier in this chapter, we attributed these changes to frequent fires. In sum, it seems that in Taylor Slough, the sparrow has declined through a combination of making some of its habitat too wet and some of it too dry.

6.5.9 Population D

This population, too, has declined from its 1981 level. Managed releases of water into this area, particularly in 1993, seem the most plausible explanation for the declines. However, except for the analyses reported in the next chapter that employ remotely sensed data, we have not completed a full analysis of the role of hydrology on this population.

6.5.10 Vegetation changes west of Shark River Slough

We now return west of Shark River Slough, to population A, which has still not recovered from its precipitous decline in 1993. Could changes in vegetation similar to those in Taylor Slough be responsible for preventing the species' recovery there?

We collected data on the vegetation types at each site we visited during the extensive surveys of 1981, 1992, and 1996. Such data are no more than a quick visual inspection of each site to record the dominant grasses. They do provide an extensive estimate of the broad pattern of changes in the vegetation. We grouped the prairie vegetation types into two major classes that separate the mixed and muhly grass-dominated prairies with short hydroperiods ("dry") from the sawgrass-dominated vegetation with long hydroperiods ("wet"). We then classified each site surveyed as having undergone no vegetation change, a change from long- to short-hydroperiod vegetation (wet to dry), or the reverse change (dry to wet).

Nott *et al.* (1998) showed that the changes took place between 1981 and 1992 and between 1992 and 1996. There are three sources for these changes. The first is errors of classification. Bass collected all the 1981 and 1992 data. In order to minimize classification errors, he carefully trained just one other observer in 1996 to assist him. The second source stems from the inherent difficulty of locating the exact 1981 survey sites (found by dead reckoning) with the GPS system available in 1992 and 1996. In this area, patches of mixed prairie are small and intermingled with the sawgrass. The helicopter might easily land in mixed prairie one year and sawgrass the next at what appears to be the same site, but is in fact ~ 100 m off. Even between 1992 and 1996, errors in the GPS readings (on the order of 50 m) could account for some classification errors. The final source of changes are those that really took place. These must be sufficiently numerous and directed to be convincing.

Counting each survey point as statistically independent shows that more sites initially counted as sawgrass-dominated (wetter) in 1981 were counted as mixed prairies (drier) in 1992 (96) than vice versa (59); 100 and 74 remained unchanged in the drier and wetter categories respectively ($\chi^2 = 12$, $p < 0.01$). Table 6.1 shows that 1992 was a dry year, but was followed three wet years. Between 1992 and 1996 the pattern of vegetation change was reversed. Some 103 sites changed from vegetation typical of dry habitats to that typical of wet, while only 39 changed from wet to dry; 77 remained dry and 39 remained wet ($\chi^2 = 5$, $p < 0.05$). The years 1993 to 1996 had exceptionally high water levels.

The patterns of change show a finely structured mix of sites that did and did not change during the two comparisons. Between 1981 and 1992 sites that remained or became dry lay along the higher north-south ridge. Areas in the northwest appeared to dry consistently too. Sites that became wetter were in the lower, southeast corner. In 1996, the sites in the northwest were consistently classified as drier than in 1992. Only the highest sites remained dry.

A change in one site is not necessarily statistically independent of a change in another site 1 km away. If it were, these broad geographical trends would not be obvious. This makes our χ^2 values more significant than they really are. Nonetheless, most sites do change and the fine mixing of the vegetation and slight differences in elevation makes the changes largely independent. A more formal removal of the effects of temporal and spatial autocorrelation using a modified Mantel technique (Fortin and Gurevitch 1993) revealed the same qualitative conclusions (Nott, pers. comm.).

6.5.11 The causes of vegetation changes

We have no detailed observations on the changes from the wetter, sawgrass-dominated communities to drier mixed prairies. Hydroperiod itself may be the explanation. In addition, drier communities are more likely to burn, and perhaps sawgrass does not recover from burning as fast as its competitors.

We propose the following mechanism for the change to sawgrass domination. Increased production and changes in the periphyton result from increasing water levels and longer hydroperiods (Browder *et al.* 1994), or from nutrient enrichment (McCormick and O'Dell 1996). Normally submerged periphyton mats can become floating mats and shade out submerged macrophytes (Van Meter-Kasanof 1973). Field observations suggest that as heavy floating periphyton mats dry they can flatten and kill the aboveground portion of muhly grass and other vulnerable species. In contrast, sawgrass can penetrate this thick mat. An area of several square kilometers once dominated by mixed prairie was covered by such a mat after the waters receded in 1996. This area no longer held the breeding population of the sparrow that it once had. Indeed, there would have been few places for sparrows to nest had they been there.

6.5.12 Discussion

There is a tight connection between water levels and sparrow breeding. Nests are much more likely to fail when water levels are high. Sufficiently high levels flood any nests that survive predators. High water levels west of Shark River Slough are largely a consequence of managed flows from upstream areas to the north of Everglades National Park. In 1993, record flows across the S12 spillways raised the water level over 20 cm, and the sparrow population declined precipitously. Relatively high water levels in 1994 to 1996 kept the population low.

The sparrow occupies mixed prairies with short hydroperiods. It avoids sawgrass-dominated areas; these have longer hydroperiods. In the east in Taylor Slough, a pumping station increased water levels, changed the vegetation from muhly grass- to sawgrass-dominated, and so caused the population to decline. In the west, similar changes have appeared over a wide region since the high water levels that started in 1993.

A question that remains is whether it is possible to measure these large-scale changes in the vegetation at a fine spatial scale and at frequent intervals. Remote sensing offers that promise, and we shall return to this topic in the next chapter.

6.6 Summary

At the start of this chapter, we presented a series of hypotheses — some more credible than others — to explain the changes in sparrow numbers. In the order in which they appeared, here is a synopsis of our results.

- *The sparrows did not disappear; we just haven't been looking for them in the right places.* This is the least credible hypothesis. It has never been associated with plausible suggestions of where the missing birds may be hiding.

- *Population fluctuations are a normal part of the ecology of all small birds, especially those with small, restricted populations.* We showed that the changes in bird numbers are not only statistically significant but fall outside the range expected for normal populations.

- *Flooding is a natural part of Everglades hydrology. We have always had wet years and dry years.* That may be correct, but we showed that the flooding that caused the population declines is the result of deliberate management decisions. Those decisions have caused flooding far in excess of what would be expected from natural variability.

- *Flooding causes only temporary damage to the habitat on which the sparrows critically depend.* We rejected this hypothesis by demonstrating that the habitat has been modified over the long term. It is a sufficiently important demonstration that we return to explore it in the next chapter.

- *Colonists from the healthy eastern populations will quickly restore the western population.* This was not a credible hypothesis when it was first proposed. The birds are known to be highly philopatric, the distances involved are great, and the hypothesis does not address the question of whether the eastern populations had an excess of individuals. Most telling of all is that the western population has not recovered.

- *The eastern areas suffer from a much higher frequency of fires, mostly anthropogenic, accounting for repeated extirpations in population F and the northern part of population C.* We confirmed this hypothesis.

- *Habitat in populations C and D has been permanently altered by the change in water regimes due to pumping of water into Everglades National Park just north of Taylor Slough Bridge.* This is confirmed for the southern part of population C by detailed vegetation analyses. A similar hypothesis seems to be the best explanation for the changes in population D.

- *Three years of almost continual flood caused significant damage to sparrow habitat that is only now, six years later, regaining its former extent.* This is another hypothesis that we have confirmed. However, it is one to which we will return in the next chapter to explore further.

- *Sparrow numbers are recovering slowly as their breeding ecology suggests they should.* As Chapter 3 demonstrates, only when the great majority of the nesting pairs in a population can all rear two or more broods can the population grow significantly from one year to the next. The observed failure of the western population, A, matches what we expect from this demographic analysis.

6.7 Appendix

Table 6.3: Data used for the analysis of the effect of fire on sparrow numbers, as counted during annual helicopter surveys. Survey sites were classified as inside, outside, or on the edge of the 1994 burn .

Survey site	Burn	Number of sparrows counted									
	class	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
mahog-13	edge	0	0	0	0	0	0	0	0	0	1
mahog-16	edge	0	0	3	3	4	4	4	3	2	5
mahog-18	edge	1	0	0	3	0	1	0	0	4	0
mahog-20	edge	0	0	2	2	2	3	2	2	3	4
mahog-24	edge	4	2	5	3	4	3	3	3	3	3
mahog-27	edge	1	1	0	0	0	1	0	0	0	0
mahog-28	edge	2	2	0	2	0	1	1	3	3	1
mahog-5	edge	0	0	0	0	0	0	1	0	0	0
mahog-14	in	0	0	0	0	0	0	1	0	0	1
mahog-15	in	0	0	0	0	0	2	1	0	1	1
mahog-21	in	0	0	1	0	0	2	2	1	0	0
mahog-22	in	0	0	0	0	0	0	0	1	0	1
mahog-23	in	0	3	2	0	0	4	1	2	4	3
mahog-29	in	4	5	4	1	1	4	0	4	2	2
mahog-30	in	3	1	4	0	0	4	1	3	2	3
mahog-10	out	0	0	0	2	0	0	1	0	3	0
mahog-11	out	0	1	0	0	0	0	0	0	0	0
mahog-19	out	2	0	3	6	4	3	1	2	1	2
mahog-2	out	0	0	0	0	0	0	1	0	1	0
mahog-26	out	0	1	0	0	0	0	0	0	0	0
mahog-3	out	0	0	0	0	1	1	0	0	0	0
mahog-31	out	3	1	1	2	2	0	3	2	2	3
mahog-32	out	5	3	4	2	4	5	1	1	2	0
mahog-35	out	0	0	0	0	1	1	0	0	1	0
mahog-36	out	1	0	4	1	0	1	1	0	1	0
mahog-37	out	2	0	0	0	0	0	0	2	0	0
mahog-38	out	3	3	2	3	5	2	2	2	0	1

Survey site	Burn	Number of sparrows counted									
	class	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
mahog-39	out	2	6	5	3	1	3	1	0	0	4
mahog-4	out	2	0	0	0	0	0	0		0	0
mahog-40	out	3	4	3	2	2	5	3	2	0	2
mahog-44	out	3	2	4	2	3	2	2	4	3	3
mahog-45	out	1	4	1	0	1	2	0	1	2	1
mahog-46	out	1	1	2	1	1	2	0	2	1	1
mahog-47	out	2	2	3	0	5	2	1	0	1	0
mahog-48	out	3	3	4	1	2	4	2	2	2	1
taylr-1	out	0	0		2	0		0	3	2	1
taylr-15	out	5	4	4	4	0	2	2	2	3	3
taylr-16	out	2	1	2	2	0	4	1	3	1	0
taylr-2	out	0	1	0	0	3	0	0	0	0	0
taylr-28	out	4	2	1	0	2	2	3	0	2	3
taylr-29	out	4	2	3	2	0	5	1	4	3	3
taylr-39	out	5	4	4	1	1	3	3	0	4	6
taylr-40	out	3	3	0	1	1	3	0	1	1	3
taylr-46	out	5	4	2	0	0	3	2	2	1	3
taylr-47	out	4	3	0	0	0	2	0	2	0	2
taylr-7	out	4	3	2	3	0	3	2	0	4	3
taylr-8	out	1	2	0	0	0	0	0	0	0	1

Chapter 7

Habitat Modeling

7.1 Introduction

7.1.1 The legal background

Countries differ in the vigor with which they protect biodiversity and in the particular laws they pass to do so. In the United States of America, one of the most effective laws is the Endangered Species Act. It prohibits direct take — the killing or harming — of federally listed endangered species. From its inception there has also been the implication that it prohibits indirect take (the destruction of the ecosystems on which species depend). That provision was challenged in a legal case, *Sweet Home vs. Babbitt*, argued in front of the Supreme Court of the United States on 17 February 1995. In the context of the Spotted Owl (*Strix occidentalis*), an Oregon group challenged the responsible cabinet member, Secretary of the Interior Bruce Babbitt, arguing that only direct take, and not habitat destruction, violated the law. In a brief of *Amici curiae* scientists, one of us (SLP) among others (Cairns *et al.* 1995) argued that habitat destruction is most often the cause of species endangerment and extinction.

The Supreme Court agreed with that position. In doing so, they raised a scientific question that transcends national boundaries: how are we to demonstrate that human actions harm the habitat on which a species depends? In the case of the owl, the action, extensive logging of the old growth forests on which the birds depend, was obvious. Of course, it need not be.

In Chapter 6, we demonstrated that the unnatural flooding of the breeding habitat of the Cape Sable Seaside Sparrow directly caused its precipitous decline in the western half of its range (Curnutt *et al.* 1998, Nott *et al.* 1998). The flooding resulted from the diversion of the area's drainage, Shark River Slough, to the west of its natural path and a change in the timing of its seasonal ebb and flow. Concomitant with those changes, areas in the east became overdrained and more susceptible to anthropogenic fires. Bird numbers are significantly reduced in burned areas for two years postfire, even on areas with good (deep) soils.

We also showed that unnatural, prolonged flooding had modified the landscape by converting the birds' preferred habitat (mixed prairie, often with a substantial percentage of muhly grass [*Muhlenbergia filipes*]) into less-suitable habitats dominated by sawgrass (*Cladium jamaicense*). Inevitably, this demonstration was based on a combination of detailed but very small plots (typically no more than a few tens of square meters) and larger plots where very quick assessments of vegetation cover were made during the helicopter survey. The legal force of the Supreme Court's *Sweet Home* decision motivates a more detailed analysis of these changes. The ideal seems impossible: we need spatially detailed, spatially extensive, and frequent observations of habitat. In this chapter, we will demonstrate that flooding and unnaturally frequent fires have indeed altered sparrow habitat in such a way as to preclude the bird's use of the habitat over long periods. We will do this by employing remote sensing.

7.1.2 An outline of the chapter

The chapter proceeds in three stages. The first explains how we predict sparrow habitat. In brief, by precisely locating the nests of sparrows during the breeding season, we identify the spectral signatures of their territories on satellite images. This signature is based on the spectral response of the vegetation comprising a sparrow's territory. The response is embodied in the pixels in the satellite image. Each pixel on an image is a six-element vector, each element representing a "color" — a wavelength either within or beyond visual detection. The combination of these spectral signatures for a sufficient sample of territories produces a prediction of the habitat available to the sparrows on the date of the satellite image.

The second stage shows that we can predict habitat in years where we have no nest location data, based on the locations of nests in subsequent years. We adduce both ecological reasons and empirical evidence supporting our methods. We also provide an analysis of the habitat predictions linking water management decisions to their effects on the habitat.

The third stage is a detailed technical analysis of the errors we find in our predictions. We identify these errors using the annual rangewide surveys of the sparrow's abundance and distribution. Some of these errors are failings of the predictive model; we argue that many more are "errors" the birds make for one reason or another.

We will present two key results.

- Across the eight years of the study, large year-to-year fluctuations in predicted habitat confirm the culpability of water managers. Flooding in 1993, 1994, and 1995 greatly reduced the habitat predicted to be suitable for the sparrow compared to 1992.

- The predicted suitable habitat west of Shark River Slough was at a low ebb in 1995 and recovered slowly, but consistently, in the years from then until 2000, when num-

> bers dropped again. This formal, technical demonstration matches exactly the subjective opinion expressed by Bass and Pimm from their visual inspections during the annual surveys of the sparrow population. By 1999, the predicted suitable habitat had not yet recovered to its preflood state. Nevertheless, the habitat is recovering faster than the slowly recovering bird populations.

Neither of these results are surprises, for they were suggested by our previous papers (Curnutt *et al.* 1998, Nott *et al.* 1998). Nonetheless, we consider the details presented here to be important in both a national and a broader context. Importantly, our data suggest that water management practices have damaged huge areas of vegetation across Everglades National Park and have done so for extensive periods and in a way that jeopardizes the survival of a federally listed species. This constitutes a "take" within the meaning of the Endangered Species Act. Moreover, its demonstration is independent of, and shows an effect lasting longer than, the direct effects of flooding.

To be more emphatic: these data provide direct evidence of water managers harming the habit of the sparrow. Because of the *Sweet Home* decision they are sufficient to prompt legal actions, even if the results of the previous chapters were not available.

More broadly, we have used satellite imagery to predict potential habitat and estimate its fluctuation from year to year, and calibrated these changes against known bird numbers. This is a procedure with few, if any, precedents.

Floods and fires directly harm Cape Sable Seaside Sparrows and their nests. The ecological question we ask here is whether they have also harmed the habitat on which the birds depend. If so, a second question follows: how quickly does the habitat recover? Clearly, the birds cannot recover until their habitat does.

7.2 Stage I: Predicting the habitat

To produce a map of a species' habitat using satellite imagery, we needed to incorporate all the features of a species' natural history that are identifiable on the image. For the sparrow, our field experiences suggested a minimum of three features: vegetative structure, proximity to woody vegetation, and patch size.

The first stage was to identify what spectral responses correspond to suitable sparrow habitat. Different vegetative structures give different spectral responses or *signatures*. In Figure 5.1 it is possible to distinguish between the wetter vegetation in the central part of Shark River Slough and the drier prairies on either side. In Figure 6.6 it is possible to see the effects of different water levels. At a finer resolution, it is possible to distinguish many more subtle vegetative features.

We located 261 nests using a Global Positioning System (GPS) and then matched each of these nests to their corresponding pixel on the satellite images. The resolution of these images (i.e., the pixel size) is 29 × 29 m. These pixels formed the basis of the prediction of potential sparrow habitat.

The second stage involved proximity to woody vegetation. Predators, such as Red-shouldered Hawks (*Buteo lineatus*), perch on bushes and shrubs when looking for prey, such as the sparrow. Nesting close to woody vegetation likely exposes sparrows to an increased risk of predation. So we asked: how close to woody vegetation do the birds nest? After answering that question, we eliminated areas that were too close to woody vegetation.

In the third stage, we eliminated patches that were too small to hold a breeding territory.

7.2.1 Obtaining the spectral signatures

This stage has three parts. First, we corrected the satellite images so our GPS data matched the image. Second, we made spectral signatures of suitable sparrow habitat using the nest pixels. Last, we applied these spectral signatures to the image to map the habitat.

Images and rectification

We used Landsat Thematic Mapper images taken during the breeding seasons of 1992 through 1999. When possible, these were from April or May, the months of peak breeding activity. In 1996, no cloud-free image was available in April or May and we used one from March 21. In 1997, all images in the breeding season were cloudy.

Landsat Thematic Mapper images consist of seven spectral bands ranging from blue (0.45–0.52 μm) to thermal (10.4–12.5 μm). Using the thermal band reduced the accuracy of our results because the prairie is essentially at thermal equilibrium, so we eliminated it from our analyses.

We first defined a set of 66 control points that we could unambiguously identify both on the satellite image and on the ground or on accurate maps. We recorded the coordinates of these using a GPS accurate to < 2 m in accessible areas and 1:24,000 quadrangle maps in inaccessible areas. We used these to correct for misalignments and distortions in the satellite images. This process, known as rectification, smoothly stretches the image to produce a least-square fit to the control points. The difference between the predicted positions of the control points and their true values had a root mean square error of 2.9 m, that is, 10% of the linear dimension of each pixel.

Making spectral signatures

Using the differentially corrected GPS, we took coordinates for 261 nests from 1996 through 1999. We eliminated nest locations judged to be of questionable accuracy and those closer than one pixel (29 m) to a road. (Presence of a road within a nest pixel contaminates the spectral signature.) This left 232 usable nests. For a given year in the analysis we used only a subset of these nests, discarding those that fell on clouds, shadows, or other features corrupting the image.

Using only the nest pixel provided no information on the spectral characteristics of the surrounding habitat within the territory. Sparrows defend homogenous territories of about 2 ha (Chapter 2). In an ideal world, we would have precise maps of sparrow territories and build our spectral signatures from those. However, in most cases we had only the nest location to work from. Therefore, we needed to select pixels that adequately represented the true territory. To select those pixels we tried two methods.

The *central place foraging* method assumes sparrows place their nest in the center of their territory. This would minimize the distance flown to feed nestlings and the distance to defend territory boundaries. We used the 25 nearest pixels (2.1 ha) that were not obviously unsuitable (i.e., woody vegetation or water). Twenty-five pixels permits a compact, if not quite circular pattern, with the nest location centrally located.

The *minimum spectral distance* method assumes sparrows place their nest in a typical part of the territory. We selected the 25 contiguous pixels having the minimum Euclidean spectral distance from the nest pixel over all spectral bands. We defined contiguous pixels as those touching along one of the four sides but not diagonally.

Our field experience, including the territories we mapped, tells us that territories are often irregular in shape with nests placed near their boundaries, suggesting this second method should be the better one. Indeed, our results supported this. The second method classified more habitat in areas with birds and less habitat where there were none. In what follows, we used only the minimum spectral distance method.

Making and summing classifications

For a particular nest and its associated 25 pixels, we calculated the minimum and maximum value within each of the six spectral bands. This produced a six-dimensional box within which we deemed all enclosed pixels to be one sparrow's opinion of suitable habitat. We did this for all the available nests and territories and combined those opinions.

We could combine those opinions in a large variety of ways. Samples based on few nests would likely perform less well than those based on large samples. Moreover, in some years we had no nests at all. To get the largest samples we could combine nests from different years, but this runs the risk of combining years with different nesting conditions (e.g., birds may have nested in different places each year because of different water conditions). To resolve these difficulties, we compared their predictions. We present those results after explaining the final two stages.

7.2.2 The bush layer

We found that sparrows do not nest near woody vegetation, presumably because of increased predation risk. Using aerial photography of the intensive study plots, we measured the distance of 235 nests and 235 random points from the nearest bush. Figure 7.1a shows the frequency distribution of these nests and points, and Figure 7.1b their cumula-

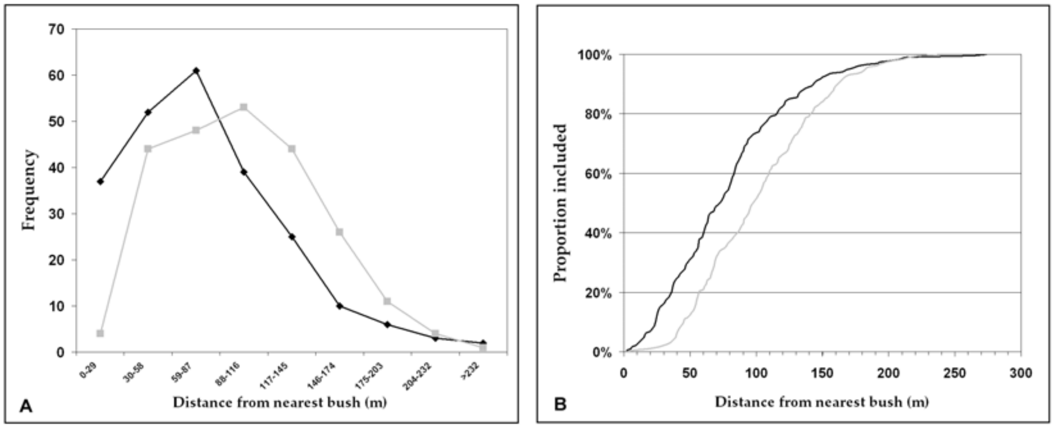

Figure 7.1: Distance of nests (gray) and random points (black) from the nearest bush. (A) The frequency distribution of the distances of 235 sparrow nests and 235 random points from the nearest bush. Each bin in the distribution is 29 m, the size of a satellite-image pixel. (B) The cumulative frequency distribution of those same points. The distributions of nests and random points are different (Kolmogorov-Smirnov test, $p < 0.001$).

tive distributions. The distribution of nests is shifted away from woody vegetation when compared to what one expects for randomly selected locations. Very few nests were within $\sim$ 29 m of a bush (or one pixel on the satellite image). There were fewer nests within 58 m and 87 m (2–3 pixels) than one would expect.. As a compromise between excluding too much sparrow habitat and including too many areas too close to woody vegetation, we eliminated classified habitat within 2 pixels ($\sim$ 58 m) of a bush.

Woody vegetation is high in chlorophyll, so it is green compared to the buff tones of the prairie grasses. The satellite images capture these obvious features. Indeed, the satellite images provide better ability to make these distinctions than the human eye owing to the sensitiviy of the satellite instrument to high reflectivity of leaf structures in the near infrared. Because of the large spectral differences between woody vegetation and other prairie vegetation, we used the ISODATA algorithm (Jensen 1996) to automatically find signatures corresponding to woody vegetation. Accuracy assessment with aerial photography showed this algorithm had an error rate of 8% for commission errors and 29% for omission errors. It detected most large woody vegetation and clusters of smaller woody vegetation, but misclassified areas with only a few small bushes.

7.2.3 Eliminating small habitat patches

Because sparrows need enough suitable habitat for a breeding territory (mean $\sim$ 2 ha; see Chapter 2), we eliminated patches of habitat smaller than 25 pixels (2.1 ha) from the predicted habitat. We used 25 pixels to be consistent with the territory size used in making signatures.

7.3 Stage II: Evaluating the predictions

Any attempt at prediction prompts two questions: "of what?" and "by what?" The first answer is simple: we want to predict the amount of habitat present that is suitable for sparrows. The second answer is more subtle. Certainly, we could predict distributions of birds in each population in each year from nest locations in each population and in each year. But prediction usually seeks efficiency. The efficiency we seek is the ability to predict distributions in all populations in all years from a sample of nests that are from only the more accessible populations and only from some of the years. The first part of the evaluation stage explores how accurately we can do this. The second part is an analysis of the habitat predictions within each population. It links water management decisions to their effects on the habitat and the population.

Each of these components uses the annual rangewide surveys of the sparrow's abundance and distribution. Tests in the intensive study areas indicated an observer can hear a singing sparrow up to 200 m away, an area of about 13 ha (Chapter 5). We calculated how much predicted suitable habitat was within a circle of 200-m radius about the survey point. If the model predictions were good, then the survey should have found birds more often in areas where the model predicted more habitat. In a graph of sparrow presence versus amount of habitat predicted (Fig. 7.2a) there should be few sparrows below a minimum threshold for predicting presence and many sparrows above the threshold. We used the size of a breeding territory (2 ha) as the threshold.

7.3.1 Predicting habitat in years without enough nests

We only have nest locations from 1996 onward, and 1996 and 1997 have too few nests for good results. However, we need to predict habitat from 1992 onwards. An efficient solution would allow us to use nests from *all available* years on *every* year's imagery. This would provide a large sample size and allow predictions in every year. An inefficient solution would obtain if there were large variation in nesting habitat from year to year. If sparrows did not nest in very similar places each year, then a nest in 199*x* would not likely be within a territory in 199*y*. Both ecological and empirical evidence support the idea that the solution we developed is an efficient one.

The ecological evidence is the consistency of habitat within our study sites. They are primarily in areas that have not flooded or burned since 1992. A criterion for originally selecting these locations was that they had a consistent sparrow population and thus suitable habitat. Therefore, we posited that areas in which sparrows nested during the detailed surveys, 1996 through 1999, were also suitable habitat in prior years. Sparrows nest in very

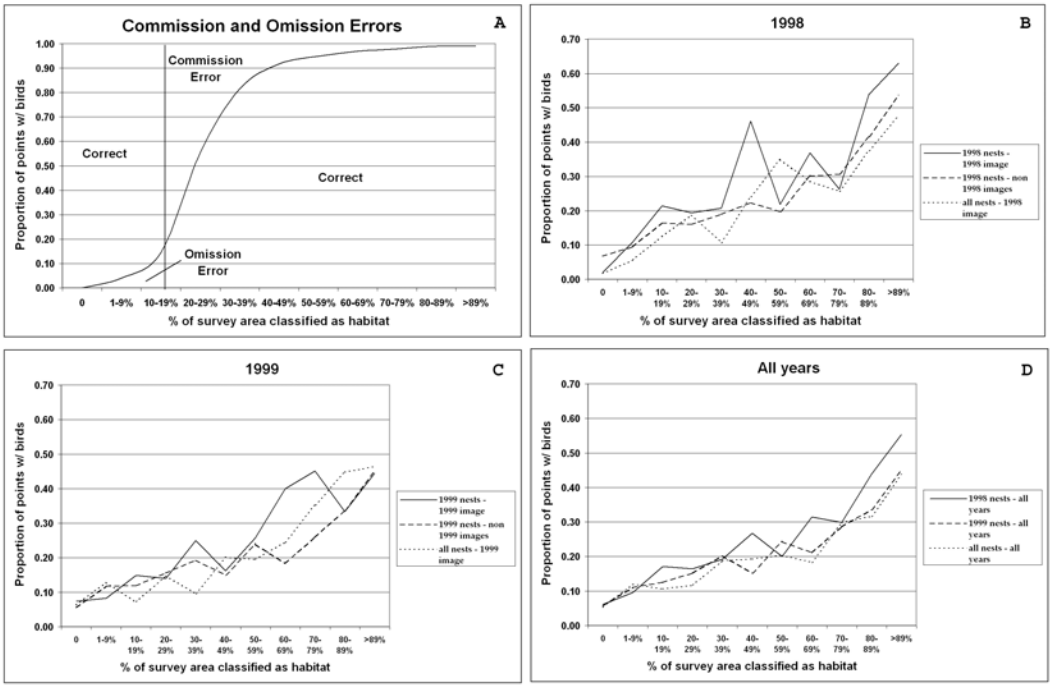

Figure 7.2: The proportion of survey sites containing one or more sparrows as a function of the proportion of the survey circle that our model classified as suitable sparrow habitat. (a) Ideally, there will be a threshold below which we do not find birds and above which we do, presumably near the size of a breeding territory (2 ha or 16% of the circle), as we indicate here. (b–d) In reality, the results have noticeable variability but do show a positive relationship between the amount of habitat in a survey circle and the number of sparrows detected there. Lines represent predictions from different combinations of nests (1998, 1999, or all years) and imagery (nest year or non-nest year) data sets. "All years" is a summation of the results from every year's imagery using a given set of nests.

similar places each year, so a nest in 199*x* would almost certainly be within a territory in 199*y*.

Figure 7.2 (b–d) shows the empirical results supporting our assumption. These graphs compare using nest data from 1998, 1999, and from all years on various years' imagery to predict suitable habitat. (We had too few nest locations in 1996 and 1997 to analyze these years separately.)

Ideally, we would get a graph comparable to Figure 7.2a, showing a positive relationship between habitat predicted and probability of finding birds. Below some threshold amount of habitat (the vertical line), there would be insufficient habitat to hold birds.

Should we find birds in such areas we would have an *omission error*. (Our model errs in omitting places where birds occur.) Above this threshold, we should find birds and, were we not to do so, we would have a *commission error*. Ideally, both omission and commission errors would be small, and there would be a sharp transition about the threshold. In reality, the graphs are more variable, but the relationship still holds.

Figure 7.2b shows the results of using 1998 nests to make signatures and predict habitat on 1998 imagery. It gave a strong, but variable, increase in the proportion of survey points with birds as the amount of predicted habitat increased, as we expected. When using 1998 nests on non-1998 images a similar pattern occurred. Thus, 1998 nests predict habitat just as well in other years as they do their own. Using 1999 nests on the 1999 image and other years gave a similar result (Fig. 7.2c). Thus, 1999 nests work as well.

We offer no formal tests of what we mean by predictions “working well.” For one prediction to be better than another, it would have to predict a smaller proportion of sites holding birds when there was only a small area of classified habitat (lower omission error) and a larger proportion when there was a large area of classified habitat (lower commission error). Inspection of the figures shows that the lines cross repeatedly, with no tendency for within-year predictions (1998 nests on 1998 image, 1999 nests on 1999 image) to be consistently better. Indeed, to the extent we might claim any consistency it is for nests from all years to predict a given image better than the nests from its year. (Thus for the 1999 image [Fig. 7.2c] nests from all years had lower omission and commission errors than did the 1999 nests alone.)

Figure 7.2d shows a summation of results from using 1998, 1999, and all nests to map sparrow habitat. Again, none of the curves differed substantially or consistently from each other. These results indicate the year of the nest does not alter the efficacy of the predictions. Likely, nest locations are consistently good habitat, at least within the time span of this study.

We conclude that nests from one year are usable for making habitat signatures in other years. To gain the maximum sample size we used all nests to map habitat in each year. This took into account the opinions of the most sparrows, and thus predicted the most habitat.

7.3.2 Habitat analysis

To estimate the total potential habitat, we combined the final habitat classifications for all years. Looking at the six populations together, we estimated 459 km^2 held potential habitat in one or more years. Among the populations, A and B had the most with 138 km^2 (30% of the total) and 116 km^2 (25%) respectively. Population E was third with 82 km^2 (18%), and C, D, and F had 31 km^2 (7%), 54 km^2 (12%) and 38 km^2 (8%) respectively.

Not all of these areas were suitable habitat each year. In any given year, floods, fires, and other environmental factors reduced the potential habitat. Looking at the annual average amount of this suitable habitat revealed a different pattern than looking at only total potential habitat. Overall, the habitat suitable for the birds each year averaged 240 km^2 (52% of the potential). Population A averaged only 38 km^2 (28%) of its potential, reflecting the large amount of habitat destroyed by floods in 1993 and 1995 and the slow recovery thereafter. Population D, also affected by flooding, averaged just 20 km^2 (37%). Populations B and E were relatively constant and had the highest average amount of habitat with 85 km^2 (73%) and 54 km^2 (66%) respectively. Populations C and F averaged 19 km^2 (61%) and 23 km^2 (61%) respectively. Now, how much of this suitable habitat did the birds occupy in a particular year?

Figure 7.3 shows the predicted amounts of suitable habitat and their variation from year to year as well as estimates of the area occupied by sparrows. To calculate these numbers, we took the number of birds heard on the survey in each population (see Table 5.2), multiplied by eight territories (the survey counts only one territory in eight, Chapter 5) and then by 2 ha, the average size of a territory. For example, in 1992, we counted 146 birds in population A, and estimated the population size as $146 \times 8 = 1168$ territories, which should occupy 2336 ha, or 23.36 km^2. The predicted suitable habitat for that population in that year was 82 km^2.

Figure 7.3 hints at an important and plausible pattern, though one about which our small sample size (six populations) precludes drawing strong inferences. Populations with frequent disturbances support fewer birds. Populations A, B, D, and E demonstrated this relationship with respect to floods (circles in Fig. 7.3). Populations A, D, and E suffered varying degrees of flooding and supported few sparrows, whereas B was not flooded and supported many sparrows. In populations C and F, fire (asterisks in Fig. 7.3) was the dominant influence. Our habitat estimates do not reflect fire's influence, but the relationship to sparrows is clear. Sparrows do not live in areas that burn frequently.

Population A had the largest fluctuations in habitat. Flooding reduced habitat from 82 km^2 in 1992 to 7 km^2 in 1993, a 91% decrease. Simply, most of the area was underwater. In the same years, the area occupied by sparrows declined from 26 km^2 to 4 km^2. In 1994, the water level was lower than in 1993. As a result, the habitat rebounded to 58 km^2, 71% of preflood levels. However, most of this habitat was again flooded soon after the image date and sparrow breeding failed (Nott *et al.* 1998). The occupied area stayed extremely low, at less than 1 km^2. The 1995 flood reduced the suitable habitat to just 9 km^2.

In 1996, the water level at the image date was almost the same as in 1994 (< 4 cm higher). Yet the predicted habitat in 1996 was only 25 km^2 compared to 80 km^2 in 1994. Our personal observations explain the large difference. Even though the area was not flooded, plant cover was very sparse, and a thick layer of periphyton covered much of what had been sparrow habitat. The thick mat was a consequence of nearly three years of constant inundation.

In the following years, the water remained low and a slow recovery of sparrow habitat ensued. This suggests the prairie was able to quickly recover from the single flood in 1993, but three sequential years of unnatural flooding caused long-term damage from which the habitat has yet to fully recover. The sparrow population shows little recovery,

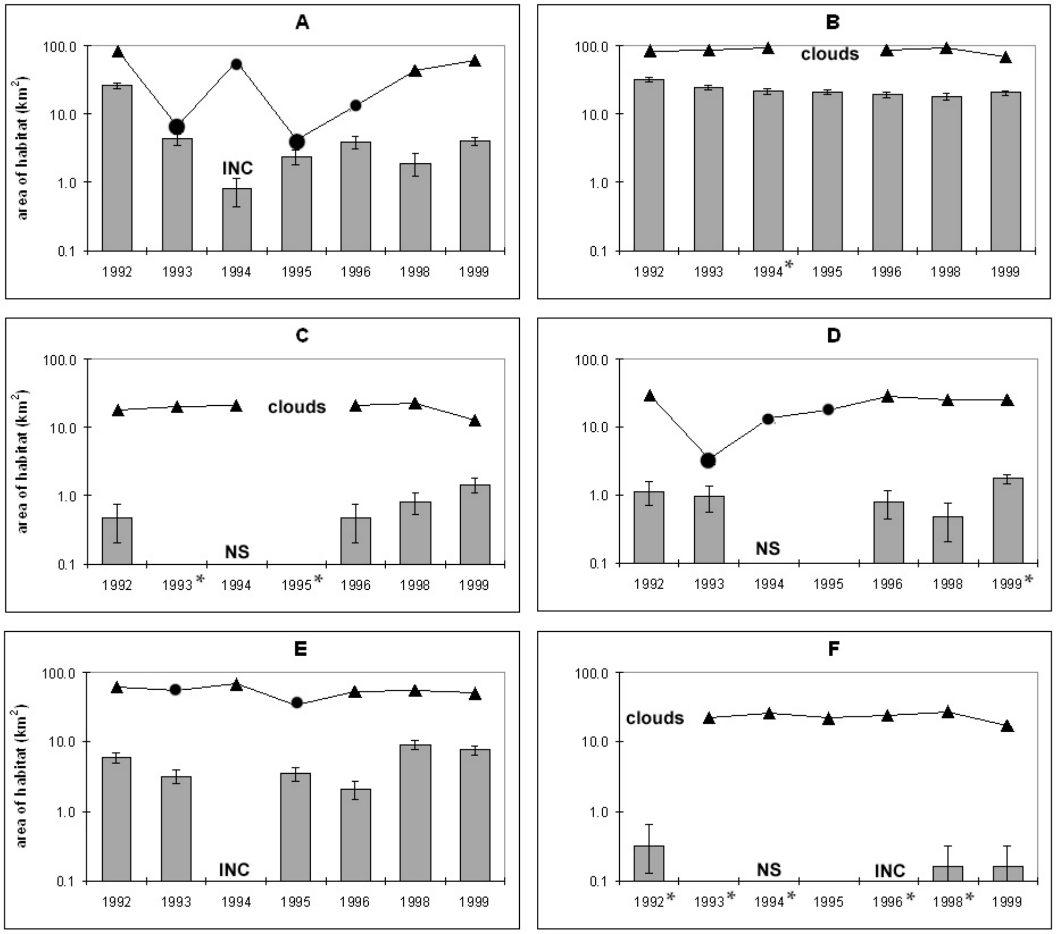

Figure 7.3: Area (km^2) occupied by sparrows (columns) and area of habitat classified as suitable (lines). We calculated the occupied area by multiplying the number of birds counted in the survey (from Table 5.2) by 8 to estimate the total number of breeding territories. Each territory is 2 ha or 0.02 km^2. The y-axis is a logarithmic scale. Bars are ± one standard error. Triangles = no flooding; small circles = moderate flooding; large circles = extensive flooding. * indicates years with fire(s) in that population. NS = no survey; INC = incomplete survey.

with occupancy in 1999 of only 4 km^2 of the 60 km^2 available. There appears to be a significant lag time between habitat recovery and sparrow population increases.

Population B was the only population that had a relatively constant amount of habitat and number of birds. It was largely unaffected by flooding and was not subject to high fire frequency.

Population C showed a relatively constant amount of habitat but few birds. In 1981, it had 4 km^2 of occupied habitat. Then, between 1990 and 1995 nearly the entire area burned one or more times. Consequently, the population dropped to an undetectable level by 1993 and was not detected again until 1996. After then, the population increased slightly but is still at a precariously low level.

Population D suffered a large decline in habitat because of flooding in 1993, going from 30 km^2 in 1992 to 3 km^2 in 1993. It then experienced moderate flooding until 1996. Since then, the amount of habitat has been relatively constant, but the location has varied by year. This population had high occupancy in 1981 but relatively few birds in 1992, possibly because of a large fire in 1990. The floods from 1993 to 1995 depressed the population even further. Since 1996, the population has remained small.

Population E had a small decrease in habitat from the 1993 flood, and the 1995 flood caused a decline from 68 km^2 in 1994 to 34 km^2 in 1995. The occupied area stayed relatively low from 1992 to 1996, ranging from 2 to 6 km^2, likely due to the flooding in 1993 and 1995. In 1998 and 1999, the occupied area increased to 9 and 8 km^2 respectively. This higher occupancy may have resulted from the consistent level of habitat since 1996.

Population F showed a small but constant amount of habitat. However, this area burned every year from 1981 to 1994 and again in 1996 and 1998. As a result, sparrows never occupy most of the habitat.

7.4 Stage III: Why do good birds make bad choices?

In the previous section we used satellite imagery to produce maps that were predictive models of the sparrow distribution. The preceding section confirmed the overall predictions, but there were errors.

With *errors of omission*, we encountered birds, but the model failed to predict sufficient habitat. In *errors of commission*, the model predicted sufficient habitat, but the survey found no birds. The purpose of this section is to examine the causes of these errors. We will separate those errors due to the model from those due to inappropriate choices the birds made. We then ask why do birds make bad choices?

These bird errors have important consequences for conservation. Quite generally, if organisms are not occupying suitable habitat, then that habitat is not contributing to the population's survival. Thus, measuring the amount of habitat alone may give an overly optimistic view of the species' plight. Similarly, organisms that are in unsuitable habitat do not contribute to the population's survival because they are unlikely to successfully produce offspring. Thus, population numbers alone may also give an overly optimistic view. First we explain how we identify these errors, and then we discuss them in detail.

7.4.1 Sources of error

Of the 3997 survey points over 8 years, 658 have held one or more birds. The model successfully predicted that 494 (75%) should have held birds, leaving 164 ($658 - 494$) omission errors. Of the 3334 survey points without sparrows, the model successfully predicted that 2030 (61%) should not hold sparrows, leaving 1304 ($3334 - 2030$) commission errors. Both omission and commission errors have five potential causes: bird errors, model errors, survey errors, image errors, and threshold errors:

Bird errors: Birds may make mistakes in their choice of territories, placing them in inappropriate places or not placing them in suitable ones.

Model errors: The model may incorrectly predict the habitat.

Survey errors: Surveyors may make errors when surveying the sparrow population, missing birds that are present or recording birds by mistake when they are absent.

Image errors: The satellite image may not capture an important event affecting the habitat.

Threshold errors: Our threshold for predicting presence, 2 ha, may be incorrect.

Threshold errors are a dilemma. Increasing the threshold increases omission errors while reducing commission errors and vice versa. We used the size of a territory (2 ha) because it is the lower limit of possible threshold values and it is ecologically defensible. Sparrows need at least 2 ha, but we do not know how much more they might need. We prefer to risk overestimating habitat than risk missing important areas.

We must now try to assess the relative frequency of the remaining errors, and to do this requires a “field guide” to their distinguishing characteristics. First we address omission errors.

7.4.2 Omission errors

Bird errors

Birds may make two kinds of omission errors, temporal and spatial. The first is where birds are in a suitable area that becomes unsuitable from one year to the next, but they remain there. Cape Sable Seaside Sparrows rarely move more than a few hundred meters between years (Lockwood *et al.* 1997, 2001, Dean and Morrison 1998). A diagnostic of this error is the presence of birds in predicted unsuitable habitat when, in the previous year, birds were present and the model judged the habitat suitable. For example, in Figure 7.4a we successfully predicted the presence of sparrows in three of four sites in 1992 (yellow dots). In 1993 (Fig. 7.4b), two of these sites still contained birds but we predicted no habitat because of flooding (red dots). These birds remained in the area even though suitable habitat had disappeared.

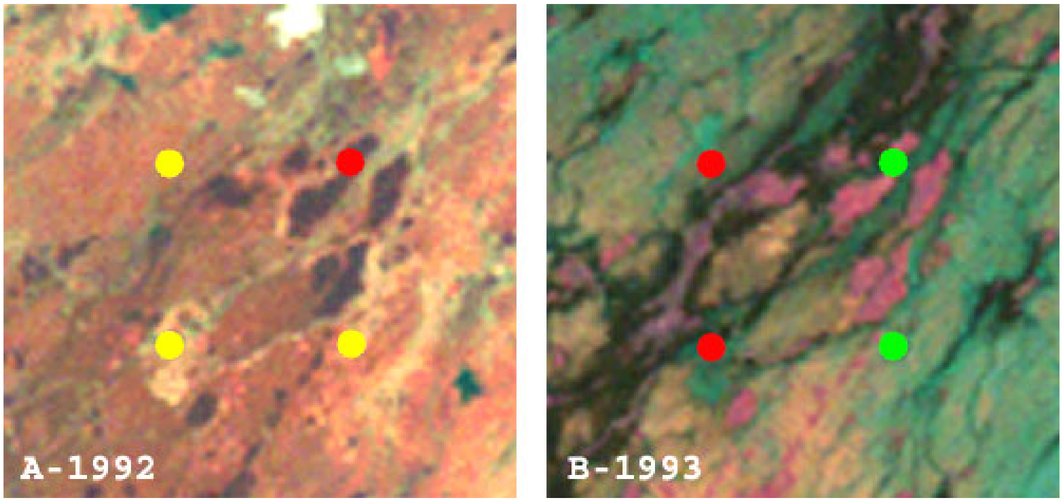

Figure 7.4: Examples of *temporal bird omission errors* and a *bush model error*. The Landsat image in (A) is of the northern portion of population A in 1992. (B) is a 1993 image of the same area. These images are in false color and employ three spectral bands, 5, 3 and 2, for red, green and blue respectively. In 1993, the prairies were flooded and the water absorbed much of the mid-infrared light (band 5) leaving a bluish-green color. Yellow dots are survey points where our model predicted birds and they were present. Red dots are survey points where the model did not predict sparrows, but they were present. Green dots are where the model did not predict sparrows and they were not present. In 1993, two sites that had birds in 1992 still contained birds even though flooding destroyed the habitat. The red dot in 1992 is a bush model error. Although the location appears in the middle of a tree island, the helicopter would have landed near the trees, not within them. Our model did not predict enough habitat within a 200 m radius of the survey point (all habitat < 60 m from tree islands and other woody vegetation were excluded) but nonetheless, one or more birds were counted here.

Spatial errors occur when birds in densely populated, productive habitat force other birds into adjacent marginal habitat. A diagnostic is the presence of birds in habitat the model predicts to be unsuitable with birds present in at least one adjacent point with habitat the model predicts to be suitable. These areas must also have a history of two or fewer sparrow occurrences during the study period and be near a large, presumably full population. For example, Figure 7.5 shows the southern portion of population B in 1994. We successfully predicted most of the sparrows but failed to predict three sites along the southern margin.

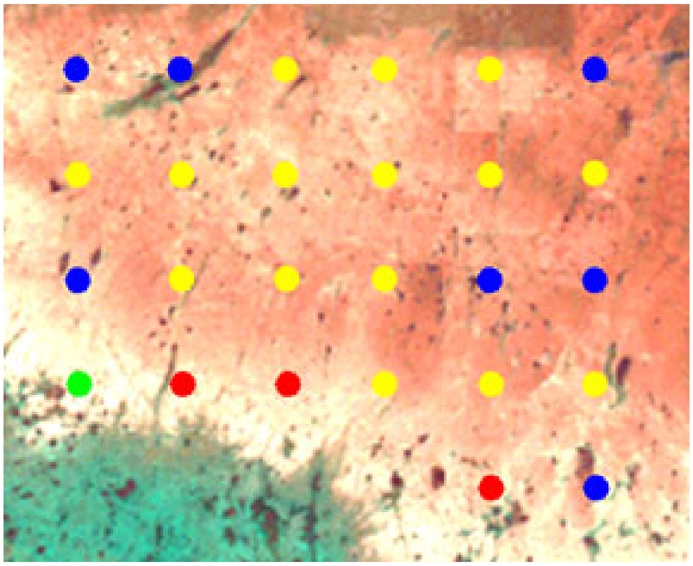

Figure 7.5: Examples of *spatial bird omission errors*. A 1994 image of the southern portion of population B. This population is the largest and is densely populated with birds. Yellow dots are sites with birds that the model successfully predicted. Blue dots have no birds but the model predicted they should have birds (commission errors). Green dots have no birds and no habitat. Red dots are sites with birds that the model does not predict should have birds. The three red dots occur in an area that usually does not hold birds and is flooded in some years (omission errors). The bluish-green area in the southwest is water and the white areas along its edge are mostly periphyton, sparse vegetation, and exposed limestone.

Model errors

Our model does not always successfully predict suitable habitat. Two sets of criteria distinguish these model omission errors from bird omission errors.

1. *Bush model errors*: The model eliminated the area because it had too much woody vegetation, but it consistently holds birds. This can happen when the helicopter lands outside a tree island when the correct coordinate is within it. The actual survey point can then be closer to sparrow habitat than the model would predict. Figure 7.4a shows an example of a bush model omission error.

2. *Prairie model errors* are areas that consistently had birds ($\geq$ 3 times) but which our model did not classify as habitat, even though we saw no evidence of fires or floods making the habitat unsuitable. Figure 7.6 shows a prairie model error. The central red dot is a site that consistently held birds, the area around it consistently had suitable

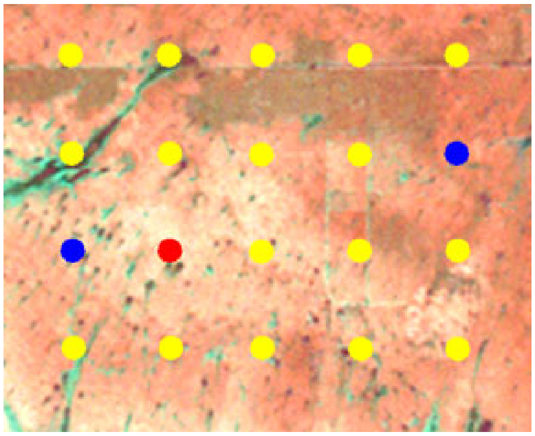

Figure 7.6: Example of *prairie model omission error* in a 1993 image of the southern part of population B. Yellow dots are survey sites successfully predicted to have sparrows. The red dot is an error where sparrows were present but the model did not predict habitat. Blue dots were classified as habitat but had no sparrows. The red dot is a site that had birds in every year of the study. The area surrounding it has habitat occupied by birds. Yet, the model did not classify the area as suitable in 1993 or most other years, and there is no evidence of floods or fires.

habitat with birds, but the model rarely classified this area as suitable for reasons we do not understand. A large number of errors from population A in 1992 are also in this category. In that case, we had no signature of the sparse sawgrass habitat that occurred in A in 1992 and thus misclassified it as unsuitable. We explain this in detail later.

Survey errors

Survey omission errors involve false detections of sparrows. They appear as birds in locations unusual for sparrows, likely as single birds, and occurring only in single years. We have no examples of these errors. Surveyors only count sparrows if they sing, and they are very familiar with the sparrow's song from years of experience. In addition, no other bird in the prairie has a similar song. (The songs of very distant Red-winged Blackbirds (*Agelaius phoeniceus*) and Eastern Meadowlarks (*Sturnella magna*) can sometimes fool the inexperienced, which is why we do not use inexperienced surveyors.) We will not discuss these errors further.

Image errors

Image omission errors occur when image problems cause a suitable area to be classified as unsuitable. They have two sources. Clouds in the satellite imagery may obscure suitable habitat in a survey area, causing an omission error. Therefore, before our analyses we removed any survey point that was cloudy in the satellite image. It is also possible that the habitat suitability changed between the image date and survey date. For example, if an area was underwater on the image date, the model would not classify it as suitable. However, if the water receded before the survey the habitat may have become suitable, causing an omission error. The reverse could happen as well. Evidence of flood between the survey and image dates identifies these errors. To avoid such errors, all of the images in this study are during or within three weeks of the survey dates. We found no image errors and will not consider them further.

We now turn to commission errors, in which the model predicts birds in places where they are absent.

7.4.3 Commission errors

Bird errors

Bird commission errors stem from the sparrow's limited dispersal. Fires or floods can eliminate sparrows from an area and damage the habitat. Thereafter, the habitat may recover, but the birds may take several years to reoccupy it. Areas of predicted suitable habitat that appeared in one year, and then became occupied by sparrows in future years, confirm this type of bird error.

So, too, do areas that held habitat and sparrows in the past, had predicted suitable habitat in the year analyzed, but no birds. Figure 7.7 shows an example from an area in population E. In 1996, only four sites (yellow dots) held birds, while most of the predicted habitat was unoccupied. By 1998, the sparrows had expanded to occupy 11 additional sites.

Model errors

In model commission errors, the model predicts there should be birds, but the survey finds none. These errors have four causes.

1. *Bush model errors* resulted in areas with too much woody vegetation that we did not identify as such with the satellite imagery (Fig. 7.7b). We identified these using the qualitative vegetation records from the extensive survey, and aerial photography when available.

2. *Fire model errors* resulted when the area burned too frequently. We calculated the burn frequency using fire maps from 1980 to 1999. Sites burning in the previous year or more than twice in the previous 10 years identified fire model errors.

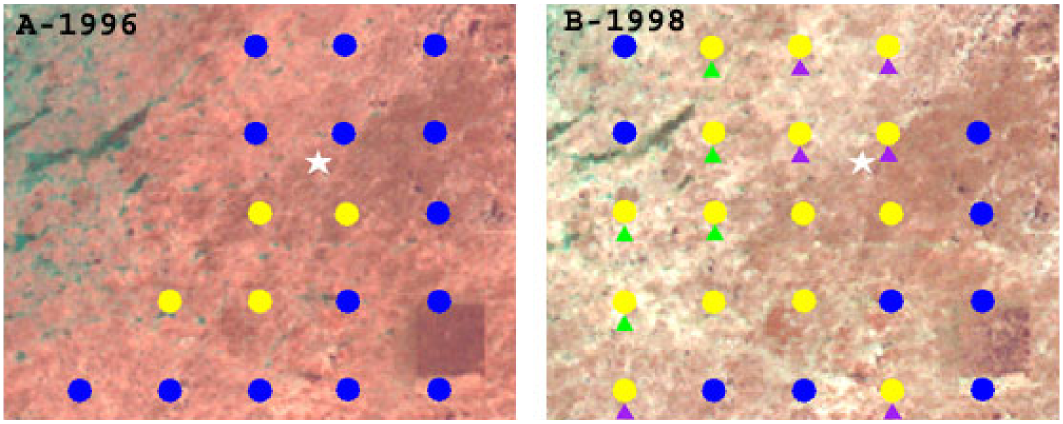

Figure 7.7: Examples of *bird commission errors* and *bush model commission errors*. Landsat images from 1996 (A) and 1998 (B) of the northern part of population E. Yellow dots are sites with predicted habitat and sparrows present. Blue dots had predicted habitat but no sparrows. Fires in 1989 and flooding in 1993 and 1995 reduced this population to only four sites in 1996. As the floodwaters receded the habitat recovered, but a large amount remained unoccupied in 1996. By 1998, the population had expanded into six new sites predicted to be habitat in 1996 and 1998 (purple triangles). In addition, as the western area dried out, the habitat recovered and the sparrows expanded westward (green triangles) into areas that were flooded in 1996. Intensive fieldwork at a remote camp (white star) supported these results. This site is very densely populated and has the highest nest success rate of the three populations we monitor. The blue dots in the easternmost column are bush model commission errors. Woody vegetation fragmented the area too much to support sparrows, but the model failed to exclude it.

3. *Data model errors* resulted from insufficient data to rule out model error in cases that may have been bird or survey errors.

4. The cause may be unknown. The absence of sparrows at a survey point and in most adjacent survey points in every year distinguished these from bird commission errors. Because the sparrow population has only been monitored for a short period, some suitable areas may never have had sparrows simply by chance. Thus, we were likely to overestimate model commission errors.

Figure 7.8 shows another example of a *bush model commmision error* and a *fire model commission error*. In the bush example (A), we regularly classified an area in population E as suitable habitat but it rarely had birds. A search of the vegetation records from the helicopter survey showed that 11 of the 16 sites in error contained vegetation that rendered the area unsuitable. In the fire example (B), the model classified most of population F as

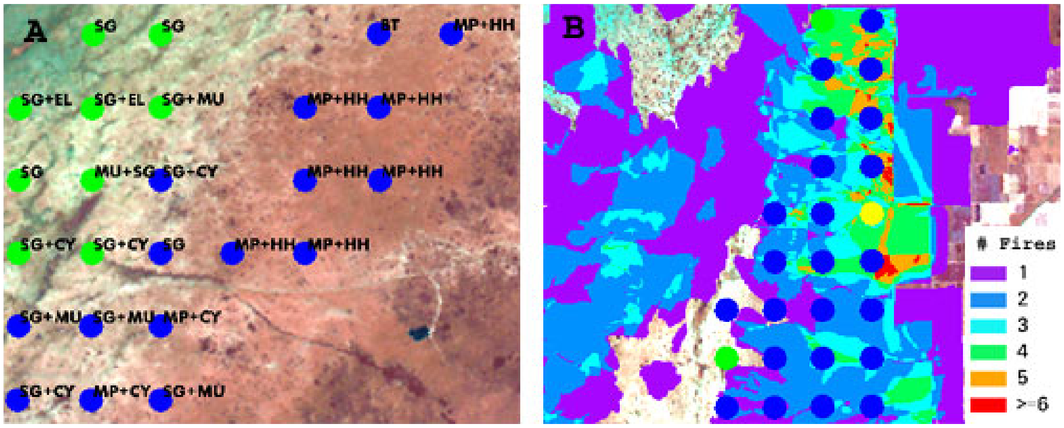

Figure 7.8: Examples of *model commission errors*. (A) The southwestern portion of population E in 1998. This area rarely had birds, yet the model classified it as suitable habitat in every year. Inspection of the vegetation records from the survey show that many of these sites contain hardwood hammocks or cypress trees, which render the habitat unsuitable for sparrows. In particular, scattered cypress trees do not appear on the Landsat images (pixel size 29 × 29 m) though they do show up on more finely resolved aerial photographs. SG = sawgrass (*Cladium jamaicense*), EL = *Eleocharis cellulosa*, MU = *Muhlenbergia filipes*, CY = cypress trees (*Taxodium distichum*), MP = mixed prairie, BT = black-top sedge (*Schoenus nigricans*), HH = hardwood hammock. (B) Population F in 1998 with number of fires over the interval 1980 to 1999 overlaid. Population F had very few birds throughout the study period, yet the model consistently classified it as habitat. However, this area had a much higher fire frequency over the past 20 years than the rest of the park. Because the model did not include fire, it failed to account for its effect on the sparrow population.

suitable. However, this area has a much higher fire frequency than elsewhere in the park, which renders it unsuitable for sparrows.

Survey errors

The survey does not always detect birds when they are present. The principal explanations are (1) the birds do not always sing and (2) birds move about their territories and will sometimes be beyond detection distance when we are surveying. When this happens, and the model classifies the habitat suitable, we get a commission error. These errors are indistinguishable from other commission errors because we do not know which survey points really had birds. If we did, then we would correct these errors. By comparing the results of two coincidental surveys in 2000, we were able to estimate that birds were likely present at 34 sites in addition to the 165 sites at which we detected them (Appendix). Scal-

Table 7.1: The three types of omission errors each year and the corresponding number of points where birds were encountered. Points with birds, but where clouds obscured the satellite image, are not included. Numbers in parentheses indicate the population that contains the majority of the errors.

Year	Temporal bird errors	Spatial bird errors	Model errors	Total	Survey points with birds
1992	14 (12 in A)	4 (4 in B)	42 (41 in A)	60 (53 in A)	163
1993	24 (19 in A)	10 (9 in B)	1	35	99
1994	0	4 (4 in B)	0	4	62
1995	15 (10 in A)	5	1	21	47
1996	9 (8 in A)	3 (3 in B)	0	12	70
1998	1	6	0	7	108
1999	16	6	3	25	109
Total	79 (52 in A)	38 (27 in B)	47 (41 in A)	164 (95 in A)	658

ing this proportion to the previous years suggests that birds should have been present at $(199/165) \times 663 \approx 800$ sites and so missed at 137 of them. With this correction, there should have been only 3845 sites without sparrows, and the model prediction of 2484 sites leaves an error rate of 35% versus our original 38%. Given the small number of these errors relative to bird and model commission errors, it is unlikely they alter any conclusions. We will not discuss them further.

Image errors

Image commission errors resulted when habitat changed from suitable to unsuitable between the image and survey dates or vice versa. This may have happened because of fire or flood damage. Evidence of fire or flood between the survey date and the image date identifies these errors. We found no image commission errors.

7.5 Results of error analysis

7.5.1 The 164 omission errors

Table 7.1 lists the classification of omission errors by year and by type, noting in which population the majority occurred. Temporal bird omission errors had their highest proportions, relative to the number of points with birds, in the flood years of 1993 and 1995 and were primarily in population A, 52 of 79 (Table 7.1). Population B had the second highest absolute number (12), but very few relative to the number of survey points with birds (364). Population D had 8 and was the second highest relatively (22 points with birds).

Flooding directly caused the high error rates in 1993 and 1995. Most of the errors are in population A, 19 of 24 and 10 of 15 respectively. In both years, opening of the S12 flood control structures during the breeding season flooded potential habitat in the western portion of the park. Related flooding also caused four errors in population D in 1993.

Spatial bird omission errors were almost entirely in populations B and E, 27 and 7 respectively from a total of 38. This is not surprising, as these two populations have had most of the birds since 1992 (Table 5.2). We found these bird errors typically along the southern and western edge of population B and the northern portion of population E. In these areas, there is a sharp division from the dry prairies to wetter slough habitats dominated by sawgrass.

Model omission errors occurred only in populations A and B. Most of these errors, 41 of 47, were in population A in 1992, and most were in the western half of the population. The 1981 survey also found birds in this western area. Flooding in 1993 caused these birds to disappear. The most likely explanation for birds being present, but the model failing to classify the habitat, is that the habitat was genuinely different from what we found after the floods. The vegetation records from the 1992 survey support this conclusion. In 1992, Bass recorded 72% of the error points in population A as having "sparse sawgrass," but it is likely there was a mixture of other grasses present as well. Elsewhere, we know that sparse sawgrass alone does not support sparrows, and we have yet to explore the original field notes to see what other grasses were present in these sites. All of the intensive study sites were dominated by muhly grass were mixed prairie with no dominant species. Thus, our model did not include the spectral signature for the "sparse sawgrass" habitat type.

When we compared the points that had birds and "sparse sawgrass" in 1992 to their vegetation in 1999, we found that this area has changed significantly from its preflood condition. Sawgrass now dominates only 18 of the 41 sites, and most of those also support other long-hydroperiod species such as *Eleocharis cellulosa*. *E. cellulosa* is the dominant species in 12 other sites. In addition, the average percent ground cover increased from 63% to 88% ($p < 0.01$). This suggests that flooding has changed the overall vegetation to the detriment of the sparrow. Moreover, the birds we saw in later years did not occur in the western area but only in the eastern half, where the model did predict habitat.

Population B had eight errors. It also had 55% of the total survey points with birds and was the easiest place to identify model errors.

7.5.2 The 1304 commission errors

Table 7.2 shows the number of commission errors by year and type, noting the populations in which the greatest number occurred. Bird commission errors were relatively low in the flood years of 1993 and 1995 (Table 7.2). They had the fewest errors while having the highest number of survey points without birds and thus potentially in error. The in-

Table 7.2: The two types of commission errors each year and the corresponding number of points where birds were not encountered. Points without birds, but where clouds obscured the satellite image, are not included. Numbers in parentheses indicate the populations that contain the most errors.

Year	Bird errors	Model errors	Total	Survey points without birds
1992	139 (39 in B, 39 in D)	158 (101 in A)	297	653
1993	113 (39 in B)	50 (22 in A)	163	638
1994	58 (45 in B)	23 (23 in A)	81	163
1995	51 (10 in B, 19 in E)	33 (11 in F)	84	427
1996	139 (59 in B)	59 (17 in E)	198	394
1998	161 (52 in B)	66 (22 in F)	227	510
1999	159 (63 in A)	95 (45 in A, 22 in F)	254	549
Total	820 (281 in B)	484 (234 in A, 90 in E)	1304	3334

complete survey in 1994 made it artificially low in errors. The floods primarily reduced suitable habitat, and thus bird commission errors, in populations A and D (Fig. 7.3). The highest proportions of bird commission errors were in dry years after the floods receded: 1996, 1998, and 1999. This reflects the lag time between recovery of the habitat in A and D and recovery of the sparrow population.

In 1993 and 1995, population A had two and four errors respectively, indicating an absence of open habitat. In 1994, there was a significant recovery of habitat, but after the 1995 flood the habitat recovery was much slower. Thereafter, a steady upward trend was evident, going from four survey points in 1995 to 63 in 1999.

The 1993 flood caused a large decrease in open habitat in population D, going from 39 bird commission errors to four. The 1995 flood apparently had little impact.

From the satellite images, it is clear that while the 1995 flood was more extensive around population A than the 1993 flood, it was less extensive around population D. This may be due to less movement of water down the L-31W and C-111 canals, which flow into population D. The other populations are higher elevation, protecting them from flood damage. Population B consistently had a high number of bird commission errors, but it is also the largest amount of habitat.

Model commission errors showed both temporal and spatial biases. They were higher in 1992 both in raw number (158) and proportionally (24% of survey points without birds) than any other year. This high error rate was entirely accounted for by population A. In 1992, population A had 101 commission errors whereas the average for other years was only 22. However, this is likely an overestimate. Some of them may be bird commission errors. We propose two possible explanations.

The first explanation stems from a lack of data before 1992. For many places, 1992 was the only year of the study that sparrows had suitable habitat, because of the effect of the 1993 and 1995 floods in later years. If the model predicted an area suitable only in 1992 and it had no birds, we cannot tell if it had birds in previous years or would have had birds in the absence of flooding in the following years. Thus, an area may have been good habitat and had birds for the last 10 years and by chance had no birds in 1992. All we know is that it had no birds in 1992, and thus it is impossible to rule out model error.

The second explanation is that the sparrows used the sparse sawgrass habitat in the west rather than the muhly grass and mixed prairie habitats in the east. Because the sparse sawgrass habitat no longer exists, we have no data to indicate if it may have been more suitable, and thus favored by the sparrow. If that were the case, we would expect the sparrows to have occupied most of the sparse sawgrass habitat before they expanded into the muhly grass and mixed prairie habitats.

Population E had a high number of model errors concentrated in its center. The model consistently found the area suitable but we never found sparrows. However, in 1981 sparrows from the main northern subpopulation did extend farther southwest into this habitat than in 1992 and later years. In addition, a small population of sparrows occurred near the southwestern end of this "misclassified" habitat in 1992. A possible explanation for this split population is a very large fire in 1989. This fire burned much of population E, but left the far northern and southern portions of the range intact. In addition, 1989 was a drought year, which could mean a lower food supply and thus higher sparrow mortality. Then in 1993, flooding eliminated the southwestern subpopulation. The combination of the 1989 fire and 1993 flood may have left population E with only a small northern subpopulation. Without survey data during this period, it is impossible to confirm this scenario and thus rule out model errors. Thus, this area may be suitable, but sparrows have yet to recolonize it.

Population F, and to a smaller extent population C, had many model commission errors because of high fire frequency. Fires exclude sparrows in two ways. First, frequent fires prevent the vegetation from becoming thick enough to support a sparrow nest, supply adequate food, or provide adequate cover from predators. Second, fires during the breeding season interrupt nesting, reducing total fecundity. The model captured some fire effects via vegetation changes that were visible in the satellite image. However, the lack of an explicit fire component caused the model to predict habitat in areas unable to support a sparrow population.

7.6 Conclusions

We find that our model is an accurate tool for understanding the dynamics of the sparrow's habitat. The model error rates were low, 7% for omission errors and 15% for commission errors. Moreover, these are likely overestimates. Most of the omission errors resulted from an inability to map (and indeed, to properly characterize) the "sparse sawgrass" habitat that existed in population A in 1992. We know of no other occurrence of this habitat. Excluding population A in 1992 leaves a model omission error rate of just 1%.

Two factors reduce the model commission error rate. First, many commission errors are also from population A in 1992. We suspect the birds preferred the sparse sawgrass habitat in the west and used it before using the suitable habitat we classified in the east. The lack of survey data before 1992 makes it difficult to confirm this scenario. Second, we undoubtedly miss some birds in the survey for reasons described earlier. Considering these two factors reduces the model commission error rate to 10%.

Most errors resulted from water managers forcing conditions on the sparrow to which they are not adapted. The sparrow's strong site fidelity and low dispersal range make it unable to quickly occupy newly available habitat (Lockwood *et al.* 1997, Dean and Morrison 1998, Lockwood *et al.* 2001). These "bird errors" demonstrate that the sparrow cannot cope with the habitat variability that resulted from floods in 1993 and 1995.

Bird omission errors resulted primarily when floods destroyed habitat from beneath the sparrow. Because of the sparrow's strong site-fidelity, it stays even when the habitat disappears. This means they have little chance of survival unless the habitat returns quickly. Such was not the case for population A, where floods in 1993 and 1995 caused damage that had yet to fully recover by 1999.

Bird commission errors are a direct measure of the open habitat into which the sparrow population can grow. As no organism is 100% efficient in occupying its habitat, we would expect there to always be some open habitat. Indeed, most of the populations have a relatively constant amount. However, the 1993 and 1995 floods meant there was essentially no open habitat in population A. Simply, there was not enough habitat to support the sparrow population and it declined dramatically. Thereafter we saw a steady increase in open habitat. However, the sparrow's low population growth rate means it will take another decade, under optimal conditions, for this population to return to preflood numbers.

The poor water management decisions made during this study have resulted in the effective sparrow population and amount of suitable habitat to be lower than they first appeared. The consequence is that a species we already knew to be threatened with extinction is actually in a more perilous situation than we previously thought. As long as water management such as occurred during this study period continues, the sparrow faces an unnaturally high risk of extinction. To prevent the sparrow's extinction, water managers must ensure both that suitable habitat is present and that the sparrows are able to occupy it.

The sparrow clearly cannot cope with ecosystem changes such as those imposed by water managers in 1993 and 1995. One of the two main populations is already at a dangerously low level. Another year of flooding could result in extinction of this population. Moreover, the species' long-term survival is now dependent on a single large population (B). If this population experiences a catastrophe, such as a fire, then the entire species would face extreme risk of extinction. It is precisely such risks that we must now consider.

Chapter 8

Risk Analysis

Very small populations usually go extinct quickly. The reasons are well understood (Pimm 1991). Populations suffer the problems of individuals finding suitable mates, of many individuals dying before the next breeding season from different causes, of loss of genetic variability and its deleterious consequences, and other unavoidable vagaries of birth and death. The importance of these chance factors diminishes quickly in larger populations. Nonetheless, experience teaches us that much larger populations can also become extinct quickly. Indeed, we know that vertebrate populations numbering in the low thousands of breeding pairs are too rare to enjoy a secure future (Collar *et al.* 1994, Baillie and Groombridge 1996, Mace 1996). Understanding the fate of these species is the much more difficult challenge that this chapter will address.

Large populations may consist of many smaller partially isolated subpopulations constituting a metapopulation. If so, the balance between frequent local extinction and recolonization from surviving populations determines the species' long-term fate (Hanski 1998). In such cases, insights from studies of very small populations are of value (Pimm *et al.* 1993, Pimm and Curnutt 1994). In other cases, an inexorable decline in numbers, perhaps driven by a readily observable reduction in habitat, leads to a clear prediction of a species' demise. Yet other species may be at risk because of the high year-to-year variability in numbers that typify many natural populations (Pimm 1991). In nature, many individuals die from the same causes, such as bad weather. Such natural population fluctuations can prove terminal for a species that is more geographically restricted than in the past.

The case history we present may be typical in requiring answers to all the questions implied by the last paragraph. What is the spatial organization of the population? Are any of its geographically determined subpopulations sufficiently small to warrant concerns over unavoidable vagaries of birth and death? What are the unnatural causes of population decline? How will these causes affect the population in the future? What are the natural causes of population fluctuations, and how can we anticipate the low levels to which they will drive the population in the future?

We explore two methods of calculating the sparrow's risk of extinction. The first employs the idea that one can characterize the natural limits of population size fluctuations over time from the study of time-series data. So armed, one can predict whether the lower limit will encompass such low levels that rapid extinction will be probable. This is a familiar recipe. It characterizes the papers in Brook *et al.*'s (2000) meta-analysis of the predictive accuracy of population viability analysis. One of us has devoted considerable thought to it (Pimm 1991). This method fails spectacularly, even though the sparrow case would seem entirely appropriate. The second method identifies the causes of the sparrow's population fluctuations, in particular, its range contractions and its ability to recover from them. By understanding the mechanisms underlying population fluctuations we deduce an altogether bleaker picture of the bird's future.

8.1 Risk Analysis 1: A phenomenological approach

What is the likelihood that a species will become extinct? Other things being equal, populations that are highly variable in their numbers from year to year are more likely to go extinct than less variable ones (Pimm *et al.* 1988, Pimm 1991). The causes of population variability are diverse. They include population factors (birth and death rates), features of the food web in which the species is embedded (e.g., whether it is a trophic specialist or generalist), and fluctuations of the host ecosystem. These factors operate at different scales (Pimm 1991). Estimating the population variance (or, equivalently, the variance in birth and death rates) and dissecting out underlying causes is a critical step in answering the key question about a species' fate. So how do we estimate this variability?

Data-rich, long-term studies to assess population variability directly will be a luxury afforded very few conservation biologists. For example, Sæther and colleagues have provided statistically rigorous dissections of the key population variables, their variances, and their time dependence for various species. In Sæther *et al.* (2000) they utilized a 20-year record along a 60-km stretch of the Eurasian Dipper's (*Cinclus cinclus*) riverine habitat, a large fraction of the population was color-banded, and the bird is widely distributed, relatively common, and conspicuous.

For many endangered species, infrequent estimates of population size will often be the only information available. For many species, we lack even this information. The urgency of the problem, however, does not allow us to request 20 years of intensive field effort before returning an answer. We might have access to long-term data on surrogates — species that are closely related or at least ecologically similar. Using one, or at best a few, estimates of abundance and a surrogate estimate of year-to-year variability, we may be able to predict risk of extinction. This is a familiar tactic (Brook *et al.* 2000).

As for many other threatened species, there are no sufficiently long-term data on year-to-year changes in this sparrow's population, or indeed on other Seaside Sparrow races. There are, however, substantial long-term records of grassland sparrow numbers in the Breeding Bird Survey (BBS). BBS data are obtained from point counts, a method very similar to the survey method we employ, and grassland sparrows from prairie states are broadly similar in their life history characteristics.

Chapter 6 reported on the study of Curnutt *et al.* (1996). They used BBS data on 10 North American grassland sparrows to explore how populations change in space and time. Two well-known relationships guided this exploration. The first is the power law relating variance of population abundance over time to average abundance across a species' geographic range (Maurer 1994). The second relationship is the tendency for a population's variability at a single location to increase over time (Pimm and Redfearn 1988). Curnutt *et al.* (1996) asked how abundance, variability, and increase in variability change over a species' geographic range and with respect to one another.

For all but one of the species they analyzed, variability increased more slowly than expected with increasing abundance across the species' range. If relative variability were independent of abundance, the slope of the logarithm of standard deviation versus the logarithm of abundance would be unity. Most of the species had slopes of ~ 0.7. This means that where a species is least common, typically at the edge of its range, its *relative* population fluctuations will be greater. To put this average slope into more accessible terms, a sample of 10 observations will span values encompassing approximately ± 1.5 standard deviations of the mean for a normally and independently distributed (statistical) population.

First, consider one of the larger Cape Sable Seaside Sparrow populations (A or B) and suppose we had counted 200 birds, leading to an estimate of 3,200 individuals. The log of the standard deviation of this population would be $0.7 \times \log 200 = 0.7 \times 2.3 = 1.6$, and so the standard deviation would be ~ 41. A range of plus or minus 41×1.5 $(= 61)$ would have the population varying between 140 and 260 counted birds, or between an estimated 2,240 and 4,160 birds. This approximates a twofold span of values over a sample of 10 points, that is, over a decade. This hypothetical situation fits comfortably with the experiences of those who count common birds over such intervals.

Now consider a site where the species is much rarer: say a mean count of 10 birds and so an estimate of 160 birds. Using the same logic, it would have a standard deviation of 5 and so abundances would span from 18 (an estimate of 288 birds) down to a count of two (an estimate of 32 birds). This is a much greater span of values than in the previous example (i.e., a factor of nine, versus a factor of about two). As Chapter 6 explained, it is large enough that local extinctions might occur naturally, by chance, at least intermittently over the span of a decade or two. Mean population counts below 10 should experience regular periods when the birds would not be counted, and where they might indeed be locally extinct.

We have not missed the significance of the assumptions of normal and independently distributed population sizes in the previous analysis. The population count in one year is likely to be dependent, probably strongly, on that of the previous year. As a consequence, for most populations, estimates of the variability of population abundances increase with increased length of record (Pimm and Redfearn 1988).

This was also the case for the grassland sparrows. Curnutt *et al.* (1996) found that of the seven species with at least 10 sampling locations of continuous data over 20 years, six showed significant increases in variability over increasing intervals. These increases in variability over time would mean that not only would we expect a sample of 20 years to encompass a wider range of standard deviations than the samples of 10 years exemplified above, but that the standard deviation itself would be larger.

We will not discuss how large the envelope of population fluctuations is with the added complication of increasing variability over time, for this has been done elsewhere (Lande 1993, Ariño and Pimm 1995). Incorporating these details, or formalizing the mathematics, does not alter the general conclusions about the sparrow: (1) The two largest populations are large enough that given normal year-to-year variability seen in other grassland sparrows, we should not expect dangerously low populations within a century (or indeed a much longer interval). (2) In contrast, the smaller populations might well fall below levels where we likely could not count them, and where unavoidable vagaries of birth and deaths may well doom them to at least local extinction.

Thus, local populations may become extinct, but at least one of the three larger populations (A, B, or E) should be available to naturally restock them. This is an entirely comforting conclusion. It stems from a rough-and-ready estimate of risk, but one certainly appropriate to the amount of information at hand.

This conclusion, however, was rudely shocked in April 1993. The western population (A), which the preceding calculation suggests might vary two-fold over a decade, declined to one-seventh of its 1992 abundance in the spring of 1993. It has remained at low levels ever since. Population D, in the southeast corner of the species' range, nearly disappeared, and the populations in the northeast (C and F) also declined. Chapter 6 provided a detailed analysis to show that these declines were statistically highly improbable given what we know about year-to-year variation in other sparrow populations.

The result was particularly discouraging to one of us (Pimm), because he had spent much of the previous decade cataloging and analyzing natural year-to-year variation in population sizes for conservation ends (Pimm 1991). Moreover, he was a founding partner, with John Lawton, (Ascot, UK), of the effort to provide a catalogue of more than 2,000 long-term time series (NERC 1999). A central objective of this compilation was to provide conservation biologists with an accessible set of estimates of natural population variability for population risk assessments.

Worse still was that the assumption of natural variability seemed a particularly sensible one. The sparrow lives almost entirely within Everglades National Park and Big Cypress National Preserve. These adjacent protected areas are very large by the standards of the hemisphere. Only about 20 national parks in Central and South America are as large or larger (Mayer and Pimm 1998). If the method of using natural variability to calculate risk of extinction should apply anywhere, this bird in these national parks would seem to be a good candidate. Why did this approach fail?

8.2 Risk Analysis 2: A mechanistic approach

Our surveys showed that the sparrow population on the western side of Shark River Slough declined dramatically after 1992. It has declined similarly since 1981 in the northeast and southeast of its range. Only two populations have remained more or less constant in size. A brief synopsis of the previous chapters is that there are three reasons.

1. The massive decline in the western population was the consequence of the inundation of the breeding habitat during the dry season by managed flows over the S-12 structures in 1993, 1994, and 1995.
2. The decline in most of the northeastern populations was due to the very high fire frequencies in these areas over the last decade or more. We erected the plausible hypothesis that the high fire frequency was due, in part, to the high incidence of unplanned human ignitions in the areas adjacent to the park. Moreover, we suggested that unnaturally low levels of water permitted high fire frequencies during the breeding season. Water that should have naturally flowed through northeast Shark River Slough to seasonally flood the eastern populations was diverted to the west through the S-12 gates. Moreover, the water was prevented from flowing back to the east by a barrier to water flow, the L-67 extension.
3. The decline in the lower part of population C and in D was due to changes in the managed water levels, which locally converted the seasonally flooded prairies that favor the birds to nearly continuously flooded, sawgrass-dominated marshes that the birds avoid.

The next step is to combine the variable area of suitable habitat with a simple demographic model of the sparrow. Such a model needs extensive data on the bird's birth and death rates. This is a time-consuming effort given the bird's rarity and inaccessibility. The central feature of our model of risk assessment is the availability of suitable breeding habitat. Our studies show this varies considerably from year to year. For this step in risk assessment, we postpone addressing the longer-term changes in vegetation effected by changes in hydrology and fire frequencies.

Chapter 2 showed that sparrows laid an average of 3.2 eggs per clutch, a number that varied little from year to year or from place to place. About half of the eggs fledged young and that fraction varied considerably. In particular, it depended on whether the clutch was laid earlier in the year and was almost certainly a first clutch, or whether it was laid later and was likely a second clutch. Rising water levels, which are common later in the year, terminated clutches. There were far fewer second clutches than first clutches, and known third clutches were so few and fledged so few young that they contributed little, if anything, to the population size of the next generation. Maximum likelihood estimates of banded birds showed that 66% of territory-holding males survived from one year to the next.

Chapter 3 combined the best estimates of these parameters and inferred others, including the survivorship of females and first-year birds. We came to the conclusion that the overall growth rate of the population was, plus or minus a few percent, close to replacement. Those few percent are a measure of the rigor of our procedures, for these data are derived from a population that has not changed perceptibly over the years during which we collected the data. That is, we estimated parameters consistent with the birds replacing each other and they have obliged us by doing so.

A typical risk analysis (sometimes called a population viability analysis or PVA) would devote considerable effort to estimating the bird's demographic parameters. We do not. While we applaud rigor and the best possible procedures, we now ask whether tight confidence intervals applied to some parameters make any difference or, worse, obfuscate the critical issues. Perhaps the most important parameters that we need to know, only serendipity will give us. How quickly do birds die when evicted from their homes by fire and flood? And how quickly does the population recover thereafter? These are inherently rare events for which our detailed estimates are merely a guide, however small the confidence intervals about them.

How quickly do birds die when conditions are bad? Even under the best conditions, 34% of the males are lost from their territories from one year to the next. We have smaller sample sizes for females that suffer the extra stress of producing and carrying eggs. We see only about a quarter of the fledged young the following year, but this must be an underestimate of their survival because some move to areas away from our extensive network of study sites. Almost certainly, however, young do not survive as well as territory-holding adults. A much greater fraction of birds will likely die under the worst conditions — prolonged, deep flooding of the habitat (which occurred from 1993 to 1995 in the western population) or extensive fires (such as that which burned most of the eastern populations in 1989).

We do not have survival estimates during these conditions and think that few studies will ever satisfactorily estimate parameters during rare events, even those that befall common species. We assume conservatively that adult survival (males and females alike) is 66% even in bad years. We assume that 50% of young survive from their hatch year to the next — a number that we feel is almost certainly too high.

How quickly can birds recover when conditions are favorable? Obviously, long-term estimates of parameters give means, not maxima. There are, however, some obvious limits on those maxima. First, suppose every pair in a population laid two clutches a year. (We have never seen anything like every pair laying a second clutch even when the conditions remain dry enough, long enough, for them to do so.) Second, suppose that the best fledge rate ever observed in a given year (60% of eggs) applied to both clutches. (We have never seen second clutches fledge the same fraction of eggs as first clutches.) Combined with the optimistic survival rates of the last paragraph, a population could increase at 61% per year. We then assume that these birds could fill up the area available for nesting without any additional mortality during their dispersal. We label this the "wildly optimistic" scenario.

The best fledge rate ever sustained for a few years in a row at a particular population was 53%. This was in population E, where numbers have steadily increased in the last few years. Even there, second clutches were less frequent and less successful than first clutches. We assumed that 60% of birds with available habitat laid second clutches and their success was the same as the first attempt. This leads to a potential growth rate of 34% per year. We still call this scenario "optimistic", because second clutches have never been observed to be so frequent or so successful.

Reducing the 60% to 50% leads to a maximum growth rate of 24% per year. We label this scenario "plausible."

Certainly we can change other parameters. Reducing the survival of the hatch year birds, a parameter that this and many other studies estimate imprecisely, has the same effect as reducing the number of young that fledge. What matters is the relative rates of increase between years; 1.61 for the "wildly optimistic" case, 1.34 for the "optimistic" case, and 1.24 for the "plausible" case. We now see which of these are consistent with our observations, and what the implications are for each population's risk of extinction.

8.2.1 The population west of Shark River Slough (A)

This population lives on a low ridge that is particularly vulnerable to flooding. Water depths of more than a few tens of centimeters prevent breeding or terminate it if it has already started (Chapter 2). Chapter 6 calculated the extent of available breeding habitat for each of the last 20 years, classifying areas into those that remain dry enough for just one brood to be raised and those that could produce two (assuming birds were physiologically capable of doing so). We then estimated the number of sparrows produced each year from the breeding and survival parameters scaled by the available habitat under the various scenarios described in the previous section. The sparrow numbers start with a guess of 2,000 birds in 1977 and follow deterministically thereafter, with the observed previous 20-year sequence of water levels repeated cyclically into the future. This starting point in 1977 allows the population to increase to its estimated 2,500 birds by the time of the 1981 survey (Fig. 8.1).

The model caps population A at 3,500 birds, an estimate of carrying capacity that does not strongly enter into the model's results, because water levels so rarely allow the birds to breed across the potential range. We determined the cap based on the maximum available habitat and typical maximum observed densities. The estimates of actual habitat conditions show, for example, that in 1977 all 2,000 birds had the chance to raise one brood, but only 11% of them were in places dry enough to raise a second, even if they were fit enough to do so.

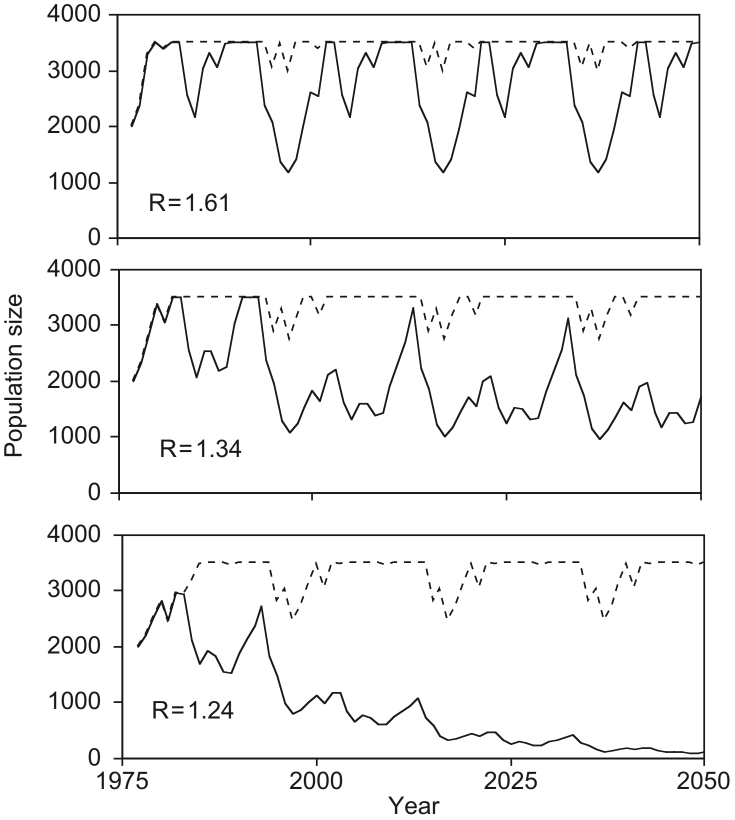

Figure 8.1: Three deterministic simulations of a model (see text) for the population west of Shark River Slough (population A). The proportional maximum change from one year to the next (R) varies from 1.61 (“wildly optimistic,” A), through 1.34 (“optimistic,” B) to 1.24 (“plausible,” C). The solid line uses the known extent of breeding habitat available for first and second clutches over the 20 years prior to 1997. It then repeats the same pattern. This extent is driven by managed water flows. Were massive dry season releases prevented, more habitat would be available for second clutches (dashed lines). Only the “plausible” model is consistent with the known population estimates in 1981, 1992, and subsequent years.

Two of the three scenarios in Figure 8.1 (“wildly optimistic” and “optimistic”) allow the population to persist. However, both optimistic scenarios fail to match two features of the rangewide survey of the birds. First, whereas both optimistic scenarios suggest an increase in numbers between 1981 and 1992, the population in 1992 was estimated to be 7% lower that it was in 1981. Unfortunately, there were no surveys in intermediate years, including some when substantial areas suffered prolonged flooding. Second, these models do not recreate the drop in population that followed the wet years of 1993 to 1995 inclusive, when the population estimates fell to fewer than 400 birds. The "plausible" model predicts fewer birds in 1992 than 1981, but even it optimistically predicts ~ 800 birds after these wet years.

An additional validation of the model and its parameters would require the sparrows to persist in the absence of these unnatural events. Were the sparrows predicted to decline, then we might suppose the model erred in not allowing the birds to recover quickly enough. We ran this "what if" alternative using a second set of models. If, during the catastrophic years, the sparrow's habitat had not been flooded early in the season, and if 100% of the habitat had been available for one brood, then the population would have thrived even under the "plausible" scenario. Indeed, it would have often reached the model's population ceiling of 3,500 birds (Fig. 8.1).

Thus calibrated, we ran our models for more sets of 20 years. They recycled the exact patterns of habitat availability, whereupon the population declined towards extinction within 50 years in the "plausible" scenario (Fig. 8.1c). It even goes to extinction in the "optimistic" one (Fig. 8.1b). What if water were not released during the breeding season? The population would dip below its population ceiling periodically but would persist indefinitely, even in the "plausible" scenario.

The catastrophic years of 1983, 1984, 1986, 1987, 1993, and 1995 were not *naturally* bad years. They resulted from deliberate, massive dry-season releases of water through the S-12 gates into Everglades National Park (Chapter 6). The contribution of rainfall to the water levels was relatively small in comparison.

So we conclude that repeating managed water flows with the pattern of the last two decades will drive this endangered species to extinction in the area that once held the largest number of birds. The survey data we have collected since 1997 confirms this speculation. The population has remained under 500 birds and it is restricted to a few square kilometers of habitat.

(Managed high water levels may also be a problem for population D, and likely similar conclusions apply to it as to population A.)

8.2.2 The populations to the north and east of Shark River Slough (C, F)

High water levels are not an issue in populations C and F as yet; indeed, it is the shortage of water that is the problem. Here, frequent fires burn the prairies. Under the best circumstances, fires severely reduce sparrow numbers for two years postfire (Chapter 6). We see little point in running risk analyses of these populations. In total, they number a few hundred birds scattered across a wide area that fires burn, in some cases, annually. Thus, the birds are already scarce and the threats to them are self-evident. More important is the question of whether fires that start in this area might spread southward to burn the only area where more than 1,000 birds remain: the southeastern population.

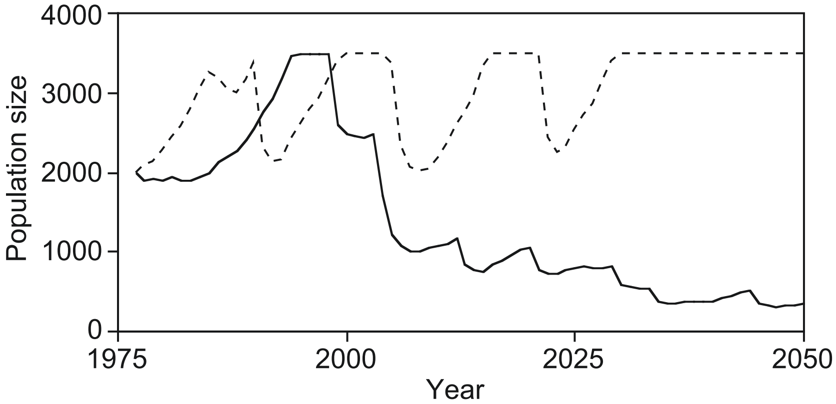

Figure 8.2: Examples of stochastic simulations of a model (see text) for the largest remaining population of Cape Sable Seaside Sparrows (B). Twenty percent of the habitat burns each year, on average, plus there are "bad" fires that burn an average of 90% of the habitat. Such fires every 20 years allow the population to persist; those every 10 years do not.

8.2.3 The southeastern population (B)

Small portions of this area burn every year, often as a consequence of fires that burn out of the pinelands to its north. Yet in 1989 nearly half of it burned as a consequence of a massive, dry-season fire. Probably all of population E burned, perhaps explaining why it is still recovering. Such fires can burn many hundreds of square kilometers in the Everglades. This size dwarfs the sparrow's range: the population in the southeast occupies only about 60 square kilometers. The policy of Everglades National Park is not to allow major fires to cross the park roads that divide this population into three parts. Nonetheless, fires of this size are hard to control in practice.

We modeled this area's population using the "plausible" scenario calibrated above. We modeled small fires assuming that every year 20% of the habitat burns and also assuming that birds within these areas cannot breed successfully that year but do not suffer any direct mortality (see Chapter 6, section 4, and in particular, Figure 6.4). We do not know how many adult birds die in fires, but it surely is more than we have assumed. We assumed that in the year after fire, 50% of the birds can breed in an area, 75% the year after that, and 100% the following year. Finally, we varied the frequency of severe fires (those that burn 90% of the bird's habitat).

Figure 8.2 provides two sample simulations with severe fires every 10 years and every 20 years. In the former case the population quickly goes to extinction; in the latter case it persists. With fires on average every 10 years, only 5% of the simulations allowed the population to increase over a 50 year period. From their original start of 2,000 birds, 50%

of the simulations resulted in the population dropping below 1,000 birds and 15% fell below 500 birds. Given enough years, all of the model runs encountered a series of fires that drove the population to extinction.

In sum, the southeastern population is in danger of extinction from extensive fires that occur as frequently as one every 10 years. Given that we have observed such fires in or near this population at that frequency, we conclude that this population is also at severe risk of extinction.

8.3 Conclusions

We predict that the sparrow population west of Shark River Slough will decline to extinction if the pattern of managed flows through the S-12 structures for the last 20 years repeats. If these unnatural breeding season flows through the S-12s are stopped, this population should flourish. The populations in the northeast have already declined to near extinction. These declines will continue unless the fire regimes are changed. On its own, the population in the southeast runs the risk of extinction because of episodic, large-scale fires. The fate of population E (now the second largest population) is interesting because it may illustrate a population that was burned to oblivion in 1989 and is still recovering.

Our models omit some obvious features. We have not included the effects of prolonged inundation or frequent fires on the vegetation. These processes alter the vegetation in ways that preclude the birds' use of areas for several years (Chapter 7). Incorporating these impacts would likely lead to even greater concerns about the sparrow's future.

The predictions of our models arise from our knowledge of the bird's breeding biology and of the area's water and fire regimes. They are not "curve fitting" exercises. Importantly, the results predict the timing and magnitude of the changes in those data. This confirms that the models are both sensible and sufficiently complete to capture the essential features.

The predicted decline to extinction of the southeastern population is a prediction of future events and thus one not confirmed by our short-term data. Notice a subtle problem: if the currently least-affected population is doomed, why does it hold so many sparrows? Should it not have gone extinct earlier? There are two nonexclusive answers. First, it, too, is affected by episodic fires, such as the fire in 1989, that might be relatively recent phenomena brought on by management changes and likely to be outside previous experience. Second, the sparrow has become locally extinct on occasion and then recolonized from other populations. This possibility makes good sense. Years of naturally high water west of Shark River Slough would harm the population there. Concomitant flooding in the northeastern populations would suppress the frequency of natural fires there and, consequently, the possibility of the fire's spread to the southeastern populations. In contrast, in dry years, the population west of Shark River Slough would be expected to flourish, even if the eastern populations ran higher than average risks due to fires. Simply, a high-risk year west of the slough would be a low-risk year east of the slough and vice versa. A complete exploration of these possibilities will require a combined water and fire model.

Nonetheless, we offer the following tentative conclusion: the sparrow will only survive if it has at least three healthy populations. To implement this requirement, the breeding areas west of Shark River Slough must not be flooded in the breeding season, and water levels should be raised in the northeast of Shark River Slough to reduce the incidence of fires.

The general conclusion for conservation is that species are not immune to massive anthropogenic impacts from outside even within one of the hemisphere's largest and best funded national parks. Everglades National Park is not large enough for calculations of risk based on natural population fluctuations to be sensible. Such calculations demonstrably gave the wrong answer for the sparrow.

Appendix A

The AOU Committee Report's Concerns

A.1 Introduction

Human actions endanger species' survival, so protecting an endangered species constrains human actions. Not surprisingly, some who feel those constraints may challenge the science on which management actions are based. Some of these challenges will be scientifically legitimate and require an independent assessment. Even when those challenges lack credibility, the opportunity to seek the help and advice of other scientists is welcome.

Our work on this species has been the subject of two external reviews. The first (Orians *et al.* 1996) evaluated our conclusions about the effects of the high water levels of 1993 to 1995. The second was a more focused effort on the sparrow. It led to a review by the American Ornithologists' Union (Walters *et al.* 2000). They raised many issues, while effectively silencing a large number of criticisms of our work. Of particular relevance here are the recommendations the committee made about our surveying methods.

The American Ornithologists' Union external peer review committee (Walters *et al.* 2000, but henceforth referred to as the "AOU committee") recommended that we undertake a second count within a year to measure the accuracy and reliability of the method. Two surveys were completed in 1999 but one was much later than the other. (We did not receive the AOU's recommendations in time to do otherwise.) The later survey found fewer birds in populations where reproduction is poor (compatible with the suggestion that birds had abandoned territories after breeding). In the more productive populations, the second survey numbers were higher, raising the possibility that we were counting floating individuals from elsewhere (or even young birds of the year). We also completed two surveys in 2000, both within April and May across much the same range of dates, with two different survey crews using identical methods.

Table A.1: The frequency of numbers seen on the first survey (rows) compared to the second survey (columns).

	0	1	2	3	4	5	6	7
0		30	11	5	2			1
1	28	10	8	6				
2	16	8	6	4		1		
3	7	4	4	4		2		
4			1		2			
5								
6		1						
7								

We feel that the AOU committee's concerns about the survey can be distilled into two questions:

1. How repeatable (or consistent) is the survey?
2. How accurate are the population estimates based on the correction factor of counts × 16?

A.2 How repeatable is the survey?

The experience of 1999 illustrates the concern: the numbers on one count were quite different from those on the other. In the extreme, this must be the case: were we to count birds in (say) October, it is very unlikely that we would hear many singing. The second 1999 count lasted three weeks after the first and into the season when we knew many birds were not breeding.

Were there to be major discrepancies between two counts undertaken over the same interval during the peak of breeding, we could not easily explain differences except by a failure of survey method. There are, however, many reasons why we should *not* expect even these surveys to be replicates, and why, by inference, we should be concerned about the accuracy of the survey results in general. These include different observers and variation in the birds' propensity to sing across the breeding season.

Are the data in Table A1 inconsistent with each survey being a true replicate? For instance, should we be concerned that single birds were detected at 28 sites on the first survey in which none were detected on the second? (There were 30 sites for which the converse was true.)

The nature of the survey means that only the statistically naïve would think that the counts would be identical on both surveys. Although we make every effort to land the helicopter in exactly the same location on each survey, the limitations of the Global Positioning System (GPS) prevent that. (Until recently, GPS signals were scrambled to limit their accuracy.) Even if the signal were not scrambled, the birds move within their territories. These are roughly 2 ha in size; at its most compact, a territory might be a circle of 80 m radius. The correction factor of 16 assumes that we will count all birds within 200 m. Yet, a bird could be a mere 41 m away on one count and at the other end of its territory, 201 m away — and thus out of range — on the next.

This suggests the distribution of sampling outcomes should be Poisson, a distribution that has a long history in statistics. For example, if the true density of territories is such that there is one per sampling area across the entire survey area, then the distribution of counts of territories will have outcomes $0, 1, 2, \ldots$ described by a Poisson distribution with mean $= 1$. Under this circumstance, there is a 37% chance that no birds will be encountered, a 37% chance that one bird will be encountered, then 18% for two, 6% for three, 2% for four.

The standard deviation of Poisson outcomes equals the mean, so the standard error follows simply by dividing the observed mean by the square root of the sample size. Confidence intervals then follow in the usual way.

So is the model right?

One way to test it is to ask whether the number of birds seen on one survey is inconsistent with the number of birds on the other. The simple example just given allows us to calculate that the chance of seeing single birds on both surveys is $0.37 \times 0.37 = 0.14$, that is, 14%. There is the same chance of seeing no birds on both surveys. And, in this particular case, there is a 28% chance of seeing one bird on one survey and no bird on the other or vice versa. There is a 4% chance of finding no birds on one survey and three on the other, or vice versa.

The point of this preamble is that this provides a model of how consistent the survey should be, and so the germ of a recipe for testing whether the survey fails that expectation. There is one added complication. We are not omniscient, and so we do not know the true sparrow density at each point. Our best estimate is the mean of the two surveys. In Figure A.1, we plot the log frequency of those mean values. The shape, a logarithmic reduction in frequency with increasing abundance, is typical of many populations.

We now imagine that this provides a reasonable description of the variation of the true mean density. There are n_1 sites with a density of 0.5, n_2 sites with a density of 1.0, and so on. This allows us to calculate how many sites would have (i, j) birds seen on the first and second surveys respectively, where $i = 0, 1, 2, \ldots$ and $j = 0, 1, 2, \ldots$ when the true density is $0.5, 1.0, \ldots$. At every density, of course, there are identical outcomes $i = 1$, $j = 1$, for instance. So the expected number of sites where one bird is counted on the first survey and one on the second is the sum of the probabilities across all the true densities weighted by the frequency of those densities.

Summing these expected values across all possible outcomes leads to a small underestimate of the observed total, because there is a fraction of sites where no birds are seen on the first count and none on the second but where the true density is not zero. (See the

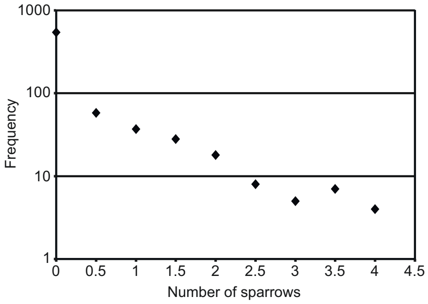

Figure A.1: The frequency of average values of sparrows encountered per survey site. (Note the log scale for the frequency.)

Table A.2: Expected numbers of birds seen on one count versus numbers seen on the other.

	0	1	2	3	4	5	6	7
0	34.25	22.67	9.34	3.36	1.17	0.40	0.14	0.05
1	22.67	18.68	10.07	4.68	2.02	0.83	0.33	0.13
2	9.34	10.07	7.02	4.04	2.07	0.99	0.44	0.18
3	3.36	4.68	4.04	2.76	1.64	0.88	0.43	0.19
4	1.17	2.02	2.07	1.64	1.10	0.65	0.34	0.16
5	0.40	0.83	0.99	0.88	0.65	0.41	0.23	0.11
6	0.14	0.33	0.44	0.43	0.34	0.23	0.13	0.07
7	0.05	0.13	0.18	0.19	0.16	0.11	0.07	0.03

earlier example.) So we correct for that under-count by multiplying the frequencies by the constant required to match the observed and expected counts.

This matrix sums to $\sim$ 199 individuals (Table A.2; expected values need not be integers), but only 165 (= 199 − 34) would be recorded because the $0, 0$ values do not appear. (165 is the observed total of sites with one or more birds counted during the survey.) One way to summarize these expected values is to sum the sites where the first and second counts do not differ, differ by 1, differ by 2, and differ by 3 or more.

The differences between observed and expected are not significant (Table A.3; as tested by a χ^2 test.)

In sum, the differences between the two surveys are exactly what one expects given the nature of the sampling process. Given the large list of factors that could inflate the differences between the two surveys, this is a quite remarkable result.

Table A.3: Comparison of expected versus observed differences. A difference of zero means that counts did not differ, 1 that they differed by 1, and so on.

Difference	Expected	Observed
0	30.14	22
1	78.73	84
2	34.85	40
> 3	21.64	19

A.3 How complete is the survey?

In the section after this one, "An analysis of detection probability," we present the results of an effort to replicate the helicopter survey count methodology on precisely fixed locations in areas where the number of neighboring territories is known exactly. Much of what follows justifies the decisions we make on the helicopter survey. For instance, we do not count birds into June, late in the morning, when the wind picks up, and when it is misty. (In the last case, the helicopter cannot land.)

Amid the plethora of results that follow is a consensus statement that under good conditions the chance of detection is "better than 60%." Does this mean that our survey consistently counts too few birds and so the population estimates are too small as a consequence? The answers are "no" and "not that it would matter if the answer were yes."

The second answer is the easier to explain. Even if the counts were underestimates, none of the inferences we have drawn (and on which the U.S. Fish and Wildlife Service's Biological Opinions are based) would be altered. The damage done by releasing massive flows of water through the S-12 gates, for instance, reduced the population to a mere 10% of its pre-1993 level. That statement, and the consequences that follow from it, would not be not changed if we multiplied the actual bird counts by 16 (as we do) or any other number.

The first answer is rather more interesting. "Better than 60%" is nearly exactly what we expect on the basis of the Poisson model we employ. For a true density of one bird per 200-m radius, the exact answer is $100\% - 37\%$ or 63%. Quite simply, birds move about their territories and, so, for reasons explained above, not all birds will always be in earshot.

Figure A.2 is a geometric example. The small clear circles are territories of 80-m radius and the larger, stippled circle is the 200-m detection radius. These territories are packed unreasonably closely, and real territories are not circular and so cannot be packed thus. But for an illustration, we ask how many birds can be heard and how many birds must be heard if all birds sing during the survey. The answer is 11 and 3 respectively. On average, the numbers heard will be in between. If one takes the average as 7 and expresses it as a fraction of the maximum (11), it comes to 63%.

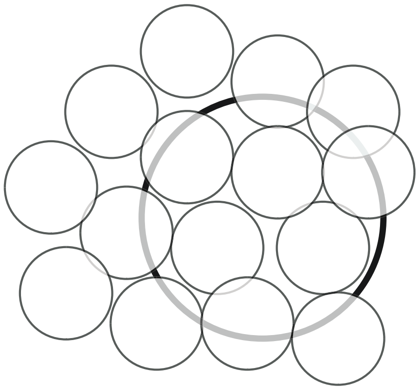

Figure A.2: A hypothetical example of territories (small circles) within a survey radius (large circle). So how many birds will be encountered on average?)

The point is that an unbiased, efficient survey should detect birds *only an expected fraction of the time*, and our estimates are close to that expectation.

Of course, what we would still like to know is what fraction of birds with territories entirely within the survey radius were counted? (They should always be counted.) We do not have that information at present; this will require the results of GIS work, presently underway by one of us (JLL). On the other hand, the fraction cannot be too low or else the average detection fractions fall below values consistent with the survey results. For the time being, we have no evidence to reject the hypothesis that our survey methods provide a good estimate of the sparrow's total numbers.

A.4 An analysis of detection probability

Detection probability, the chance that we will record a male sparrow during standard point counts, is influenced by a variety of factors (e.g., weather, observer, and species), all of which decrease the likelihood that a true count of individuals can be taken. This bias should be explicitly incorporated into estimation protocols to avoid inaccuracies in abundance calculations. In June 1999, we established a series of point-count locations within our intensive study plots. Beginning in April 2000, we visited these locations and mimicked the extensive survey procedures for counting resident males. By comparing the count results to detailed territory maps, we can directly calculate detection probabilities. These probabilities can then be incorporated into error estimates for the extensive survey.

The correction factor of 16 is based on the fraction of total area sampled (a) and detection probability (p), such that $ap = 1/16$ (Walters *et al.* 2000). Below, we directly calculate p, and variations in p, by conducting fixed-radius point counts within intensive study plots

Table A.4: Beaufort scale of wind speed modified for use in marl prairies, Everglades National Park.

Beaufort Number	Field Criteria
0	No wind.
1	Slight wind such that the very tops of the grasses were moving.
2	Wind such that the entire stalks of grasses were moving.
3	Moderate wind such that leaves on trees in hammocks were moving.
4	Strong wind such that tree branches in hammocks were moving.

and then comparing these counts to the results from detailed territory mapping. The mapping efforts represent the "true" number of individuals within a 200-m radius of the point count location. Once the detection probability is calculated, a correction factor can be estimated under all conditions explored (e.g., wind speeds, density groups, and time of day).

A.4.1 Methods

We conducted fixed-radius point counts from 14 April to 17 July 2000. We established point count locations 400 m apart within seven 600 m × 800 m plots. Six locations were within population B and one was within population E. Counts were made following the procedures described above (and in Bass and Kushlan [1982] and Curnutt *et al.* [1998]). All individuals heard singing, or sighted, were recorded for up to 7 min after arrival at the point-count station. We could not simulate the arrival and departure of a helicopter; however, traveling by foot through a breeding area may have broadly similar effects on resident males. When generally disturbed (i.e., when not defending a nest), males tend to perch atop sawgrass (*Cladium jamaicense*) seedheads and sing. We varied our start times across study plots such that all times between sunrise and 11:00 a.m. were covered. During each count we recorded the observer, visibility, water depth, and wind speed. Wind speed was estimated using the Beaufort scale with adjustments for use in marsh habitat. The Beaufort scale used ranged from 0 to 4 with each increase in scale indicating an increase in wind speed (Table A.4).

We began mapping the territories of banded and unbanded males on 25 March and continued to update these maps until 17 July 2000. A crew of two or more visited each plot at least one day per week for at least 3 hr. Observers located sparrows using spotting scopes or binoculars, and marked the location of their territories using colored survey tape. Some territories were marked after a member of the resident pair was captured in a mist net. Territory location was recorded using a GPS and subsequently recorded on an ArcView map. Point-count locations were also recorded using GPS, and these locations were overlaid onto the territory maps for each plot. We then counted the number of territories wholly or partially within a 200-m radius of each count location based on these maps.

The total number of marked territories wholly or partially within 200 m of a point count station represents the “true” number of sparrows. We then scaled the number of individuals detected during each point count by this value. This proportion is the detection probability. It is possible for the observer to overestimate the number of sparrows within the 200-m-radius detection zone (e.g., birds not resident within 200 m venture into the point count radius and are counted). Thus, probability of detection can range from 0 (i.e., no birds were detected although some were mapped) to > 1.0 (i.e., more birds were detected than were mapped).

Mean detection probability was calculated according to time of day, wind speed, water level, observer, plot, month, and density levels. Start times were categorized into five nominal categories: Between 6:00 a.m. and 7:00 a.m., between 7:00 a.m. and 8:00 a.m., between 8:00 a.m. and 9:00 a.m., between 9:00 a.m. and 10:00 a.m., and after 10:00 a.m. We compared the mean detection probability between these four start times using ANOVA. Similarly, we compared mean detection probability between observers (7) and months (4) using ANOVA. We looked for changes in detection probability with water level and wind speeds using simple linear regression and ANOVA. We measured water depth relative to the soil surface. All water measurements were made at the point count station at the start of each count period.

It is possible that detection probability will change as sparrow abundance changes. To test this, we divided the point count locations into two density groups. Locations that held fewer than four territories within 200 m of the point count station were considered low density. Locations with more than five territories were considered high density. We tested for differences in mean detection probability between the two groups using a t-test.

A.4.2 Results

Seven observers made a total of 254 point counts between 14 April and 17 July 2000. The maximum number of birds detected during any one point count was eight, and the minimum was zero. The maximum number of territories mapped within a 200-m radius of a point count location was nine, and the minimum was zero. Detection probability averaged 0.58 (standard error $= 0.02$) and ranged between 0 and 1.67. On 14 occasions (5%) more birds were detected than were shown on territory maps. Overestimates occurred across the season and the different start times with no noticeable pattern. On 11 occasions (4%), no birds were detected in areas that contained one or more mapped territory (i.e., a false negative occurred). The vast majority (95%) of errors in detection involved underestimates. Visibility very rarely fell below 200 m, twice falling to 150 m and once to 60 m. Thus, during 99% of the counts it was possible to easily see birds within a 200-m radius of the count location. Wind speeds varied between zero and four in the Beaufort scale, with a modal value of one. The earliest start time was 6:48 a.m. and the latest was 10:14 a.m. Most counts (84%) were made between 7:00 a.m. and 9:00 a.m.

Detection probability was not influenced by the depth of standing water according to ANOVA ($F = 2.4$, D.F. $= 1$, $p = 0.12$). Water depths varied from 0–17 cm with a mean depth of 3.31 cm (standard error = 0.30).

Detection probability varied significantly according to time of season (i.e., month), time of day, sparrow density, and wind speeds. Time of season (month) had a statistical influence on detection probability (ANOVA, $F = 5.90$, D.F. $= 3$, $p < 0.001$). However, there was no obvious pattern to these differences. The highest mean detection probability recorded was among June counts (0.70, $n = 65$) and the lowest mean detection probability was in July (0.47, $n = 41$). April and May probabilities were 0.51 ($n = 58$) and 0.57 ($n = 92$) respectively.

Mean detection probability declined monotonically with time of day and higher wind speeds. Counts conducted after 10:00 a.m. produced the lowest mean detection probabilities (0.30, $n = 4$). Point counts that started at 9:00 a.m. and 8:00 a.m. had mean detection probabilities of 0.37 ($n = 30$) and 0.50 ($n = 96$) respectively. The highest mean detectability occurred during counts made between sunrise and 8:00 a.m. (0.70, $n = 114$). These differences were statistically significant (ANOVA, $F = 15.4$, D.F. $= 3$, $p < 0.0001$). Detection probability and wind speed were negatively correlated ($F = 30.1$, D.F. $= 2$, $p < 0.0001$). The correspondence of effects for wind speed and start time are not independent. Wind speed tends to increase as the morning wears on ($F = 43.8$, D.F. $= 3$, $p < 0.0001$).

Finally, detection probability decreased as density increased. Count locations with three or more mapped territories had an associated detection probability of 0.61. Count locations with seven or more mapped territories had an associated detection probability of 0.49. These two means were statistically different ($t = 2.50$, D.F. $= 1$, $p = 0.01$).

A.4.3 Discussion

The range of detection probabilities provided here provides advice to the extensive survey that we have long understood. Detection probability can be quite high depending on conditions. An early morning, low-wind count is often better than 60% accurate — what one would expect under the Poisson model. However, this probability drops by half as the morning progresses and the wind increases. To maintain a high rate of accuracy in counts, it is our recommendation that point counts are restricted to earlier than 9:00 a.m. and under wind conditions of two or less on the Beaufort scale. Although wind speed tends to increase later in the morning, this is not always the case. We encountered mornings when wind speeds remained low past 9:00 a.m. Thus, discretion in applying this recommendation is necessary, as it may be possible to conduct accurate counts late in the morning on some occasions.

We found no discernable pattern in detection probability during the typical time frame of the extensive survey, despite observing significant differences in detection probability by month. We purposefully excluded juveniles in this calculation despite our recording flocks of juveniles regularly past mid-June. We observed some of these juveniles “practicing" their song, and thus they may be easily mistaken for breeding males by inexperienced observers. By late June, all observers were very familiar with sparrows as they had been finding and following nests since March. They could easily distinguish juveniles by sight and sound. This may not be the case for personnel conducting the extensive surveys as they are typically not as intimately familiar with sparrow behavior. Thus, it is our further recommendation that point counts are not conducted past the first weeks of June as observers may inadvertently include young of the year in their counts.

There was a discernable difference in detection probability between low- and high-density locations. The low-density locations included here are comparable to densities observed in the Shark Valley plot before 2000. This study plot is imbedded in what is now one of the most sparsely populated areas of the sparrow's range. In these low-density areas, detection probability was high (0.61) indicating that, if sparrows were present, they were likely to be counted. However, there also appeared to be a saturation level beyond which observers had a difficult time distinguishing all resident males. Detection probability dropped to 0.49 in locations that held five or more territories. This led to the slightly counterintuitive result that the extensive survey is more likely to underestimate the number of males within densely populated areas than in sparsely populated areas.

A.4.4 Other relevant factors for the extensive survey

The AOU external review board also suggested the use of female departure calls as a method for surveying female sparrows. We observed what we believe to be departure calls made by the females of this subspecies under much the same circumstances as described in MacDonald and Greenberg (1991). However, the detection distance for this call is well within 50 m of the nest, and it cannot be heard given the slightest wind. This is in sharp contrast to departure calls given by other marsh-nesting birds (Greenberg, pers. comm.). We find that counting females by listening for departure calls is not practical in this context.

A.5 The AOU committee response to the repeated survey

In the winter of 2000–2001 three members of the AOU committee independently commented on our response to their earlier concerns about survey methods. In this section, we reproduce those comments and supply our response to them.

A.5.1 Reviewer 1

> In 2000, the CSSS research team added an assessment of detectability as part of its annual survey program. Following suggestions of the AOU review committee, the researchers conducted a number of point surveys in areas where the number of pairs of Cape Sable Seaside Sparrows is known (based on color

> banded birds). For me, this field exercise and analysis are much more powerful than the repeated survey analysis and I will focus my comments on this calibration.

We agree. Indeed, this is an important reason why we invest effort in maintaining color-banded populations across intensive study sites in the three main populations.

Predictably, detection probability (sparrows counted on point-count survey divided by marked males with territories overlapping count circle) varied with time of day, time of year, wind speed, and sparrow density. Under "good" conditions, detection probability was 0.6. We further argue that this is as high as can be expected if all singing males are detected, because no attempt was made to weigh the presence of birds in the 200-m circle by the portion of their territory within that circle. The conclusion is that correction factors can be incorporated based on the predictable changes in detection probability; it is, however, unclear as to when or if such correction factors will be applied.

> My main concern with this conclusion is that it is unclear from the document how many historical surveys were conducted under conditions that now require correction factors. My other question (having done a lot of this kind of survey work in other regions) is whether enough days in the optimal season are available so that counting does not have to be done under poor conditions.

The expectation that even under the best possible conditions, only $\sim 60\%$ of the birds will be detected, stems from the assumption of a Poisson sampling distribution. The variation about this level — when conditions are not good — could be corrected in several ways. One might be using different correction factors under different conditions. In our experience, this is a poor solution when those factors can only be measured imprecisely. Our solution has been to *only survey when the conditions are good*. We survey for only 2–3 hr each morning (we are limited by helicopter range and fuel capacity), we do not fly when conditions are not good, and we stop early if, in particular, the wind starts to blow. We employ very few observers, all of whom are very experienced.

> One interesting result is that detection probability declines with density. This has been found with other surveys and is apparently a result of people underestimating the number of singing birds when a number of birds are singing.

This is an interesting point. Its effect on the bird counts, however, is quite small. Almost all of the observations involve only one or two birds per site. If (say) sites with five birds were mostly sites with six birds, the estimated numbers of sparrows would increase only very slightly.

> It seems to me that there is much more information that can be derived from the type of calibration conducted. The analysis in this report has focused on determining the detectability coefficient. However, by presenting the data as

> a regression between the number detected and the "true" number of territorial sparrows and conducting some ANCOVA analyses, we could get a handle on the detectability at low densities (intercept), change in detectability with density (slope), and the reliability of the count (amount of scatter — correlation coefficient). Wind speed and time of day could be treated as covariates. It would be most interesting to plot out this regression for points conducted during the optimal count conditions. If territory maps are available, then one ought to be able to estimate the proportion of territories contained in the 200-m circle. Along these lines, I wonder what can be learned from more information about the plot maps. For example, how many of the birds detected are unmated males, and what is the origin of the males detected on surveys that weren't part of the territory maps.

While we are currently working on plot maps and birds detected by point counts on them, the main point is that we avoid those conditions that would affect the counts' accuracy.

> I have a couple of other more technical comments: What is the specific evidence that observer experience did not affect detection probabilities? Should some sort of program (such as DISTANCE) to correct for differences in the distance of the bird be used to convert detections into density estimates.

The evidence was overlooked by this reviewer; it appears earlier in this chapter. While it is possible (perhaps likely) that detection declines with distance to the bird, the "factor 16" correction includes this. We see no reason to change it.

> Finally, the confidence intervals and much of the arguments on the accuracy of the counts depend upon the use of a Poisson distribution. However, if the sparrows are patchily distributed, can a Poisson distribution be invoked? I have yet to see actual territory maps or an analysis of the spatial distribution of sparrow territories. From comments in the report, I gather that such as analysis is in the works.

The Poisson distribution accepts that sparrows may live in patches, but it does require that the sparrow detections are statistically independent. (That is, there is nothing that prevents the expected value being (say) five detections per site or two detections per site, so long as the individual detections are not contingent. Were they to be contingent, then one would get too high a variance on repeated surveys. This is the point of the repeated survey analysis presented above. Were one to see (say) many locations where there were 10 birds on one count, then zero on the next (and vice versa), the Poisson assumption would not hold. This would be the case were birds to be in flocks. As the analysis shows, the numbers we encounter are entirely in accord with the Poisson assumption.

A.5.2 Reviewer 2

> The most exciting element of this chapter is the information on detection probabilities obtained by collecting census data on intensive study plots in which the population was known. One of the panel's primary recommendations with respect to research was to obtain such information. Even these initial results are interesting and informative. The overall detection probability was 0.58, whereas it has been assumed to be 1 previously.

Not so! The Poisson expectation is that the average number of detections matches the underlying true density. However, it recognizes that (for instance) even when the true density is 1.0, no detections will be made in roughly 37% of the surveys. These omissions are counterbalanced by the times where more than one detection is made.

> Detection probability varied from 0 to 1.67 depending on observer, season, time of day, wind speed and population density. Knowing the effects of these factors will enable improvements in the census protocol, and indeed the authors suggest limiting counts to conditions meeting certain criteria based on their findings. Adhering to these criteria should reduce variance in detection probability and thereby enable more accurate population estimates.

We do indeed adhere to these criteria and have already done so.

> The panel also recommended incorporating estimates of detection probability into the census, and using estimates of detection probability in calculating sampling error associated with population estimates. That detailed inferences about changes in population were being made based on census data that lacked any variance estimate was a major issue in the panel review.

Again, this is not so. When we have made inferences, we have always assumed that the census data were Poisson distributed. For such data, the standard deviation equals the mean, and so the standard error of the mean is the mean value divided by the square root of the sample size.

We disagree that the sampling error is our principal concern. What matters are the inferences we draw from them. Estimates with tiny sampling variances may not tell us anything of ecological interest; all populations fluctuate. Conversely, those estimates with greater statistical uncertainties may still be ecologically informative when supplemental data are available.

> Perhaps data on detection probability are as yet too few, but still, it is disappointing that no attempt is made to determine the precision of the 2000 census data. Instead, the 2000 data are portrayed and discussed much like previous census data, despite the panel's criticism. Furthermore, two analyses are conducted to demonstrate the accuracy of the data, both of which the panel specifically discounted as useful approaches: replicate counts and application of the

> Poisson distribution. The panel noted that detection probability cannot be estimated well from replicate counts. The authors do not use their replicate counts for this purpose, but instead argue that consistency within replicates indicates that counts are accurate.

Our response contains two elements: an estimation of sampling variance (from the repeated surveys) and an estimation of detection probabilities. As explained in response to earlier comments, these have separate functions, ones this reviewer has misunderstood.

> The counts do not appear very consistent to me. For example, at the station at which the most birds (7) were detected during the first survey, none were detected during the second. As for use of the Poisson distribution, it addresses only one of the two components of sampling error (i.e., it does not address the component associated with detection probability), and even for this component it is better to use the actual distribution of count data rather than assume an underlying distribution (Walters *et al.* 2000).

The reviewer's first comment is without any associated statement of probability. As explained in the analysis, across several hundred observations, the chance of seeing zero birds on one count and seven on the next falls within broad expectations. Indeed, the example we provide could involve zero birds being present on one count and nine on the next.

> To provide just one example of the difficulties in interpreting count data in the absence of an estimate of variance, I turn to counts of population A in 1998, 1999 and 2000. The authors conclude from these data that population A has been constant in size during this period. However, the count in 1999, and 2000 was twice that in 1998. Has the population size changed? It is impossible to say without an estimate of sampling error.

Once again, we refer the reader to introductory statistics textbooks that would instruct him in how to calculate standard errors from Poisson distributed statistics. In this particular case, the answer depends largely on whether one expects a trend in numbers (in which case several years can be combined for inferences) or one must treat the samples without any prior inferences.

In response to this, and similar questions, Chapter 5 now identifies each of the inferences we draw.

A.5.3 Reviewer 3

> The authors specify two quantities that they believed to have been of interest to the AOU committee: repeatability (consistency) and accuracy. I would have restated these as accuracy and precision, and I note that they are often combined

> into a statistic such as mean squared error that provides an excellent metric for evaluating estimator performance.

We are quite happy to call these repeatability and accuracy. The mean square error follows simply from the Poisson distribution assumption in the normal way.

> The exercise with the repeat counts for 2000 was difficult for me to follow, but I believe that the conclusion that emerges is that both counts can be described by a Poisson distribution with the same parameter, λ. This would suggest similar detection probabilities for the two surveys if the population were closed between sampling periods.

Exactly so.

> That is nice, but a primary concern in the AOU review did not involve changes in detection probabilities within season, but from year to year and thus across water conditions. So I still believe it is important to try to incorporate efforts to estimate detection probability each year of the survey. Repeat surveys within a year are not useful for this purpose, and, in my opinion, the extra effort should instead be channeled into distance sampling, multiple observers, temporal removal modeling or some other approach for estimating the detection probabilities associated with point counts (the addendum to this chapter is yet another approach to detection probability estimation).

As explained above, repeated surveys address one issue, estimation of detection probabilities quite another. The reviewers generally missed the efforts we expend in assuring that all the sampling is done by highly trained observers under optimal conditions. Simply, it is better to avoid differential corrections than to estimate them.

> The discussion in the material addressing the question: "How complete is the survey?" includes the idea that underestimation of abundance is not necessarily a problem in estimating rate of change. Certainly this is true, but the potential problem arises when detectability varies from year to year or from one set of environmental conditions to another. It is this year-to-year variation that is best dealt with by annual efforts to estimate detectability. In the absence of such estimation efforts, one must assume/hope that detection probability is constant over time, because temporal variation in detection probability will be confounded with true changes in abundance in the estimates of population change. This becomes especially important when changes in environmental conditions (e.g., water depths) are believed to influence true abundance but may also influence detectability.

We have no reason to expect that, under identical conditions, birds will be more difficult to detect singing in one year than another. There is a crucial point. Under conditions of high water, we rarely hear birds singing. That is because they are not singing, not because we do not detect them when they are. Why would birds sing when the only place for their nests is under a meter of water? What matters is not the number of birds alive in any one year, but the number of birds that have the chance to breed. Our estimates are of breeding populations, not populations — as, in practice, are almost all estimates based on singing males.

> The addendum to this chapter was very interesting and goes directly to the kind of study that seems most relevant to me. It is clear that the author considered the AOU report recommendations seriously and designed a very interesting investigation of sources of variation in detection probability. Previous work using territory mapping suggests to me that this approach may not provide the best fix on "true" numbers of birds. Also, I am accustomed to estimating a detection probability that corresponds to the birds actually present at the time of the sampling (so you can't get estimates > 1 unless you miscount), rather than one that includes a number of birds thought to "reside" in a sampled area. So I recommend considering other approaches for direct estimation of detectability.

Not so! Not only can one get estimates > 1, it is essential that one do so in order for the Poission distribution to work. The reviewer's error here is to assume that observers and birds are completely fixed in space. Were this model to obtain, we would employ a binomial model with p, the estimate of detection given that a singing male is present. As explained, neither the surveyor is fixed (because of GPS considerations) nor are the birds fixed (they move around their territories). There will, indeed, be occasions when, by chance, birds will have arranged themselves closer to the observer than expected.

> Nevertheless, I like the basic approach of this work very much, and it may well turn out that use of territory mapping is the best that can be done. The results are not unexpected, as variation in detection probability was found to be associated with observers, time of day, wind speed, and true bird density. I believe that this kind of detailed work is excellent and that it should lead to the recommendation to try to estimate detectability directly every year of the survey (as opposed to the 2 alternatives of (1) hoping detection probability is the same every year, or (2) trying to identify every single factor that may influence detectability and to then control for these factors or include them as covariates or develop models for them). Whether this estimation involves territory mapping, distance sampling, multiple observers, temporal removal, or another approach is best determined by those involved in the work.
>
> Finally, I note that Chapter 5 did not include an effort to estimate the variances of the population estimates. As noted in the initial AOU report, such estimates should include the components of variation associated with the estimation of detectability and the spatial variation in counts of animals. The previously

> noted asymmetry of effort devoted to data collection and analysis is worth mention again. The field work that went into this report was very expensive of time, effort, and real dollars, and such an effort should produce results that are accompanied by the standard measures of statistical precision. Such measures are not statistical fine points as they provide the information needed to permit the user to judge strength of inference. Thus, as a reader, I am provided no guidance about how seriously to view the estimates presented in Table 2, as my interpretation should be determined almost entirely by my understanding of the possible sources of bias (e.g., the manner in which detectability was incorporated) and by the associated measures of sampling variation (these are absent from this report).

This reviewer's comment about "no guidance" suggests he misunderstands our statistical model. Once the Poisson sampling is established, the sampling variance follows in obvious ways that are explained in basic statistics books. However, we once again stress that the estimates of variance are means to an end and not an end in themselves.

Appendix B

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