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The 2000 Cape Sable Sparrow Annual Report

Edited by

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Introduction

For the last two years, we chose to put our annual report on our work on the Cape Sable sparrow on the web to facilitate discussion and to provide the information needed by those who make management decisions about this endangered bird and the ecosystem on which it depends.

The set of all three years (1998, 1999, and 2000) provides a comprehensive archive of our work.

This year the web page will likely be delayed for a few weeks as we transfer the materials from the home of the reports for the previous two years

<http://web.utk.edu/~grussell/csshtml/csss.html>.

to their new home at the Center for Environmental Research and Conservation (Check the personal web page of Professor Stuart Pimm at www.cerc.columbia.edu.) The first version of this report is being produced in Adobe Acrobat format and distributed by e-mail. Until the new web site is complete, this year's report may requested in this form from StuartPimm@aol.com.

First time readers

The materials for these three annual reports were produced sequentially. As with all research, we obtain new information each year, sometimes modifying our interpretations as the new data require. Working through all this material can be daunting, so we offer some simple recommendations for navigation.

As a first step, read *The recovery of the Cape Sable seaside sparrow through restoration of the everglades ecosystem* by

Lockwood, J. and T. Fenn. 2000. The recovery of the Cape Sable seaside sparrow through restoration of the everglades ecosystem. *Endangered Species Update*.

This paper by Professor Lockwood and her colleague provides a short, succinct summary of the ecology of this species. It appears as chapter 1 of this report.

Second, read

Curnutt, J. L., A. L. Mayer, T. M. Brooks, L. 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.

And

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* 1:21-29.

These pairs of papers deal with the demography of the sparrow and causes of its decline up to the 1997 field season. They appear in the 1998 report.

Finally,

Lockwood, J.L. K.H. Fenn, J.L. Curnutt, D. Rosenthal, K.L. Balent and A.L. Mayer. 1997. Life history of the endangered Cape Sable seaside sparrow. *Wilson Bulletin* 109(4): 720-731.

This paper provides an early overview of the sparrow's breeding biology, the general features of which have not been changed by another four years of fieldwork (though the details certainly have.) It, too, appears in the 1998 report.

You should now considered yourself a veteran reader and progress to the next step.

Veteran readers

The previous two annual reports contain chapters comparable to this one in that they update the papers published in international peer-reviewed journals discussed in the previous section. In addition, they contain manuscripts were in preparation at the time but that have now been accepted for publication (or will likely be submitted in the near term.)

The work on the sparrow's risk of extinction that first appeared in *Balancing on the Brink* (see the 1998 report), and as Pimm and Bass (in preparation) in the 1999 report, appears here as chapter 2. It should be quoted as:

Pimm, S. L. and O. L. Bass, Jr. (in press). Range-wide risks to large populations: the Cape Sable sparrow as a case history. In Beissinger, S. and D. R. McCullough, *Population Viability Analysis*, The University of Chicago Press.

Professor Lockwood and her colleagues have produced updates of their work on the bird's demography in the annual reports subsequent to their paper. And there have been brief mentions of the banding efforts led by Mr. David Okines. Banding and nesting studies of rare species take many years to acquire sufficient sample sizes. Chapter 3 is our first effort to summarize these efforts for publication since 1997. This work has been submitted but not yet accepted. It should be quoted as:

Lockwood, J. L., Fenn, K. H., Caudill, J.M., Okines, D., Bass, O. L. jr., Duncan, J. R. and S. L. Pimm (in prep). Demography of the Cape Sable seaside sparrow within Everglades National Park

The work undertaken by Professor Robert Powell and Mr. Clinton Jenkins employing remote census technologies to modelling the changes in sparrow habitat has produced color imagery in several papers and in previous reports. This year the work is near completion and appears as Chapter 4. Although the paper has not yet been submitted, it should be quoted as:

Jenkins, C. N., Powell, R., Bass, O. L. Jr. and S. L. Pimm (in prep.) Demonstrating the destruction of the habitat of the Cape Sable seaside sparrow.

This paper contains this year's most important result and we abstract the introductory material here for emphasis.

Countries differ in the vigor to which they protect biodiversity and in the particular laws they pass to do so. In the United States of America, one of the more 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 take indirectly — through the destruction of the ecosystems on which species depend. That provision was challenged in a legal case, Sweet Home versus Babbitt, argued in front of the Supreme Court of the United States, on February 17th 1995. In the particular context of the Spotted Owl, an Oregon group challenged the responsible cabinet member, Secretary of the Interior Babbitt, arguing that only direct take violated the law and not habitat destruction. In a brief of Amici Curiae scientists, one of us (Pimm) and 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 raise 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.

Our particular concern is the Federally-listed Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) a bird found only within the seasonally flooded marshes in the Everglades of South Florida. In previous publications, we demonstrated that the unnatural flooding of its breeding habitat 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 over-drained and more susceptible to anthropogenic fires. Those fires also harm the birds directly.

We left open the possibility that flooding and fires also damaged the habitat and so the birds as a consequence. In this paper, we will demonstrate that flooding has indeed altered the habitat in which the sparrow occurs, done so in a way to preclude the bird's use of the habitat, and over a period of years longer than the flooding itself.

The paper proceeds in two stages. The first explains how we predict sparrow habitat. The second stage is an evaluation of those predictions.

We will present two key results.

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

(2) 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 1999. This formal, technical demonstration matches exactly the subjective opinion expressed by Bass and Pimm from their visual surveys. By 1999, the predicted suitable habitat had not yet recovered to its pre-flood state. The habitat is recovering faster than the slowly recovering bird populations. It is the repetition of precisely such a scenario that we predict could lead to the species' extinction (Pimm and Bass, 2000).

Lest the significance of this text still be unclear, let us be blunt. We do not issue opinions of biological jeopardy under the provisions of the Endangered Species Act: the Fish and Wildlife Service does. But in this text is an explicit recommendation. In addition to harming the birds directly, water managers have damaged them indirectly by destroying essential habitat over a large area and over many years.

The final chapter, (5), arises from the recommendations of the Walter's committee (see the 1999 report) that we repeat the annual helicopter census of the species to obtain an estimate of the accuracy of the survey methods. We tried to implement such a count in 1999, but unaccountable delays in establishing the Walter's committee meant that the second survey was much later in the breeding season than the first. For reasons we understand, the two surveys were not replicates. This year, the surveys were completed within the same period at the height of the nesting season. Chapter 5's remarkable claim is that the surveys are indeed

replicates of each other and that the survey provides an unbiased and efficient sampling of the population.

Please take note of the following advisory. We make this report available soon after the completion of each year's field season to facilitate discussion and to help managers make the best possible choices.

The material presented here, unless it has already been published, appears here in draft form.

Chapter 1.

The recovery of the Cape Sable seaside sparrow through restoration of the Everglades ecosystem.

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Abstract

The Cape Sable seaside sparrow (Ammodramus maritimus mirabilis) has been listed as federally endangered since 1967. Its small population size and unique ecology have perpetuated conservation concern. The ultimate factor in this sub-species' decline is the alteration of the everglades ecosystem. Range-wide surveys conducted since 1992 have documented 90 percent declines within some sub-populations leaving the sub-species vulnerable to extinction in the near future. Although the life history of the sparrow is typical of grassland birds, its demographic characteristics leave it highly vulnerable to even short-term alterations of fire and flood regimes. A multi-billion dollar restoration plan has been launched in an effort to return everglades' hydrology to a more natural state. However, even with this plan, the Cape Sable seaside sparrow is in danger of extinction. As shown for the plight of the Dusky seaside sparrow (Ammodramus maritimus nigrescens), a close and now extinct relative of the Cape Sable seaside sparrow, management actions must be swift to avert the extinction of short-lived, habitat specialists such as this sparrow.

Introduction

Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) population numbers have declined nearly 50 percent between 1992 and 1996 (Curnutt et al. 1998). This federally listed sub-species currently exists within the protected lands of Everglades National Park (ENP) and adjacent Big Cypress National

Preserve. These two biological preserves (together nearly 8,500 km² in area) form one of the largest protected areas in North America, yet fail to function as a preserve for this and many other inhabitants (Mayer and Pimm 1998). Because large-scale hydrologic changes reflect patterns of population decline in the Cape Sable seaside sparrow, this bird is perceived to be the 'canary' in the 'coal mine' of the everglades. At present, the 20-year plan to restore original everglades hydrology promises recovery of the ecosystem. For short-lived species such as the sparrow; however, special attention must be paid to interim protection.

Historical perspective

Historically, the everglades were a 'river of grass' encompassing an estimated 28,205 km² of unbroken, freshwater prairie (Mayer and Pimm 1998). Extending from Lake Okeechobee in the north to Florida and Biscayne Bays in the south, water drained across the flat terrain as a 'sheet,' its peak averaging 64 km wide and 0.5 m in depth (Mayer and Pimm 1998). The heaviest flows (up to six km/hr) occurred during the wet-season (June to January).

South Florida was sparsely populated before the turn of the century (Tebeau 1968). High variation in water flow made south Florida an unpredictable place for most economic ventures, especially commercial farming (Mayer and Pimm 1998, Snyder and Davidson 1994). In 1850 the U.S. Congress passed the Swamp Lands Act which encouraged development in south Florida by 'reclaiming' flooded lands for agriculture (Light and Dineen 1994). This act, and another passed in 1948 (the Central and South Florida Project), set in motion a series of hydrology changes culminating in the construction of 2,200 km of canals and levees and over 40 pumps and spillways (Mayer and Pimm 1998). Lake Okeechobee was impounded in the 1930s, permanently altering the hydrologic link between the lake and the freshwater prairies to the south (Light and Dineen 1994).

These changes enabled south Florida to become one of the largest producers of winter vegetables and domestic sugarcane in North America (Snyder and Davidson 1994). Coupled with flood control, economic growth enabled the human population to reach four million by 1990 (Light and Dineen 1994). As early as the 1940s, officials recognized that this growth created additional demands on available water. Consequently, three Water Conservation Areas (WCAs) were included in flood control measures and established just north of ENP (Figure 1). These areas receive most of the run-off from Lake Okeechobee and the Everglades Agricultural Areas. They provide freshwater sources for agriculture, residential areas, and recreation. They also function as a 'filter' removing agricultural run-off (e.g., phosphorous) from water entering natural areas such as ENP (Light and Dineen 1994).

Between the WCAs and federal biological preserves, 67 percent of the original

everglades ecosystem is protected from urban development. Although nearly half of that area is managed largely for biological resources, there is a limit to preservation efforts as only the lands, not the historical water flows, were protected. Since the re-plumbing of south Florida, water flows from the WCAs into the principle tributary of the lower everglades (Shark River Slough) via six spillways (Figure 1). Levees split the slough into eastern and western halves (Light and Dineen 1994). Western Shark River Slough receives most of the water, while the eastern slough (and other eastern tributaries such as Taylor Slough) receive little. The result is that prairies fringing western Shark River Slough are unnaturally wet for longer periods each year and the eastern prairies have desiccated (Nott *et al.* 1998). These prairies are home to the only six sub-populations of the Cape Sable seaside sparrows known (A-E, Figure 2).

Figure 1. Map of the present Everglades watershed, including major canals, sloughs and political boundaries of parks and preserves (reproduced with permission from Mayer 1999).

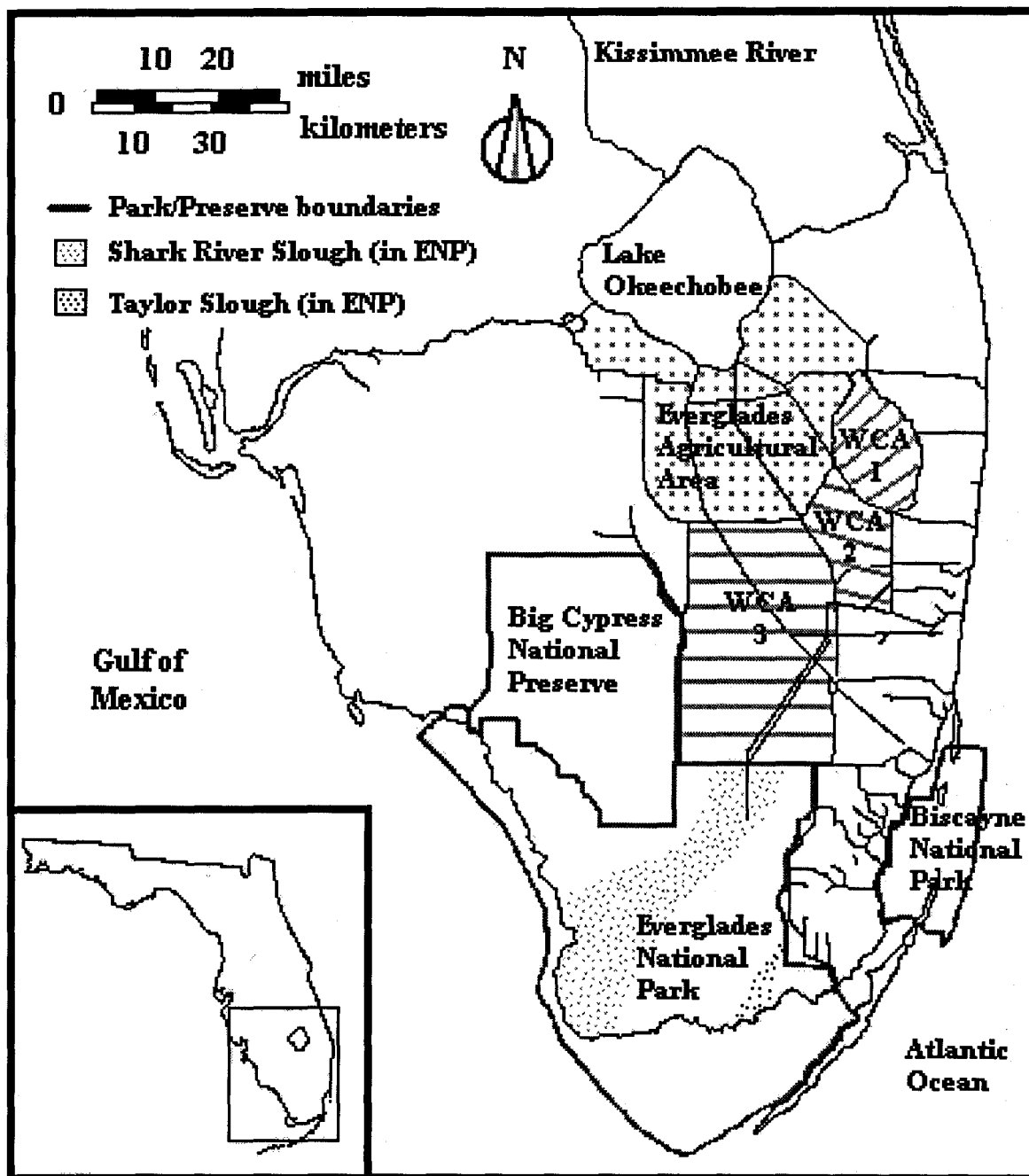
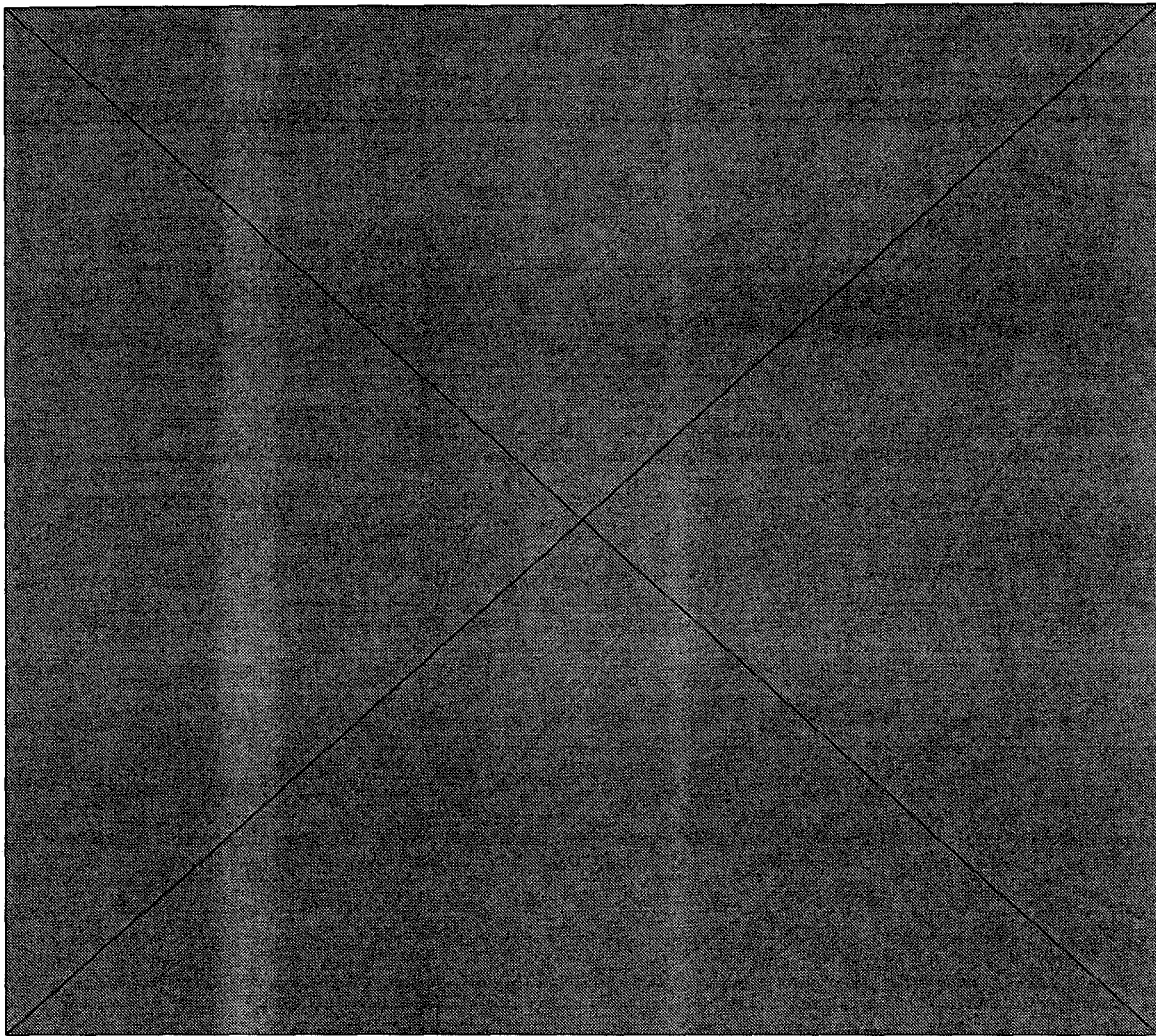


Figure 2. Location of Cape Sable seaside sparrow sub-populations within Everglades National Park and Big Cypress National Preserve.



The Cape Sable seaside sparrow, a small, drably colored bird, has never been common (Curnutt *et al.* 1998). First described in 1919 by Arthur Howell, this sub-species was thought to exist only within the freshwater marshes that grew on Cape Sable early this century (Werner and Woolfenden 1983). A hurricane that made landfall over Cape Sable on September 2, 1935, forever changed the Cape's vegetation and landscape (Mayer and Pimm 1998, Curnutt *et al.* 1998). The sparrow was not found on Cape Sable after that event. In fact the species was believed extinct until L.A. Stimson's 1951 documentation of inland populations in freshwater prairies (Stimson 1956). Because most seaside sparrows live within tidal marshes, this discovery made the sub-species an ecological oddity (Post and Greenlaw 1994). As a likely consequence of the sparrow's phoenix-like identity

and its unusual ecology, the U.S. Congress placed the Cape Sable seaside sparrow on the first endangered species list enacted in 1967 (Curnutt *et al.* 1998).

Current status

In 1981, ENP researchers conducted range-wide point counts of the Cape Sable seaside sparrow breeding population. Points were located one km apart and accessed via helicopter (Kushlan and Bass 1983). This survey yielded sparrow population estimates of over 6,000 individuals, with more than 2,000 located in each of two 'core' sub-populations (A and B) (Kushlan and Bass 1983). Similar estimates resulted from the next survey in 1992. In 1993, however, estimates dropped 90 percent from 2,500 to 400 individuals within sub-population A (Curnutt *et al.* 1998). Sub-populations C, D, and F each declined from over 400 individuals to fewer than 80 in the ensuing years (Curnutt *et al.* 1998). Annual surveys since 1993 have shown no reverse in these declines (Pimm and Bass 1999). Only the central sub-populations (B and E) contain relatively stable numbers from year to year.

To understand these declines, we have monitored nests and color-banded individuals from nine study plots (each 0.50 km²) within sub-populations A, B and E (Lockwood *et al.* 1999a,b). From six years of study, we know the following aspects of the sparrow's demography. The breeding season can last from late March to August depending on the onset of summer rains (Lockwood *et al.* 1997, Werner 1975). A pair can fledge at least three broods per breeding season with early broods more likely to fledge young than later broods (40 percent vs. 16 percent Mayfield success scores respectively). Sparrows prefer to nest in one m tall sparse sawgrass (*Cladium jamaicense*) stands mixed with bunchgrasses typical of seasonally dry areas (Lockwood *et al.* 1999b). Nests are built approximately 16 cm from the soil surface with a standard variation in height off the ground between 2 and 30 cm (Lockwood *et al.* 1999a, Werner 1975). Adults feed nestlings grasshoppers, spiders, dragonflies, and lepidoptera larvae, all locally abundant food sources (Lockwood *et al.* 1997). The principle threat to nests is predation, probably by water snakes or rats (Lockwood *et al.* 1997).

Adults are site-fidelic, often returning to the same 200 m territory every year to breed (Lockwood *et al.* 1999a). When sparrows are not breeding they do not travel far. Using radio telemetry, Dean and Morrison (1998) recorded sporadic long distance movement over five km, but most tagged individuals stayed within one km of their nesting grounds. We have never re-sighted an individual banded in one sub-population within another (Lockwood *et al.* 1999a). Adult sparrows live a maximum of four years and just less than half of the adults in any given year will die (Lockwood *et al.* 1999a). Hatch-year individuals exhibit low survival their first year out of the nest but they are more likely to move over longer distances (up to one km) (Lockwood *et al.* 1999a).

Although these demographic attributes are typical of most grassland birds, they become a unique liability in the context of current alterations in everglades water flow. In the western prairies of ENP, satellite images and ground-based hydrologic monitoring stations show several high water events between 1993 and 1996. In some years, water levels reached 50 cm above ground level (Nott *et al.* 1998). This exceeds the average nest height off ground by 34 cm and the highest nest ever recorded by 20 cm. These large water flows did not result from rainfall *per se*, but were due to released WCA water (Nott *et al.* 1998).

In the eastern prairies, altered hydrology has changed temporal fire patterns that, in turn, have impacted sparrow breeding habitat. Although periodic fires maintain freshwater prairies by preventing the encroachment of shrubs and hardwood trees (Kushlan and Bass 1983), comparisons between fire records and sparrow surveys demonstrate the following: 1) sparrows regularly occupy sights that have burned one year prior, and 2) historically occupied areas that burn every one or two years rarely hold sparrows today (Curnutt *et al.* 1998).

Since sparrows live a maximum of four years, short-term disruption of reproduction (such as fire or flood) can significantly effect population numbers (Lockwood *et al.* 1999a). In areas where adult sparrows cannot breed for two or three consecutive years, most adults die without replacing themselves in the population. This situation is exacerbated by the sparrow's limited clutch size. A pair of adult sparrows averages two young per nesting attempt. Theoretically, if all adults in an area successfully fledge one brood, population number will simply remain stable. (In practice, population numbers still decrease due to the low survivorship of juveniles.) Population increases are only possible when individuals successfully fledge two to four broods per breeding season (Lockwood *et al.* 1999a).

When short-term disruptions occur over a wide geographic range, recovery is further hampered by the sparrow's limited dispersal over long distances. Low numbers will persist because immigration rarely occurs across sub-populations. There is little chance for the 'rescue effect' whereby individuals from a stable sub-population immigrate into a declining one.

A final concern is that high water and frequent fires are causing long-term changes in habitat structure (Nott *et al.* 1998, Lockwood *et al.* 1999a). Known to be a habitat specialist, this subspecies will not breed in prairies lacking specific structural cues (Lockwood *et al.* 1999b).

Restoration and future management

Restoring historical 'natural' water flows was a goal of a bill passed by the U.S. Congress in 1992 (Mayer 1999). The restoration plan aims to rectify environmental damage done by the 1948 Central and South Florida Project while

maintaining adequate flood control and freshwater supplies for the local populous (Governor's Commission for a Sustainable Florida 1995). Though the plan is promising, the task is monumental. Current estimates place the completion of the restoration at 20 years (Mayer 1999). The existent configuration of canals and levees simply provides no physical route to quickly redirect water flow from the over-flooded west to over-dry east (Pimm and Bass 1999).

Given the observed steep declines in Cape Sable seaside sparrow numbers over two or three years, there is no guarantee the sparrow can survive the 20 required to restore its breeding habitat. Consider the damage its close relative, the Dusky seaside sparrow (*Ammodramus maritimus nigrescens*), sustained between 1960 and 1980. The Dusky seaside sparrow was once found around Titusville, Florida. Like the Cape Sable seaside sparrow, the Dusky inhabited seasonally flooded marshes and existed in distinct geographic populations. Also like the Cape Sable seaside sparrow, the Dusky declined when hydrological changes left breeding grounds flooded or fire prone.

From an estimated 2,000 pairs on Merritt Island in the 1950s, DDT had already reduced populations 70 percent by 1957 (600 pairs) (Sykes 1980, Trost 1968). A bad situation was made worse when mosquito control impoundments flooded breeding habitat. The Dusky declined another 90 percent to 70 pairs by 1963 (Sykes 1980, Trost 1968). The threat was understood and the Dusky's habitat requirements documented (Trost 1968). Piecemeal studies to determine whether the birds would respond favorably to restoration of 'natural' hydrologic patterns satisfied endangered species legislation (Walters 1992) but left only one individual on Merritt Island by 1977 (Sykes 1980, Baker 1973, Sharp 1969).

The population of Dusky seaside sparrows located in the marshes along the St. John's river was estimated at 984 males in 1968 (Sharp 1970). Although it took two years to purchase U.S. National Wildlife refuge land here for the endangered bird, it took only one to gain a permit to build a highway through one densely populated colony (Walters 1992). Highways and development outside the refuge reduced the largest colony from 100 to 12 birds (Baker 1978). Inside the refuge, an open ditch drained Dusky habitat while six fires from neighboring farms burned over 4,000 acres. By 1977 fewer than a dozen birds of the 143 counted in 1970 were left on the refuge (Baker 1978). Despite urgent requests for fire lines as early as 1975, they were not completed (nor was the ditch plugged) until 1979. By that time, only nine males were left (Walters 1992). The last wild Dusky seaside sparrows were taken into captivity in 1980. The last individual, referred to as Orange for the legband he wore, died in captivity in 1987.

Conclusion

In many ways the current recovery prospects of the Cape Sable seaside sparrow

mirror those of the Dusky from the early 1960s. Recovery seems feasible. The sparrow's demography and habitat requirements are known; the hydrologic changes that impact that habitat are understood. Unlike the Dusky, the Cape Sable seaside sparrow enjoys advantages such as higher population numbers, a range entirely within federally protected lands, and consensus on the need to restore the ecosystem on which it depends.

Nevertheless, these advantages do not guarantee success. With such obvious parallels between the management needs of the Dusky and those of the Cape Sable seaside sparrow it is incumbent upon managers to avoid the known pitfalls that lead to extinction. More than anything else, the story of the Dusky illustrates how critical the timing of management decisions are in dealing with short-lived habitat specialists. Each delay in decisions to purchase refuge land, construct fire lines, and seasonally drain impoundments, carried the cost of a few more Dusky seaside sparrows. Though the restoration of the Everglades ecosystem is a commendable and significant undertaking, it in no way alleviates the need for short-term, and often difficult, management actions. Without such actions, the Cape Sable seaside sparrow may become a martyr for the threatened ecosystem about which it once raised awareness.

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Chapter 2.

Range-wide risks to large populations: the Cape Sable sparrow as a case history

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Abstract

Very small populations — those numbering a few to a few dozen breeding pairs — often go extinct quickly. The reasons for their doing so are well-understood and relatively easy to model. Considerable experience teaches that much larger populations that occur across much wider ranges can become extinct quickly too. Understanding the fate of these species is the much more difficult challenge that this paper will address. The species of concern is the Cape Sable sparrow.

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 on the basis of past experience of the species of concern or some similar species. 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. We show that this method failed spectacularly even when applied to a situation where it would seem entirely appropriate. Our second method identifies the causes of the sparrow's population fluctuations. In particular, we consider the factors the cause its range to shrink and its ability to recover from such shocks. By understanding the mechanisms underlying population fluctuations we deduce an altogether bleaker picture of the bird's future.

Introduction

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

Large populations may be composed of many smaller partially isolated sub-populations. If so, the balance between frequent local extinction and recolonization from surviving populations determines the species' long-term fate (Hanski 1998). In such cases, the 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 their numbers that typify all natural populations (Pimm 1991). In nature, many individuals die from the *same* causes — bad weather, for instance. Such natural population fluctuations can prove terminal for a species that is now more geographically restricted than in the past.

The case history we shall 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 sub-populations sufficiently small to warrant concerns over those "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 to what low levels they will drive the population in the future?

The species of concern is the Cape Sable sparrow (*Ammodramus maritimus mirabilis*), a drab, olive-brown bird, so obscure and lacking in charisma that it was not discovered until well into this century. First, we present some brief remarks about its natural history and about the southern Everglades to which it

is restricted. These remarks summarize Lockwood et al. (1997), Curnutt et al. (1998), and Nott et al. (1998).

Next 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 those fluctuations. 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 Brook et al.'s (2000) meta-analysis of the predictive accuracy of "population viability analysis". One of us has devoted considerable thought to it (e.g. Pimm 1991). We shall show that this method failed spectacularly even when applied to a situation where it would seem entirely appropriate. A 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.

The Cape Sable sparrow and the ecosystem on which it depends

The sparrow is considered to be a subspecies of the widespread seaside sparrow, albeit an ecologically and geographically distinct one. It is not a "seaside" sparrow ecologically as it inhabits freshwater rather than saltwater marshes. In addition to its unique habitat, it is geographically isolated. The nearest surviving subspecies, *A. m. peninsulae* is 300 km to the north. Although first discovered in 1918 on Cape Sable, vegetation changes after the massive hurricane of September 1935 made the Cape unsuitable for it.

The U. S. Fish and Wildlife Service included the subspecies in the first list of endangered species on March 11, 1967, (32 Federal Register 4001). Its restricted range and the fate of the population on Cape Sable were the primary justifications. The subsequent rapid extinction of the Dusky seaside-sparrow (*A. m. nigriscens*) in northern Florida lent support to that decision.

Shark River Slough is the primary drainage in the southern Everglades of Florida (see figures 1 and 2, chapter 1). To its west lies the higher ground of the Big Cypress and, to the east, the Atlantic coastal ridge. Expanses of marl prairie lie between the main drainage of Shark River Slough and these two modest ridges. In contrast to the main Slough, these prairies are inundated on average only from three to seven months per year. These seasonally flooded wetlands to the east and west of the slough are the particular ecosystem on which this bird depends.

Currently, nearly all the overland flow in the Shark River Slough drainage originates from the four S-12 gated spillways at the northern boundary of Everglades National Park (see figures 1 and 2, chapter 1). The east-west distribution of these structures covers about half of the pre-drainage expanse of

Shark River Slough. Historically, most of the overland flow occurred toward the *eastern* edge of Shark River Slough — as suggested by the figure. The S-12 structures, however, are on the *western* edge: it across these structures that the water actually flows.

This artificial hydrology affects the two expanses of marl prairie on either side of the slough in opposite ways. The western marl prairies naturally remained dry for much of the year. They were inundated seasonally by rainfall and overflow from the slough. They are now subject to the vagaries of water releases from the S-12 structures.

The southeast corner of the Florida peninsula held the largest expanse of marl prairie. Bounded by the eastern edge of Shark River Slough, it spread southeast, encompassing the southern terminus of the Atlantic coastal ridge. It ended at the thin line of mangroves along the northeastern shore of Florida Bay. To the north, the marl prairies once extended in a long arm to central Dade County. This expanse of potential sparrow habitat suffered two major assaults. The more drastic was the conversion of the eastern portion of prairies to residential and agricultural lands.

Much of the remaining prairie, at and around the eastern boundary of Everglades National Park, is over-drained and subject to frequent fires. Fires in the wet season (June to October) are caused by lightening strikes and are generally small and patchy because the ecosystem is already wet. They can occur throughout the region. Those at the end of the dry season, (March to late May) are frequently caused by human carelessness and tend to burn large areas along the Everglades eastern boundary but sometimes deep into the natural areas.

Curnutt et al. (1998) estimated that nearly half of the original prairie has been destroyed or degraded. As for many species for which we must assess the risk of extinction, the ultimate cause of endangerment is the massive reduction in suitable habitat.

Bass and Kushlan (1982) conducted the first extensive sparrow survey in 1981. We repeated the survey in 1992 and annually thereafter. Across a 1 km x 1 km grid of more than 600 sites, we record the number of sparrows seen or heard within a 10 minute interval. We take particular care to visit all locations that might hold sparrows and do not observe birds at most of the sites we survey. This suggests that we do not miss many (if any) sites that hold birds.

To estimate the actual numbers of sparrows from the number we observed on our survey, we multiply each singing male by 16. This correction is based on the range at which we can detect the sparrow's distinctive song — it encompasses $1/8^{\text{th}}$ of a square kilometer — and on the assumption that one female

accompanies each singing male. Work on our intensive study plots confirms this calibration (Curnutt et al. 1998).

Using this calibration, we estimated that the total population of this species was over 6000 in both 1981 and 1992. The birds are not distributed continuously, but are grouped into six sub-populations of varying sizes (see figure 2, chapter 1)). Sub-population A (west of Shark River Slough) was the most numerous in 1981 (~2700 birds) and B held fewer birds (~2300). Sub-population B held more than A in 1992 (~3000 versus ~2600). Sub-population E consistently held ~600 birds. The other three sub-populations held between 100 and 400 birds, although we found no birds in F in 1992.

What is the likelihood that this bird will become extinct?

Risk analysis 1: a phenomenological approach

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 1991, Pimm et al. 1988). 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 (whether it is a trophic specialist or generalist, for example), and 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 ecologists. For example, Saether and his colleagues (see for instance, Saether et al. 2000) have provides statistically rigorous dissections of the key population variables, their variances, and their time dependence for various species. In the example quoted, they utilized a 20 year record along a 60 km stretch of the bird's 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 all the information available to those who must estimate the species' risk of extinction. 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 — closely related or at least ecologically similar species. 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 long-term data on year-to-year changes in Cape Sable sparrow populations, or indeed on other seaside sparrows. 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.

Curnutt et al. (1996) used BBS data on 10 North American grassland sparrows to explore how populations behave simultaneously 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 examined the increase in a population's variability at a single location 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. Were relative variability to be 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 . Simply, where a species is least common — typically at the edge of its range — it will be relatively most variable.

Let us put this average slope into more accessible terms. For a normally and independently distributed, (statistical) population, a sample of 10 observations will span values encompassing approximately ± 1.5 standard deviations of the mean.

First, consider one of the larger sub-populations (A or B) and suppose we actually counted 200 birds, ($\log 2.3$) leading to an estimate of 3200 individuals. The log of the standard deviation of this population should be $0.7 \times 2.3 = 1.6$, and so the standard deviation should be ~ 41 . A range of plus or minus $41 \times 1.5 (= 61)$ would have the population varying between 140 and 260 counted birds or between an estimate 2240 and 4160 birds. This approximates a two-fold span of values over a sample of ten points, that is, over a decade. It 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 160 birds. Using the same logic, it would have a standard deviation of 5 and so abundances should span from 18 (an estimate of 288 birds) down to a count of 2 (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). 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 two paragraphs' analysis. The population count in one year is likely to be dependent, probably strongly so, 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 the case for the grassland sparrows too. Curnutt et al. (1996) found that of the 7 species with at least 10 sampling locations of continuous data over 20 years, 6 showed significant increases in variability over all time periods. 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 will itself be larger.

We will not rework the example of how large is the envelope of population fluctuations with the added complication of increasing variability over time. More rigorous discussions of population extremes appears elsewhere (Lande 1993, Ariño and Pimm, 1995). Incorporating these details — or formalizing the mathematics — does not alter the general conclusions about the Cape Sable sparrow:

(1) The two largest sub-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 sub-populations might well fall below levels where we could not likely count them — and where unavoidable vagaries of birth and deaths may well doom them to at least local extinction.

Thus, local sub-populations may become extinct, but at least one of the three larger sub-populations (A, B, or E) should be available to naturally re-stock 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.

The conclusion was rudely shocked in April 1993. The western sub-population, for which the preceding calculation suggests might vary two-fold over a decade, in fact 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. Curnutt et al. (1998) 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 shock was particularly painful to one of us (Pimm), because he had spent much of the previous decade in 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) in the effort to provide the catalogue of more than 2000 long-term time series (now available at <http://www.sw.ic.ac.uk/cpb/cpb/gpdd.htm>). A central objective of this compilation is to provide conservation biologists 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 Cape Sable sparrow is found 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 twenty national parks in Central and South America are as large or larger (Mayer and Pimm 1998). If the method of "use natural variability to calculate risk of extinction" should apply anywhere, this bird in these National Parks could seem to be a good candidate. Why did this approach fail?

Risk analysis 2: a mechanistic approach

Our surveys showed that the sparrow declined dramatically since 1992 on the western side of Shark River Slough. It has declined similarly since 1981 in the northeast of its range and in the southeast. Only two sub-populations have remained more or less constant. The key results of Curnutt et al. (1998), Nott et al. (1998) and Lockwood et al. (1997) are:

- 1 The massive decline in the western sub-population was a consequence of the inundation of the breeding habitat during the dry season by managed flows over the S12 structures in 1993, 1994 and 1995.

- 2 The decline in most of the northeastern sub-populations was due to the very high fire frequencies in these areas over the last decade or more. We erect the plausible hypothesis that the high fire frequency is due in part to the high incidence of unplanned human ignitions in the areas adjacent to the park. Moreover, we assert that unnaturally low levels of water permit high fire frequencies during the breeding season. Water that would have naturally flowed through northeast Shark River Slough to seasonally flood the eastern populations was diverted to the west through the S-12s. Moreover, the water was prevented from flowing to the east by a barrier to water flow called the L67-extension.
- 3 The decline in the lower part of C and in D was due to managed changes in the water levels that have locally converted the seasonally flooded prairies that the birds favor to near continuously flooded, sawgrass-dominated marshes that the birds avoid.

For this step in risk assessment, we will postpone the longer-term changes in vegetation effected by changes in hydrology and fire frequencies. 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.

The obvious next step is to combine this feature of 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 and, to that end, we have long invested considerable energies in banding birds and finding their nests. In recent years, we have banded about 100 individuals per year and find as many nests. This is an achievement of which we are proud given the bird's rarity and inaccessibility: all but one of the sub-populations are reached only by helicopter.

Given this effort, the reader might expect that we would now 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.

We review what is known about the sparrow's demographic parameters elsewhere: Lockwood et al. (in prep.) update an earlier effort (Lockwood et al. (1997). In brief, the sparrows lay an average of 3.2 eggs per clutch, a number that varies little from year to year or from place to place. About half of the eggs become fledged young and that fraction varies considerably. In particular, it depends on whether the clutch is laid earlier in the year (almost certainly a first clutch) or later (likely a second clutch). Rising water levels (common later in the year) terminate clutches. There are far fewer second clutches than first clutches and known third clutches are so few in number and fledge so few young that they contribute little, if anything, to the population size of the next generation.

Maximum likelihood estimates of banded birds show that 66% of territory holding males survive from one year to the next. Lockwood et al. (in prep.) combine the best estimates of these parameters and infer others (including the survivorship of females and first year birds). They come to the entirely comforting conclusion that the overall growth rate of the population is, 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 perceptible over the years during which we collected the data. That is, we estimate parameters consistent with the birds replacing each other and they have obliged us by doing so.

Unfortunately, what we need to know to answer the key question are parameters that only serendipity will give us. How quickly will birds die when evicted from their homes by fire and flood? And how quickly will 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.

First, 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 for some will move to areas away from our extensive network of study sites. Almost certainly, however, young do not survive as well as territory-holding adults. Under the worst conditions — prolonged, deep flooding of the habitat (which occurred from 1993 to 1995 in the western sub-population) or extensive fires (such as that which burned most of the eastern sub-populations in 1989) — a much greater fraction of birds will likely die.

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 sub-population laid two clutches a year. (We have never seen anything like 100% of the pairs 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 sub-population was 53%. (This was in sub-population E, where the numbers have steadily increased in the last few years.) Even here, second clutches are less frequent and less successful than first clutches. Assume that all birds that have available, dry habitat are 60% as successfully in rearing their second clutches as their first clutches. (This is equivalent to 60% of birds with available habitat fledging second clutches and their success being the same as the first attempt.) This leads to a potential growth rate of 34% per year. This is still "very optimistic" — we label it as such — for 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 consider this to be "plausible."

Certainly we can change other parameters. Reducing the survival of the hatch year birds — a parameter for which this and so many other studies can estimate only imprecisely — has exactly the same dynamically 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 are the implications for each sub-population's risk of extinction.

The sub-population west of Shark River Slough (A).

This population sits on a low ridge and it is particularly vulnerable to flooding. Water depths of more than a few centimeters prevent breeding or terminate it if it has already started (Lockwood et al. 1997). Nott et al. (1998) calculated the extent of available breeding habitat for each of the last 20 years, classifying the areas into those that remain dry enough for just one brood to be raised, and those that could produce two (assuming they were physiologically capable of doing so.) It is simple to estimate how many sparrows would be produced each year from the breeding and survival parameters scaled by the available habitat under the various scenarios described in the previous section (Figure 2). The sparrow numbers start with a guess of 2000 birds in 1977 and follow deterministically

There is no Figure 1 in this chapter.

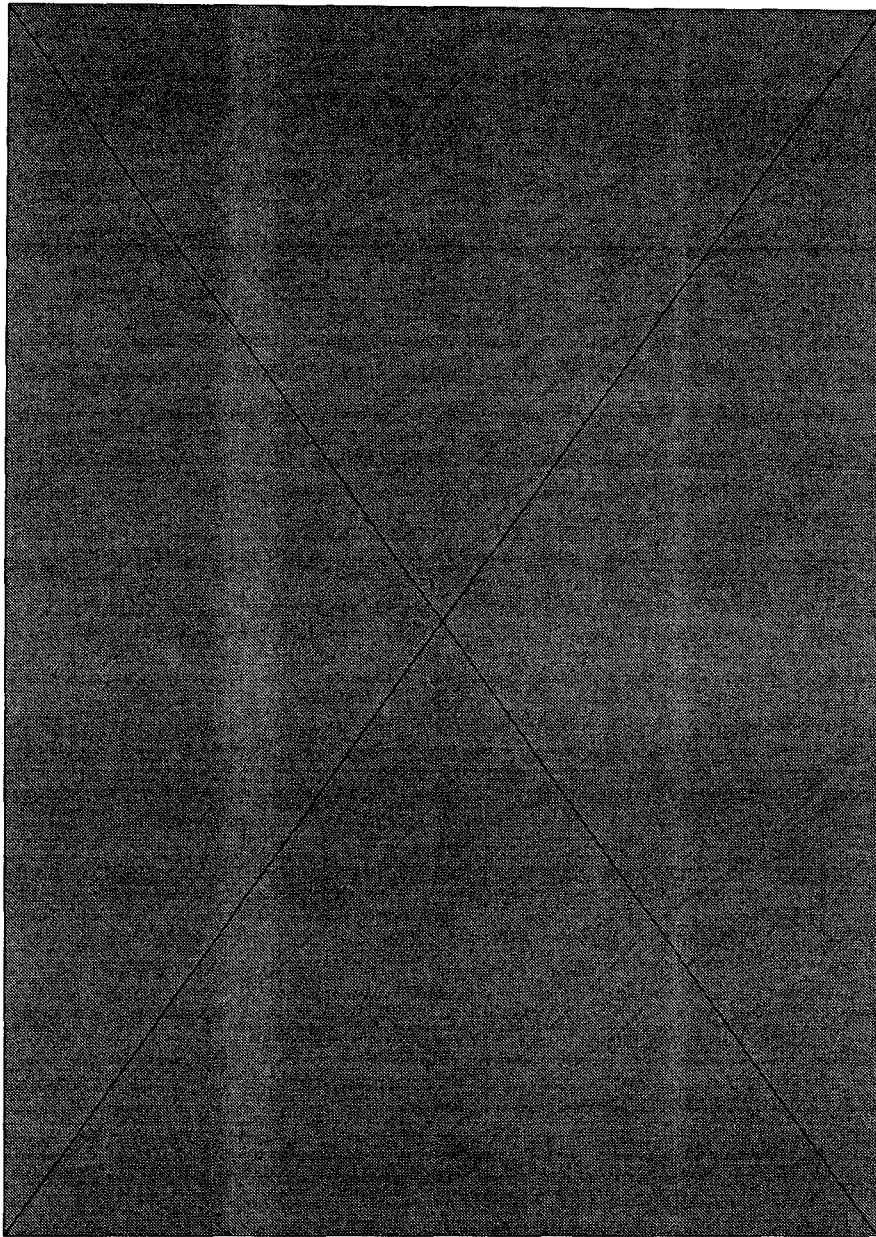


Figure 2. Three deterministic simulations of a model described in the text for the sub-population west of Shark River Slough. The proportional maximum change from one year to the next (R) varies from 1.61 ("wildly optimistic"; at top), through 1.34 ("optimistic", middle) to 1.24 ("plausible" bottom). The solid line uses the known extent of available 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). As the text discusses, only the "plausible" model is consistent with the known population estimates in 1981, 1992 and subsequent years.

thereafter with the observed last 20-year sequence of water levels repeated cyclically. This starting point in 1977 allows the population to increase to its estimated value of 2500 birds by the time of the 1981 survey.

The model caps the population at 3500 birds — an estimate of carrying capacity that doesn't strongly enter into the model's results because water levels so rarely allow the birds to breed across the potential range. (We estimate the cap based on the maximum available habitat and typical maximum observed densities.)

The estimates of actual range show, for example, that in 1977 all 2000 birds had the chance to raise one brood, but only 11% of them were in places dry enough to raise a second, even had they otherwise been able to do so.

The three scenarios of figure 2 show that only the "wildly optimistic scenario" allows the population to persist. Both optimistic scenarios fail to match two features of the range-wide survey of the birds. First, the population in 1992 was estimated to be 7% lower than it was in 1981. (There were no surveys in intermediate years and in those years there were some years when substantial areas suffered prolonged flooding.) Both optimistic scenarios suggest an increase in numbers between 1981 and 1992. 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 predicts ~800 birds after these wet years. (So, it too is rather optimistic.)

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 S12s into Everglades National Park (Nott et al. 1998). The contribution of rainfall to the water levels is relatively small in comparison.

A second validation of the model and its parameters requires the sparrows to persist in the absence of these unnatural events. Were the sparrows predicted to decline, then we might suppose the model must err in not allowing the birds to recover quickly enough. A second set of models runs this "what if" alternative. 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 under all three scenarios. Indeed, it would have often reached the model's population ceiling of 3500 birds (Figure 2).

Thus calibrated, we run our model for more sets of 20 years. It re-cycles the exact patterns of habitat availability, whereupon, the population declines towards extinction within fifty years in the "plausible" scenario (Figure 2 c). It even goes to extinction in the "optimistic one" (Figure 2 b). What if water were not

released? The population dips below its population ceiling periodically, but persists indefinitely even in the plausible scenario.

We conclude that repeating managed water flows with the pattern of the last two decades would rapidly 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.

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

Managed high water levels are not an issue in the other sparrow populations; indeed, it is the shortage of water that is the problem. Here, frequent fires burn the prairies. We do not find birds in areas that are burned as often as once every two years (Curnutt et al. 1998). 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 southwards to burn the only area where more than 1000 birds remain — the southeast population.

The southeastern sub-population (B)

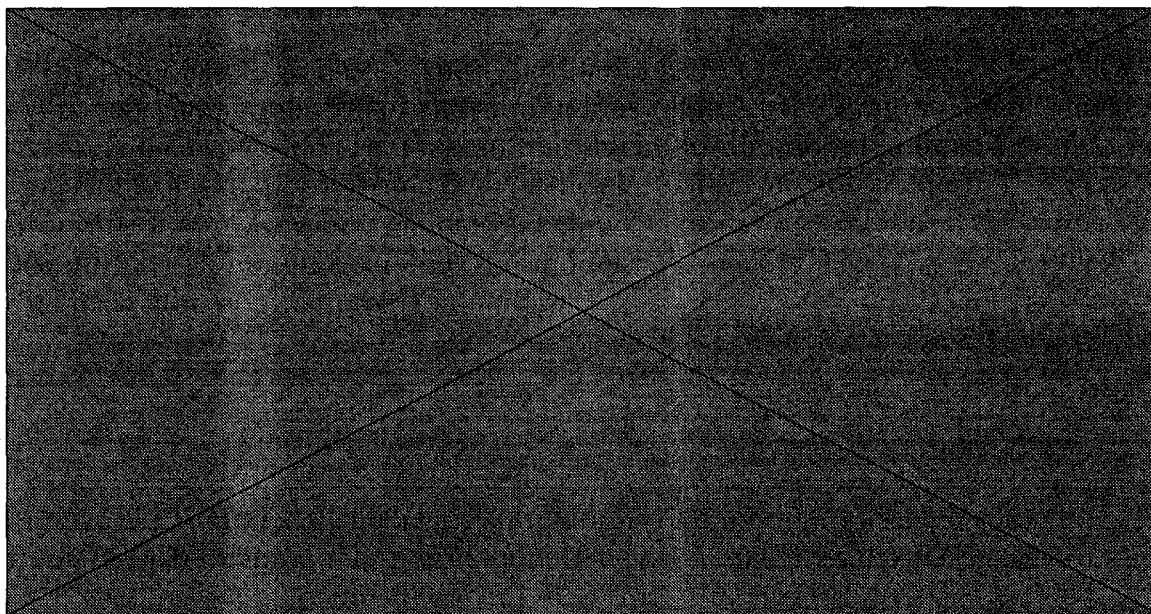
Small portions of this area burn every year often as consequence of fires that burn out of the pinelands to its north. Yet in 1989 nearly half of it burned as a consequence of a massive, dry-season fire. (And probably all of sub-population E did, perhaps explaining why it is still recovering.) Such fires 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 model this area's population using the "plausible scenario" calibrated above. We "set" small fires ($1/40^{\text{th}}$ of the available habitat) every year in 20% of that habitat. Birds within these areas cannot breed successfully that year, but do not suffer any direct mortality. We do not know how many adult birds die in fires, but it surely more than we have assumed. In the year after fire, we assume that 50% of the birds can breed in an area, 75% the year after that, and 100% the following year. Curnutt et al. (1998) show that sparrow populations increase for five or more after fires, so these estimates are also optimistic. Finally, we vary the frequency of severe fires — those that burn 90% of the bird's habitat.

Figure 3 provides two sample simulations with severe fires every ten years and every twenty years. In the former case the population quickly goes to extinction,

in the latter case it persists. These simulations are typical. With fires on average every ten years, only 5% of the simulations allowed the population to increase over a 50-year period. (That meant that the minimum population was in the first year of the simulation). Some 50% of the simulations resulted in the populations dropping below 1000 birds and 15% below 500 birds (from their original start of 2000). Given enough years, all the model runs encountered a bad run of fires that drove the population to extinction.

Figure 3. Examples of stochastic simulations of a model described in the text for the largest remaining sub-population. Twenty percent of the habitat is burned each year, on average, plus there are "bad" fires that burn an average of 90% of it. Such fires every 20 years allow the population to persist, those every 10 years do not.



In sum, the southeast population is in danger of extinction from extensive fires as frequent as one in ten years. Since we have observed such fires in or near this population at the frequency, we conclude that this population too is at severe risk of extinction.

Conclusions

We predict that the sparrow sub-population west of Shark River Slough will decline to extinction if the pattern of managed flows over the S12s for the last 20 years is repeated. If these unnatural breeding season flows over the S12s are stopped, this sub-population will flourish. The sub-populations in the northeast have already declined to near extinction. These declines will continue unless the fire regimes are changed. On its own, the sub-population in the southeast runs the risk extinction because of episodic, large-scale fires. The fate of sub-population E (now the second largest sub-population) is interesting in that it may illustrate a population burned to oblivion in 1989 that is still recovering.

Our models omit some obvious features. We have not included the effects of prolonged inundation or of frequent fires on the vegetation. These processes alter the vegetation in ways that preclude the birds' use of areas for several years (Curnutt et al. 1998, Nott et al. 1998). Incorporating these impacts would likely lead to even greater concerns about the sparrow's future.

The predictions of the current 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 to the census data. 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 sub-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 non-exclusive answers. The first is that 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 its previous experience. The second is that the sparrow has become locally extinct on occasion and then be re-colonized from other populations.

This second possibility makes good sense. Years of naturally high water west of Shark River Slough would harm the population there. There would be concomitant flooding the northeastern populations that would suppress the frequency of natural fires there and the possibility of their 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 Cape Sable 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 there.

The general conclusion for conservation is that species even within one of the hemisphere's largest national parks — and possibly its best funded— are not immune to massive anthropogenic impacts from outside them. 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 Cape Sable sparrow.

Critics may counter that this is a special case. The species occupies a wetland and perhaps wetlands are uniquely vulnerable to the vagaries of water flows upstream. Perhaps; but we are not convinced. Other large parks have unique problems that cross their boundaries. Fire, and our inclination to suppress small fires and so risk catastrophic ones, is an example that comes to mind for many parks in the western U.S.A, for example.

We argue that even for the largest protected areas we must develop mechanistic models of what causes populations to decline. Unless we do so, we will not predict future risks adequately.

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Chapter 3

Demography of the Cape Sable seaside sparrow within Everglades National Park

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Abstract:

The Cape Sable seaside sparrow is an endangered subspecies endemic to south Florida's everglades ecosystem. It exists in six spatially distinct areas (subpopulations A through F). Four of these have suffered greater than 50% declines in breeding individuals since 1992. Because of the sparrow's rarity and cautious nature, demographic information has been difficult to obtain. We describe a

five-year study aimed at collecting this data. We relate this information to modern hydrological characteristics of the everglades as this varies across the spatial extent of the sparrow's range and has been implicated in observed subpopulation declines. Greater than 60% of adult sparrows survive from year to year and 20% of juveniles return to their natal sites within two years of fledging. We find that sparrows can produce up to four broods per breeding season (March to August) and that female sparrows lay an average of three eggs per nest, two of which usually hatch. These characters vary from year to year but not spatially. The success of these nests varies from year to year and spatially. Nest success varies between sub-populations such that nests in subpopulation E are more than four times as likely to fledge young as nests within subpopulation A. Nest success within subpopulation B begins at 26% early in the breeding season, but drops to 9% after the onset of summer rains in early June. Nests are built 16 to 21cm from the soil surface making them vulnerable to high water flow events. Sparrows generally remain within a one-km area centered on their breeding grounds and we have never observed immigration between sub-populations. These demographic attributes combine to make the Cape Sable seaside sparrow extremely dependent on the hydrology of the freshwater prairies it inhabits.

Introduction

The successful recovery of any threatened species requires a knowledge of its population biology and ecological requirements (Clobert and Lebreton 1991). Describing population dynamics reduces to understanding rates of birth, death, immigration and emigration (Clobert and Lebreton 1991). Despite framing the questions in straightforward terms, providing answers is often difficult. This is especially true for the rare and cautious Cape Sable seaside sparrow (*Ammodramus miratimus mirabilis*) whose behavior and patchy distribution have hampered efforts to collect the most basic demographic information (Curnutt 1996). This subspecies, endemic to south Florida, has been recognized as federally endangered since 1967 (Curnutt 1996). In the last seven years, populations have declined by 50% or more in some areas (Curnutt et al. 1998, Nott et al. 1998). In order to institute management or restoration activities that benefit the Cape Sable seaside sparrow, we need to pinpoint the demographic factors being compromised, how they are compromised, and to what degree. Below we describe a five-year study aimed at answering these questions.

The Cape Sable seaside sparrow lives within the Everglades ecosystem of extreme south Florida (Werner and Woolfenden 1982, Kushlan and Bass 1982). This 'river of grass' is characterized by a slow overland flow originating at Lake Okeechobee in the north and entering Florida and Biscayne Bays in the south. The primary drainage system of the Everglades is a slough (Shark River Slough, Figure 2, chapter 1) that is flanked by expanses of marl prairie. These marl prairies are inundated with freshwater and support grasses and sedges (e.g.,

Cladium jamaicense, *Muhlenbergia filipes*, and *Schizachyrium rhizomatum*) that stand approximately one meter tall. Water inundates these prairies when the slough overflows (Curnutt et al. 1998). Under natural conditions, these periods of inundation occur from the onset of summer rains in early June until the beginning of the dry-season in January (Curnutt et al. 1998). During the dry months of February through May, Cape Sable seaside sparrows build low, cup-shaped nests in these marl prairies (Werner 1975, Werner and Woolfenden 1982).

Beginning in the early 1900s, a series of canals and spillways built within the Everglades began altering this overland flow of water. Management diverted water from the eastern Everglades to control flooding around the growing urban population of greater Miami and to facilitate agriculture (Nott et al. 1998, Light and Dineen 1994). The legacy of these efforts is that flows now drain into the western portion of Shark River Slough leaving the eastern marl prairies in a dry state far longer than under natural conditions. Conversely, the western marl prairies are flooded more often (Curnutt et al. 1998). Nott et al. (1998) provide evidence that these alterations in flow patterns (i.e. hydrology) have contributed to the observed sparrow population declines in the western marl prairies. Further, Curnutt et al. (1998) attribute the declines within extreme eastern Everglades to frequent fires due to over-drying.

Our study researched how these varying hydrological conditions relate to changes in Cape Sable seaside sparrow demography. However, the sparrow is only one of many threatened species within the Everglades ecosystem (Mayer and Pimm 1998). The Everglades is slated for a multi-billion dollar restoration that will take place over the next two decades (Lockwood and Fenn 2000). The goal is to aid wildlife recovery by reproducing historic water flows, yet still provide ample freshwater supplies and flood control for the local populous (Lockwood and Fenn 2000). This is a challenging task made more difficult by a vague understanding of how hydrology effects sensitive species. Our results represent a first crucial step in defining how much, when, and where water should flow into natural areas under restoration schemes.

Methods

Study areas

The sparrow's current range lies entirely within federally and state protected lands in south Florida. Although most individuals live within Everglades National Park (ENP) at present, a significant segment live within Big Cypress National Preserve (Kushlan and Bass 1982). Our study is limited to those in Everglades National Park. The population is separated into six spatially distinct 'patches' labeled sub-populations A – F (Fig. 1; see figure 2 chapter 1) by Curnutt et al. (1998). The dispersal information collected for this study addresses the spatial independence of each of these sub-populations.

Everglades National Park personnel conduct annual range-wide surveys of the sparrow (Curnutt et al. 1998, Kushlan and Bass 1982). From this information we know that the sub-populations have not followed similar population trajectories over the past decade. Of the three sub-populations we will consider (A,B, and E), the western (A) subpopulation has declined the most. This subpopulation held half the known population in the initial 1981 survey (Curnutt et al. 1998). Between 1992 and 1994, densities dropped by 90% and have yet to recover (Curnutt et al. 1998). Nott et al. (1998) attributed this decline to high water events that they assumed, given the magnitude, prevented successful nesting.

Subpopulation B has remained largely stable in numbers since 1981 (Curnutt et al. 1998). Subpopulation B now holds the vast majority of sparrows and is often referred to as the population 'core'. Subpopulation E declined in sparrow numbers by 50% between the 1981 and 1995 surveys (Curnutt et al. 1998). The reason for the decline is unclear, however this area experienced numerous fires during this period (Curnutt et al. 1998). Surveys conducted since 1997 have documented significant increases. Subpopulation E now holds 35% more individuals than were counted in 1981 (USFWS 1999).

The seven study plots within subpopulation B were chosen for their accessibility. Each approximately 0.5 km², they lie along the one maintained road (Main Park Road) and the one un-maintained road (Old Ingraham Highway) that pass through portions of the sparrow's range. In 1997 and 1998 we established new study plots within sub-populations A and E. The plot in A is approximately 0.5 km² while the plot in E is 1.5 km². Monitoring these remote plots require overnight stays and helicopter transport. Thus, these plots are visited half as often as the others.

Monitoring

We capture and band adult Cape Sable seaside sparrows using mist-nets and play-back recordings of their song (Bibby et al. 1992). Male sparrows are territorial and respond to a tape-recording of their song by flying toward the source (i.e. a recorder placed under the mist-net). Females will respond to taped play-back of songs or they can be flushed into a net. Females are caught less frequently than males. Adult sparrows are sexed based on behavior (e.g., only males will sing) or morphologically (e.g., presence of a brood patch for females or cloacal protuberance for males). It is possible to distinguish hatch-year (HY) and after-hatch-year (AHY) individuals based on plumage differences (e.g., HY birds have short and differently colored flight feathers). It is not possible to age adult birds. In 1997 we began banding nestlings on their fourth to sixth day in the nest.

All banded individuals are given a USFWS aluminum band and three celluloid color bands. The unique color combination allows us to identify individuals

throughout the breeding season and in subsequent years. We begin searching for previously banded individuals in March, marking the territories of any re-sighted or recaptured birds with colored surveyors tape. We use re-sight-recapture information to generate a survivorship estimate for males using the Cormack-Jolly-Seber statistical model from the program MARK (White and Burnham 1997). We also calculate the proportion of individuals that are re-sighted or recaptured each year and compared these return rate values between the sexes and ages.

Each year we search for sparrow nests from mid-March until early-June. In the 1996 and 1999 seasons we continued searching for nests until August. In the two seasons (1997, 1998) we did not continue past June, a separate radio telemetry project worked from early-June until the following March (Dean and Morrison 1998). We incorporate results from this study where appropriate.

To find nests we use behavioral cues (e.g., adults delivering food or giving defensive calls) and random search-and-flush techniques (Bibby et al. 1992). Nests are checked every second or third day until fledging or failure. On each nest visit, we record the number of eggs or nestlings present, the identity of the adults attending the nest, and the state of the nest itself. Each visit lasts less than a minute and neither the eggs nor nestlings are handled. Due to the aforementioned constraints on visiting plots within sub-populations A and E, occasionally the fate of nests found in these areas are unknown.

We test for differences in the number of eggs and nestlings per nest between sub-populations and years using ANOVA. If significant differences are found, we use Fisher's protected least square difference (PLSD) to do post-hoc pair-wise comparisons between means. The above information also estimates nesting success according to Mayfield techniques (Mayfield 1975, Johnson 1979). The Mayfield technique calculates the daily survival probability of a nest by avoiding the assumption that all nests found were actually observed through the entirety of the nest cycle (Mayfield 1975). Because adults are banded with a unique combination of color bands, we also follow an individual's multiple nesting attempts.

We divide all nests found according to their date of hatching such that we compare fecundity measures between the wet and dry seasons. Cape Sable seaside sparrows continue to nest after the onset of summer rains, however nesting attempts are less common (see below and Werner 1975). All nests that have a hatch date before 1 June are termed 'early-season' and all nests that have a hatch date after 1 June are called 'late-season'. The 1 June cut-off is the approximate time of year when the summer rains begin (Olmstead et al. 1980). We qualitatively compare Mayfield nest success rates between early- and late-season nests. In addition, we compare numbers of eggs and nestlings using Student's t-test.

Water flows within ENP have occasionally reached heights of 50cm above ground level within the western marl prairies (Nott et al. 1998). In such scenarios, the height at which sparrows place their nests off the ground becomes the most important determinant of fecundity. If water levels attain heights greater than the average height of the nests, most will flood and fail (Lockwood et al. 1997). For this reason, we measure the distance from the top of the soil to bottom of the nest structure (accuracy of ± 1 cm) after the young fledged. We use Student's t-test and ANOVA to compare the average height of nests off the ground between the early- and late-season and the sub-populations respectively.

We record all evidence of nest failure, including the presence of standing water in the nest and destroyed eggs or nestlings. We record apparent predation events as the unexplained loss of all nest contents between nest checks (Schaub et al. 1992). Calculation of predation rate is based on these records (Schaub et al. 1992, Lockwood et al. 1997). Predation rate is calculated as the number of predation events divided by the number of nests with eggs or young present. These rates are calculated over 10- to 14-day intervals starting each year from the day that the first nest was found.

Because Lockwood et al. (1997) present preliminary evidence of increased predation rates with increases in water level, we look for a similar effect here. We use hydrological information from an ENP monitoring station. This station (P46) is located approximately two km of all subpopulation B plots. The P46 water levels function as the independent variable; predation rates calculated for the seven subpopulation B plots are assigned as the dependent variable. Each data point represents a particular unit of time encompassing the 1996 to 1999 breeding seasons.

The locations of banded, recaptured and re-sighted individuals are recorded in Universal Transverse Mercator (UTM) Easting and Northing coordinates using a Global Positioning System (GPS). The accuracy of the GPS varies from one to 20m. These locations allows us to calculate 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). We use Student's t-test to compare mean dispersal distances between adult and juvenile sparrows.

Based on the above demographic parameters and their associated variability, it is possible to create a simple model that produces worst and best case population growth scenarios. Our purpose is not to produce a detailed viability model, but to understand how our results constrain the bird's recovery. First, we obtain the number of young produced per breeding attempt. To do this, we multiply the proportion of adults that breed by average clutch size and the daily probability that the young will survive to fledging (Mayfield score). We then divide this

value by two such that productivity can be expressed per individual. (A nest is the product of a pair of birds, obviously.) To obtain one-year population growth (X_{t+1}) we incorporate juvenile (HY_s) and adult survival (AHY_s) rates in the following way:

$$X_{t+1} = (AHY_s * X_t) + (HY_s * \text{individual productivity}) \quad (1)$$

Annual population growth is then expressed as:

$$\text{Population growth} = X_{t+1} - X_t \quad (2)$$

Results

Survival

We banded 247 adult (AHY) Cape Sable seaside sparrows between 1994 and 1998. The number of AHY individuals banded ranged from 20 to 80 per year. We recaptured or re-sighted 118 of these 247 individuals at least once in subsequent years. The majority (82) were only seen once after banding. Thirty-six adults were re-sighted two or more years subsequent to original banding. One male, banded as an adult 1994, has been re-sighted every year since; making this male a minimum of six years of age. A female, banded in 1995 as an adult, is a minimum of five years of age.

Of the 118 re-sighted adults, 93 (79%) were males. Using program MARK (White and Burnham 1997) we derive a survival model for adult males. A Cormack-Jolly-Seber model that assumes constant survivorship and recapture probability provides the best fit to our data. From this, survival rate is estimated at 0.66 (standard error = 0.06) and the recapture rate is 0.65 (standard error = 0.08). Thus, 66% of all adult males in our sampled population survive between years.

This statistical model efficiently derives survivorship estimates while accounting for the various pitfalls of using mark-recapture information (White and Burnham 1997). However, it poorly distinguishing differences in survival rates and recapture rates when sample sizes are low or mark-recapture efforts have been underway for a short time. This being the state of our data, we can not compare survival models between HY and AHY individuals, between males and females.

Return rates, or the proportion of individuals re-sighted or recaptured from year to year, are poor estimators of survival rates for a variety of reasons (Begon 1979). Yet, they do allow a glimpse into demographic differences between various groups of individuals within the population (i.e. HY vs. AHY, males vs. females). From 28% to 48% of AHY individuals return one year after banding; 20% to 37% returned two years post-banding and only 5% returned four years

after banding. We have banded 213 juvenile (HY) sparrows; most in the nest. We can only calculate a return rate for HY individuals up to two years post-banding. Return rates for HY individuals ranges from 15% to 20%; nearly half that of the equivalent return rate of AHY individuals. If we divide banded individuals according to gender, males and females show similar overall return rates. Males return at a rate between 26% and 52%. Females return at a rate between 25% and 45%. We do not have enough banding information from the various sub-populations for a spatial comparison of return rates.

Fecundity

We found 252 Cape Sable seaside sparrow nests between 1996 and 1999. Ten nests were found in subpopulation A, 212 in subpopulation B, and 30 in subpopulation E. Most nests (150) were early-season. We found 68 late-season nests and 34 could not be classified. Among the ten subpopulation A nests, only one (10%) was classified as a 'late'. Of the 183 classifiable subpopulation B nests, 60 were late-season (33%). Of the 26 subpopulation E nests that could be classified, 7 were late-season (27%).

Although fecundity has several different definitions (Clobert and Lebreton 1991), there are three measures commonly calculated for birds: the number of nests produced in one breeding season, number of young produced per nest, and number of fledglings produced per egg laid. Below we describe each measure for the Cape Sable seaside sparrow.

The first fecundity measure is the number of nests produced per breeding season. The average length of the breeding season and the length of one nest cycle (i.e. phenology) influence this value. The earliest Cape Sable seaside sparrow nest was found on 20 March 1997. This nest had two eggs, but was lost to predation seven days later. Werner (1975) reports observing young from a nest initiated in late-February. The latest sparrow nest was found 10 July, 1999. This nest eventually fledged young on 26 July. Werner (1975) reports observing nests with eggs as late as 26 July and Dean and Morrison (1998) report catching recently fledged young as late as September. T. Dean reports a nest successfully fledging young as late as 2 August 1998 (T. Dean pers. com.). Thus, Cape Sable seaside sparrows can nest from March until at least early August (122 to 142 days).

The number of clutches produced in one breeding season depends upon how much time individuals devote to pair bonding, nest building, egg laying, incubation, nestling care, and fledgling care. Most of our observations concern egg laying, incubation and the nestling period. We recorded the timing of egg laying at eight nests. In each case, the females laid eggs every day until the clutch was complete. We observed four nests from initiation of the clutch to hatching. All four females incubated the nest 12d. We observed 101 nests from

hatching to fledging. The average nestling period length for these nests was 9.15d (standard deviation = 2.12d). We have found 11 nests that were complete but held no eggs. These nests eventually held eggs an average of 2.72 days after they were found (standard deviation = 1.56d). Thus, we estimate that Cape Sable seaside sparrows require 30 to 35 days to build a nest, lay eggs, incubate, and fledge young.

The final portion of the nest cycle, the period of fledgling care, is the most uncertain. We have never re-sighted a fledgling banded as a nestling within the same breeding season and thus can add no new information to that described in Lockwood et al. (1997) and Werner (1975). Adults may overlap broods and care for fledglings as they are initiating a second clutch (essentially no time devoted to fledgling care) or they may care for young up to 20 days after leaving the nest (Werner 1975). This generates an estimate of 30 to 50 days required to complete one nesting cycle. Dividing this value into the 122 to 142 days during which sparrows were observed breeding, yields a per annum clutch production of two to four.

How many re-nesting attempts have we actually observed in one breeding season? Of the 252 nests found in our study, 27 were known second clutches, three were known third clutches, and one was a known fourth clutch.

The second component of fecundity is the number of young produced in one breeding attempt. Cape Sable seaside sparrows lay an average of 3.18 eggs per nest (standard deviation = 0.55, $N = 126$ nests). This average does not vary by year (ANOVA $F = 1.05$, $df = 3$, $P = 0.37$) or across sub-populations (ANOVA $F = 1.04$, $df = 2$, $P = 0.36$). Clutch size did not vary between early- versus late-season nests (Student's $t = 0.21$, $df = 111$, $P = 0.83$).

Cape Sable seaside sparrows average of 2.85 nestlings per nest (standard deviation = 0.86, $N = 179$ nests). This average varies according to year (ANOVA $F = 5.57$, $df = 3$, $P = 0.0011$). Post-hoc comparisons between years reveals that the number of nestlings per nest decreased in 1999. Nests held an average of 2.65 nestlings (standard deviation = 0.87, $N = 85$ nests) in 1999, a value significantly lower than in 1997 and 1998. The number of nestlings per nest did not vary according to subpopulation (ANOVA $F = 1.29$, $df = 2$, $P = 0.28$) or between early- versus late-season nests ($t = 0.38$, $df = 169$, $P = 0.71$).

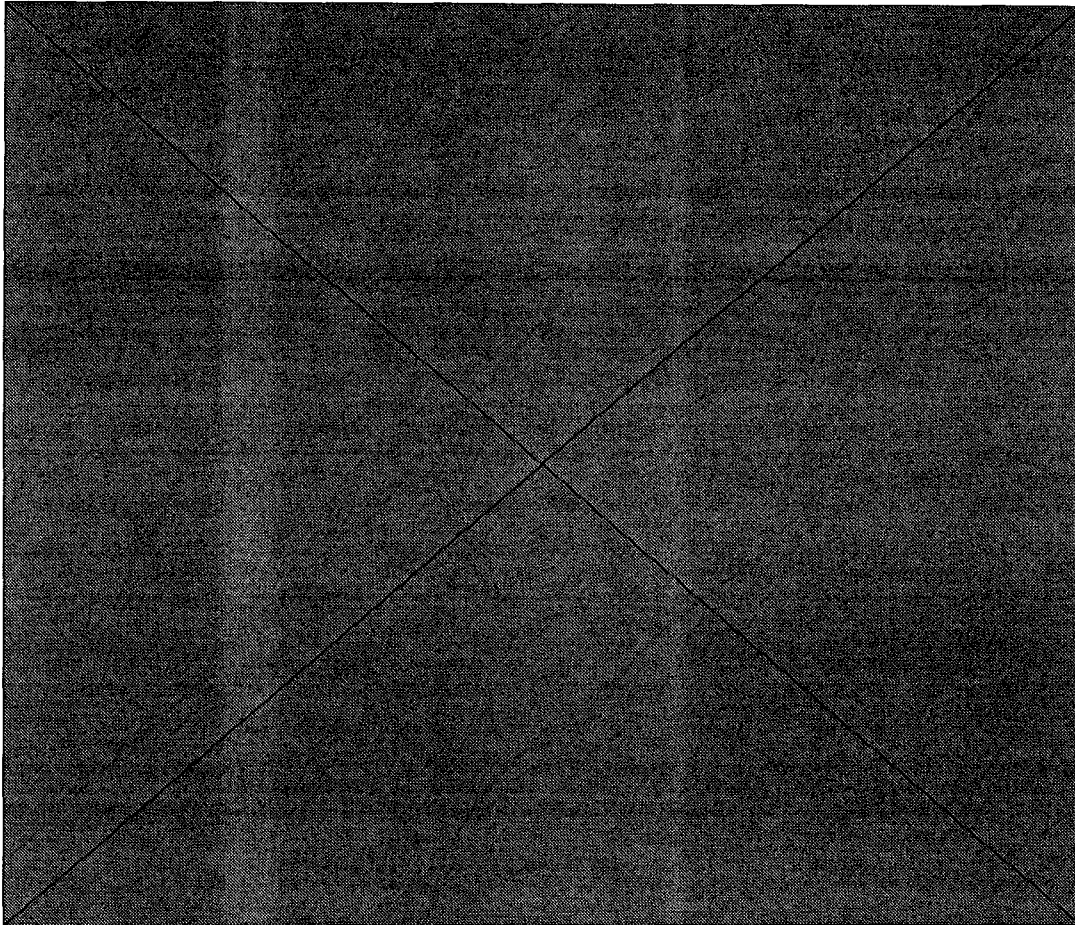
Finally, fecundity can be measured as a daily survival probability, often calculated using the Mayfield method (Mayfield 1975, Johnson 1979). Mayfield nest success rates varied considerably from year to year. Nests found in 1998 show the highest daily survival probability at 0.60. Nests found in 1999 showed the lowest daily survival probability at 0.12. Comparing Mayfield nest success rates across space, shows that subpopulation E has the highest success rate at 0.53 whereas sub-populations A has a survival probability of 0.12.

Subpopulation B was the only group with enough information to divide these probabilities according to early- versus late-season. Early-season subpopulation B nests have a survival probability of 0.26 whereas late-season nests have survival probability of 0.10.

Lockwood et al. (1997) find circumstantial evidence that higher water levels increase the rate at which Cape Sable seaside sparrow nests are lost to predation. To test if the observed temporal variations in predation pressure are due to differences in hydrology, we look for correlations in predation rate and water levels. Using all nests found within subpopulation B study plots, we calculated predation rates over 10- and 14-day intervals and compare them to the average water levels at the P46 hydrological monitoring station. Predation rates varied from 0 to 0.12 with an average value of 0.0342 (standard deviation = 0.04). The average water level at the P46 hydrological station varied from 5.5cm above mean sea level (MSL) to 53.36cm MSL with an average of 31.8cm MSL (standard deviation = 13.48cm). When we plot predation rate within the subpopulation B plots against water levels at the P46 station, the highest predation rates occur during periods of high water (Fig. 2). Most of the points in the upper left corner of Fig. 2 (i.e. those which have high predation rates and water levels) represent time periods occurring after 1 June. However, not all points in the upper left corner of Fig. 2 are late-season nests. High water levels, no matter when they occur, increase predation pressure within subpopulation B study plots.

There is no figure 1 in this chapter.

Figure 2. Predation rate plotted against water levels at the ENP P46 hydrological monitoring station. Each point represents either a 10 or 14 day period during the 1996-99 breeding seasons.



How high can water levels rise before they are detrimental to Cape Sable seaside sparrow nesting? The answer depends in part on the prevalence of predators, but it also depends on how high sparrows will build their nests from the ground. The average height that Cape Sable seaside sparrows place their nests from the ground (i.e. from soil surface to bottom of the nest structure) varies through time and, to some extent, through space. The average height of nests within subpopulation A is 16cm (standard deviation = 6cm, N = 6), within subpopulation B is 18cm (standard deviation = 7cm, N = 169), and within subpopulation E is 18cm (standard deviation = 8cm, N = 25). There are no discernable differences between these values (ANOVA $F = 0.23$, $df = 2$, $P = 0.79$). However, the variance around each of is relatively high (one standard deviation is roughly equal to at least 1/3 of the average). Although we can not detect spatial differences across large scales, on smaller scales the height of nests off the ground is highly variable.

We next pool the nests and look for differences between years and through the breeding season. The average height that nests are built off the ground increases after the onset of summer rains in early June (Student's $t = -3.05$, $df = 198$, $P = 0.003$). Nests that hatch young before 1 June sit an average of 17cm off the ground (standard deviation = 7cm, $N = 136$) whereas nests that hatch young after 1 June sit an average of 21cm off the ground (standard deviation = 8cm, $N = 64$). Similarly, average nest height varies from year to year (ANOVA $F = 4.96$, $df = 3$, $P = 0.002$). During the 1996 and 1997 breeding seasons, Cape Sable seaside sparrows built nests lower to the ground (16cm and 15cm respectively) than during the 1998 and 1999 breeding season (21cm and 19cm respectively).

Dispersal

By following banded individuals from one breeding season to the next, we calculate breeding dispersal distances for adult (AHY) sparrows. Adult Cape Sable seaside sparrows will defend a territory an average of 212m (standard deviation = 131m, $N = 30$) 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 300m.

Because we limit the spatial extent of our re-sight efforts, we are not likely to detect dispersal movements over medium to long distances. Dean and Morrison (1998) utilized radio-transmitters to document Cape Sable seaside sparrow movements over the non-breeding season. They report left-skewed non-breeding season dispersal distributions. Most radio-tagged individuals moved 100m to 150m, and all but two individuals moving less than 370m, between consecutive sightings. Dean and Morrison (1998) recorded longer range movements, sometimes up to 7km, however these movements were rare and most of these individuals returned to their breeding territories by the end of the non-breeding season (Dean and Morrison 1998). We have never re-sighted or recaptured a banded individual from one subpopulation within another. Collectively, these observations 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 (HY) individual will move from their place of hatching to the site in which they settle during their first breeding season. [These sites may or may not be breeding territories.] Individuals banded as nestlings were re-sighted or recaptured an average of 577 m (standard deviation = 98m, $N = 15$) from their place of hatching. This value is significantly different than that observed for equivalent time frames in adults (i.e. one and two year movements; Student's $t = -4.73$, $df = 42$, $P < 0.0001$). In contrast to the distribution of AHY dispersal distances, HY birds move longer distances thus producing a more even distribution of dispersal distances with a maximum natal dispersal distance of over 1km recorded. We have not yet collected enough

information on HY individuals to calculate longer interval movements.

Demographic Model

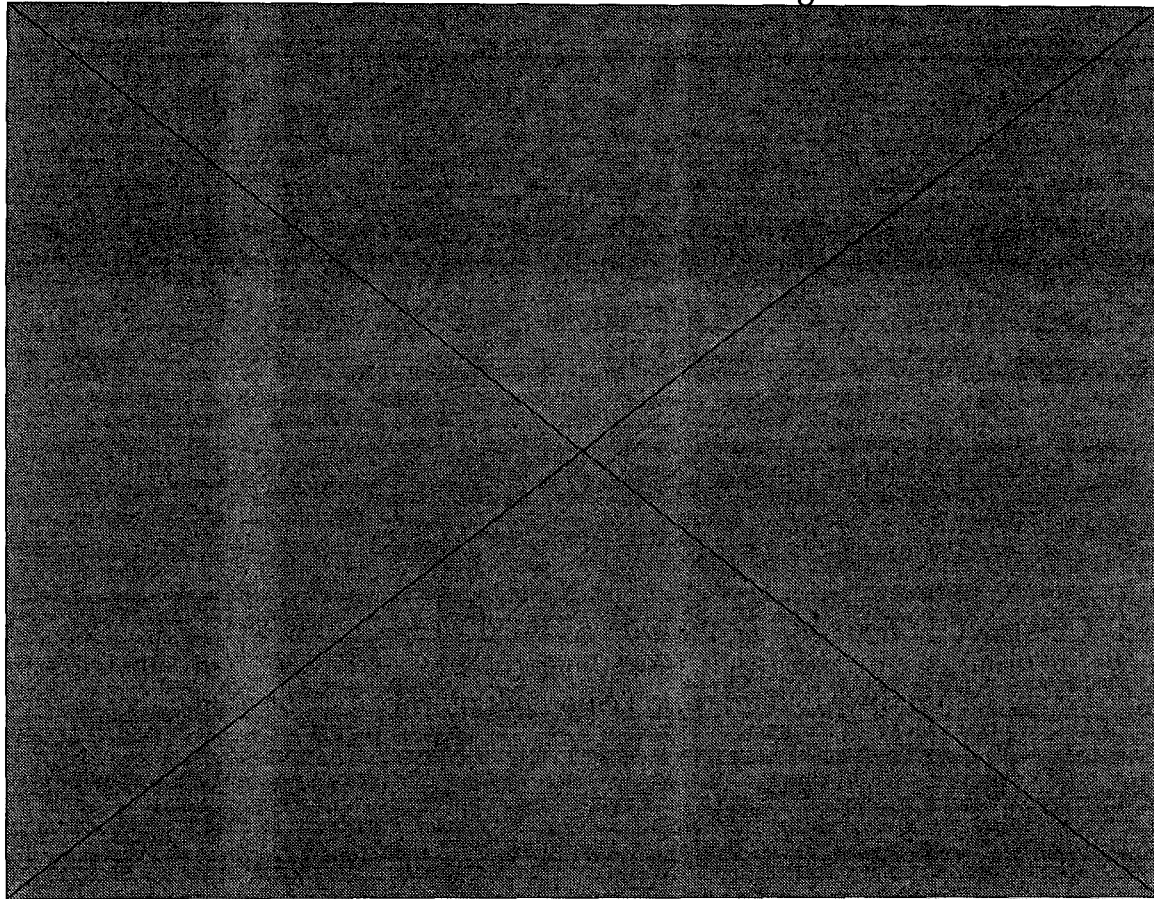
We begin by exploring the best case scenario. We assume all breeding individuals produce large clutches ($3.73 = \text{average plus one standard deviation}$) and these clutches have a daily survival probability equal to the maximum observed (0.53). We will assume late breeding attempts have the same clutch size and success rate as early attempts and that all breeding individuals that produced an early nest will also produce a late nest. Finally, we will assume adults have a high survival rate of 0.72 (average plus one standard deviation) and that juveniles survive nearly as well as adults (0.50).

When we insert these variables into equation 1, we get an annual increase of 70%. This is clearly very optimistic. It is unlikely that any segment of the sparrow population would ever enjoy conditions that will produce this annual rate of increase. Even under this wildly optimistic scenario, however, the sparrow population will not double in one year.

Next we change each variable to its lowest recorded value and re-calculate annual growth rate (Fig. 3.). When we change adult survivorship to its lowest recorded level annual growth rate becomes 58%, an 8% decrease as compared to the optimistic scenario. Changing juvenile survivorship, clutch size, or the proportion of late breeders to their lowest recorded values has similar effects, resulting in annual growth rates between 25 and 40%. The largest change in growth rate occurs when daily nest survival probabilities are set to levels observed in subpopulation A. This change, from 0.53 to 0.12 nest survival probability, results in a annual growth rate of -6%. Thus, even when we are very optimistic in all other respects, subpopulation A will decrease in numbers given its current nest success rates.

Obviously annual growth rates will become more realistic (and less optimistic) as we incorporate more observed demographic parameters. If our model is robust, when we insert the observed values for each subpopulation we should obtain annual growth rates that are consistent with observed population trajectories (see above). Subpopulation B has shown consistent numbers of individuals since the first population estimates were made in 1981. When we insert the demographic parameters described here into equation 1, we obtain an annual growth rate of 0.23%. Subpopulation E has shown an increase in individuals since 1997 and accordingly we obtain an annual growth rate of 27% using demographic data collected since 1998. Subpopulation A declined by more than 90% between 1992 and 1997. Since 1997 numbers have continued to slowly decline. Using demographic data collected since 1997, we obtain an annual growth rate of -17%.

Figure 3. Sparrow annual growth rate according to a demographic model (see text for details). Variables are adjusted from the optimistic scenario to their lowest value in order to ascertain their effect on annual growth rates.



Discussion

Cape Sable seaside sparrows are highly sedentary and extremely faithful to particular breeding locations. The various sub-populations likely do not 'trade' immigrants such that one could be the 'source' for another in decline (i.e., a 'sink': Pulliam 1998). Thus, we can expect the future of the Cape Sable seaside sparrow to be played out in several smaller arenas (sub-populations), the fate of each determined largely independent of the others.

Cape Sable seaside sparrows are unlikely to live past three years of age and at least 40% of the population will die each year. Juveniles are much less likely to return from year to year indicating that they have low first-year survivorship. These estimates are typical of small land birds (Ricklefs 1973, Perrins and Birkhead 1983) and other races of seaside sparrows (Post and Greenlaw 1994). There may be more complex survivorship dynamics within the various sub-populations, however given the nature of mark-recapture information it will

require longer time-series to uncover them.

Cape Sable seaside sparrow fecundity reaches its maximum potential early in the breeding season (March to June). Sparrows will continue to breed well into the wet-season, allowing this subspecies to recover from population declines. However, in order to realize this potential, most nests must be successful. Sparrows only produce two to three young per nesting attempt. If only early-season nests are successful, the young produced will replace breeding adults but future population levels will remain the same. [In practice, population levels may still decline due to the low survivorship of juveniles.] The presence of late-season nesting is a principal means to increase sparrow densities. Even under the best conditions we have observed (i.e. subpopulation E growing at a rate of 27% annually), it will take four years for population size to double.

These demographic traits make the Cape Sable seaside sparrow extremely dependent on the condition of the marl prairies they inhabit. Relatively short-term excesses of water, or overly dry conditions that promote annual fires, can have long-lasting impacts. Most resident sparrows will die within five years of initial impact, and if there are very few or no successful nesting attempts during this period, the effected subpopulation will inevitably decline. Further, managers can not rely on emigration from adjacent sub-populations to 'rescue' the effected subpopulation.

The above discussion outlines the more subtle effects of altered hydrology on Cape Sable seaside sparrow demography. However, all races of seaside sparrow incur the blunt effects of periodic high water events. Unusually high tides cause mass loss of active nests in other seaside sparrow races (Marshall and Reinert 1990). However, Cape Sable seaside sparrows exist within a non-tidal ecosystem. Nesting success is not influenced by tidal flooding events (Post and Greenlaw 1994, Marshall and Reinert 1990). Instead hydrological influences on nesting success come from annual variations in the summer rains and management decisions regarding water releases into Everglades National Park (Nott et al. 1998).

Cape Sable seaside sparrows place their nests near the ground making them extremely vulnerable to high water events. The height of nests from the ground varies through the breeding season, from year to year, and across small spatial scales. This variation renders inexact predictions concerning what water levels will cause mass loss of active nests. However, we can make general predictions. The highest recorded average height of nests off the ground is 21cm (late-season nest average). If we add one standard deviation to this value, we can estimate that at locations where water levels rise above 29cm during the nesting season, nearly 70% of all active Cape Sable seaside sparrow nests will flood and fail due to inundation alone (this does not include the effects of high water on nest

predation rates). Water management decisions that reflect this fundamental aspect of Cape Sable seaside sparrow biology will increase the probability that this subspecies will recover.

Predation pressure is also influenced by hydrological patterns. The higher the water level the higher the probability that a sparrow nest will be lost to predation. Most nest losses in our study we attribute to snakes because the nest structure is undisturbed. [The other assumed predator, the rice rat, often leaves feces and dishevels the nests.] Some evidence implicates the cottonmouth (*Agkistrodon piscivorus*) in predation events. These snakes are common in our study plots and T. Dean (pers. com) reports finding a cottonmouth with an adult radio-collared sparrow in its gut. If cottonmouths are the principle predators of sparrow nests, this may explain the correlation between high water levels and predation rate. Cottonmouths bask in the sun during the day, but are most active at night especially after heavy rain (Behler and King 1988).

Predation of nests is a natural event, especially for a ground-nesting species that construct an open-cup nest (Martin and Li 1992, Bosque and Bosque 1995). The implicated predator is native to the Everglades and has likely co-evolved with the sparrow. Thus, it is not clear what management action could be taken to reduce predation pressure beyond limiting artificial flooding during the breeding season.

There are clear gaps in our knowledge of Cape Sable seaside sparrow demography, such as juvenile survival and age-specific fecundity of females. However, the absence of this information should not be construed as gap in our understanding of how to manage this subspecies. Our results provide clear implications for water management, and thus define broad guidelines for restoration of a more natural Everglades waterflow.

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challenged in a legal case, *Sweet Home versus Babbitt*, argued in front of the Supreme Court of the United States, on February 17th 1995. In the particular context of the Spotted Owl, an Oregon group challenged the responsible cabinet member, Secretary of the Interior Babbitt, arguing that only direct take violated the law and not habitat destruction. In a brief of *Amici Curiae* scientists, one of us (Pimm) 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 raise 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.

Our particular concern is the Federally-listed Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) a bird found only within the seasonally flooded marshes in the Everglades of South Florida. In previous publications, we demonstrated that the unnatural flooding of its breeding habitat 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 over-drained and more susceptible to anthropogenic fires. Those fires also harm the birds directly.

We left open the possibility that flooding and fires also damaged the habitat and so the birds as a consequence. In this paper, we will demonstrate that flooding has indeed altered the habitat in which the sparrow occurs, done so in a way to preclude the bird's use of the habitat, and over a period of years longer than the flooding itself.

The paper proceeds in two 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. (The signature of 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 is an evaluation of those predictions. It has three parts. The first explains how we can predict habitat in years before we began intensive fieldwork and thus have no nest locations. It includes both ecological reasons and empirical evidence supporting our methodology. The second is an analysis of the habitat predictions. It links water management decisions to their effects on

the habitat. The third part is a detailed and technical analysis of the errors we find in our predictions. We identify these errors using the annual range-wide 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 find that errors of the kind where we predict no habitat, but where there are sparrows, are few indeed. Often they are explicable in terms of birds remaining in the same place from one suitable year to the next unsuitable one. Errors of absence from predicted suitable habitat are more common. They are most readily explainable by the bird's inability to recolonize once-suitable habitat that in immediately preceding years became unsuitable because of fires or floods.

We will present two key results.

(1) Across the eight years of the study, large year-to-year fluctuations in predicted habitat confirm the culpability of water managers. Flooding in 1993 and 1995 greatly reduced the habitat predicted to be suitable for the sparrow compared to 1992. This is a formal, technical demonstration of the figures presented in Nott et al. 1998, inferring dry prairies in 1992 and extensively flooded prairies in 1993 and 1995, from the colors of the published images.

(2) 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 1999. This formal, technical demonstration matches exactly the subjective opinion expressed by Bass and Pimm from their visual surveys. By 1999, the predicted suitable habitat had not yet recovered to its pre-flood state. The habitat is recovering faster than the slowly recovering bird populations. It is the repetition of precisely such a scenario that we predict could lead to the species' extinction (Pimm and Bass 2000).

Neither of these results are surprises, for they were suggested by our previous papers. Nonetheless, we consider the details present here to be important in both a national and a broader context. Importantly, our data conclude that water management practices have damaged huge areas of vegetation across Everglades National Park, have done so for extensive periods of time, and in a way that jeopardizes the survival of a Federally listed species. This constitutes a "take." Moreover, it is one that is independent of, and lasts longer than, the direct affects of flooding. Crucially, these data are independent of — and so additional to — all other conclusions that we have drawn in previous papers.

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

Figure 1 – Location of sparrow populations (A-F) in Everglades National Park. Water enters the park from two sources, the S-12 floodgates and a pumping station north of Taylor Slough. The S-12 floodgates are west of the natural entry point for water into the ecosystem. (The natural flow path is illuminated by the tree islands, which line up with it. They appear as pale, tear-drop shaped objects amid the darker, flooded areas of the Slough.) Whenever the S12s open they flood population A. Additionally, shifting of water to the west causes population F to become drier and to suffer an increased fire frequency. The pumping station north of Taylor Slough affects the water levels in populations C and D. Heavy pumping results in the complete flooding of D and the southeastern portion of C. Populations B and E are less affected by flooding.



The Cape Sable sparrow, its habitat, and its history

The approximately 2000 pairs of Cape Sable sparrows live entirely within 1500 km² of Florida's Everglades. The birds live in six populations separated to various degrees by the area's main drainage, Shark Slough, and areas of unsuitable (typically wood or bushy) habitat (Figure 1).

Bass and Kushlan (1982) conducted the first extensive sparrow survey in 1981. We repeated the survey in 1992 and annually thereafter. Across a 1 km by 1 km grid of more than 600 sites, we record the number of sparrows seen or heard

within a 7-minute interval. We take particular care to visit all locations that might hold sparrows and do not observe birds at most of the sites we survey. This suggests that we do not miss many (if any) sites that hold birds.

To estimate the actual numbers of sparrows from the number we observed on our survey, we multiply each singing male by 16. This correction is based on the range at which we can detect the sparrow's distinctive song — it encompasses $1/8^{\text{th}}$ of a square kilometer, roughly a circle with a diameter of 200 meters — and on the assumption that one female accompanies each singing male; Curnutt et al. (1998) provide details.

Using this calibration, we estimated that the total breeding population of this species was over 6000 in both 1981 and 1992. Of the six populations, A (west of Shark River Slough) was the most numerous in 1981 (~2700 birds) and B held fewer birds (~2300). Population B held more than A in 1992 (~3000 versus ~2600). Population E consistently held ~600 birds. The other three populations held between 100 and 400 birds, although we found no birds in F in 1992.

Table 1 lists the numbers of survey points and birds heard during each yearly survey. The number of survey points ranges from between 478 and 853. Table 1 lists from 416 to 721 because we exclude some outlying areas that hold few, if any birds. (These include Cape Sable itself where the bird was first collected and where habitat changes have subsequently made the location unsuitable for it.) Some of the earlier surveys deliberately explored areas thought unlikely to hold birds to confirm that they did not. In 1992, for instance, the survey extended across much of the deep-water areas of Shark River Slough. Recent surveys attempt to count at every location that has held birds in the past or that we think that is even remotely potential habitat. For quantitative habitat comparisons, we demarcate populations by drawing a polygon around all survey points that ever have birds or were in any of the 1997 through 1999 surveys (Figure 1).

Populations A and B were the two largest populations in 1981 and 1992 and consequently have most of the survey points (table 1). In 1994, the survey was incomplete because of mechanical difficulties. Populations C, D, and F have no survey results and E is incomplete. The 1996 survey was incomplete for population F.

Table 1. Number of birds heard (top) in number of survey points (bottom) in each population in each year. 'NS' means there was no survey and 'inc' means the survey was incomplete.

Birds heard									
Population	1981	1992	1993	1994	1995	1996	1997	1998	1999

A	156	146	24	5	14	24	17	11	25
B	147	199	154	135	130	118	177	113	128
C	27	3	0	NS	0	3	3	5	9
D	25	7	6	NS	0	5	3	3	11
E	42	37	20	7/inc	22	13	52	57	48
F	7	0/inc	0	NS	0	1/inc	1	1	1
Total	404	392	204	147	166	164	253	190	222

Points surveyed

A	338	347	338	284	340	167	228	263	297
B	137	146	149	132	159	130	135	136	133
C	40	41	40	NS	40	38	34	40	39
D	67	67	67	NS	67	56	46	50	50
E	73	79	75	16/inc	74	63	66	77	88
F	41	3/inc	41	NS	41	11/inc	35	32	36
Total	696	683	710	416	721	465	544	598	643

Although populations A and B were of similar size in 1981 and 1992, floods during the breeding seasons of 1993, 1994, and 1995 prevented the birds from nesting across much of population A. Sparrows nest close to the ground and nestlings drown or suffer increased predation during floods (Lockwood et al. 1997). Like other small-bodied passerines, the expected lifetime is about one year, so only a few old birds survived to see the drier conditions of 1996. Population B remained relatively constant throughout the study period. Populations C and D had moderate numbers of birds in 1981, but during this study period consistently have few birds.

Population E had two sub-populations in 1992. We speculate that this was the

result of the very large fire in 1989. Much of the middle and southern portions of the population burned, but part of the northern portion was undamaged. Birds in the northern sub-population were present in every year of the survey. However, in 1995 opening of the S-12 floodgates flooded part of this sub-population and there was an associated decline in numbers. Since 1996, the northern sub-population has been increasing and expanding southward. The southern sub-population held a substantial number of birds in 1992, but since then has fared poorly due to flooding. Survey records indicate that the area had more sawgrass (*Cladium jamaicensis*) in 1992 than is typical of sparrow habitat, suggesting a wet history. However, from 1989 to 1992, which were very dry years, all of this area was dry. It may be that this typically wet area became suitable for sparrows with the dry conditions and they expanded into it. Then, in 1993 and many subsequent years, the area floods and the birds disappear. Since 1993, birds occur only sporadically.

Population F is always small, likely because the area suffers frequent fires.

Floods and fires directly harm the birds and their nests. The 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.

Stage I: Predicting the habitat

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

Our first stage is to identify what spectral responses correspond to suitable sparrow habitat. Different vegetative structures give different spectral responses or *signatures*. Even in the gray-scale image in figure 1, it is possible to tell the difference between the wetter vegetation in the central part of Shark River Slough and the drier prairies on either side. In color (see Curnutt et al. 1998) and at a finer resolution, it is possible to pick out many other more subtle vegetative features.

We locate over 200 nests using a Global Positioning System (GPS) and then match each of these nests to their corresponding pixel on the satellite images. The resolution of these images — the pixel size — is 29 by 29 meters. These pixels form the basis of the prediction of potential sparrow habitat.

The second stage involves the proximity to bushes. Predators, such as Red-shouldered Hawks (*Buteo lineatus*), perch on bushes and shrubs when looking for

prey, such as the sparrow. Nesting close to bushes likely exposes sparrows to an increased risk of predation. So we ask: how close to bushes do the birds nest? After answering that question, we eliminate areas that are too close.

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

In brief, to predict sparrows present, an area must contain a sufficient number of pixels with the correct spectral signatures to enable a sparrow to establish a territory and these pixels must not too close to bushes. We now present these steps with the requisite details.

Predicting habitat 1: Obtaining the spectral signatures

This stage has three parts. First, we correct the satellite images so our GPS data will match up correctly with the image. Second, we make spectral signatures of suitable sparrow habitat using the nest pixels. Last, we apply these spectral signatures to the image to map the habitat.

Images and rectification. We use Landsat Thematic Mapper (TM) images taken during the breeding seasons of 1992 through 1999. When possible, these are from April or May, the months of the peak breeding season. 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 TM 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 reduces the accuracy of our results because the prairie is essentially at thermal equilibrium. We eliminate it from our analyses.

We took coordinates for 66 ground control points using a differentially corrected GPS (< 2 m error) in accessible areas and from quadrangle maps (1:24000) in inaccessible areas. We use 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 meters, 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 eliminate nest locations judged to be of questionable accuracy and those closer than one pixel (29m) to a road. Presence of a road within a nest pixel contaminates the spectral signature. This leaves 232 usable nests. For each year, we discard nest locations if they fall on clouds, shadows, or other features corrupting the image.

Using only the nest pixel provides no information on the spectral characteristics of the surrounding habitat within the territory. Sparrows defend territories of about 2 hectares (Werner et al. 1974, our unpublished data). In an ideal world, we would have precise maps of sparrow territories and build our spectral signatures from those. However, in most cases we have only the nest location and must work from that. Therefore, we need to select pixels that adequately represent the true territory. To select those pixels we tried two methods.

The *central place foraging method* assumes that 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 use the 25 nearest contiguous pixels (2.1 ha) that are not obviously unsuitable (i.e., bushes or water). (25 produces a compact, if not quite circular pattern, with the nest location centrally located.)

The *minimum spectral distance method* assumes that sparrows place their nest in a typical part of the territory. We then select the 25 contiguous pixels that are most similar to the nest pixel. That is, they have the minimum spectral distance from the nest pixel.

Our field experience, including mapped territories that were irregular in shape and had nests near their boundaries, suggested that this second method should be the better one. Indeed, our results support this. In direct comparisons of the first and second methods, the latter classifies more habitat in areas with birds and less habitat where there are none. In what follows, we only use the minimum spectral distance method.

Making and summing classifications. For a particular nest and its associated 25 pixels, we calculate the minimum and maximum value within each of the six spectral bands. This produces a six-dimensional box within which we deem all enclosed pixels to be predicted habitat. This is one sparrow's opinion of suitable habitat. Clearly, we can do this for all the available nests and territories and combine those opinions.

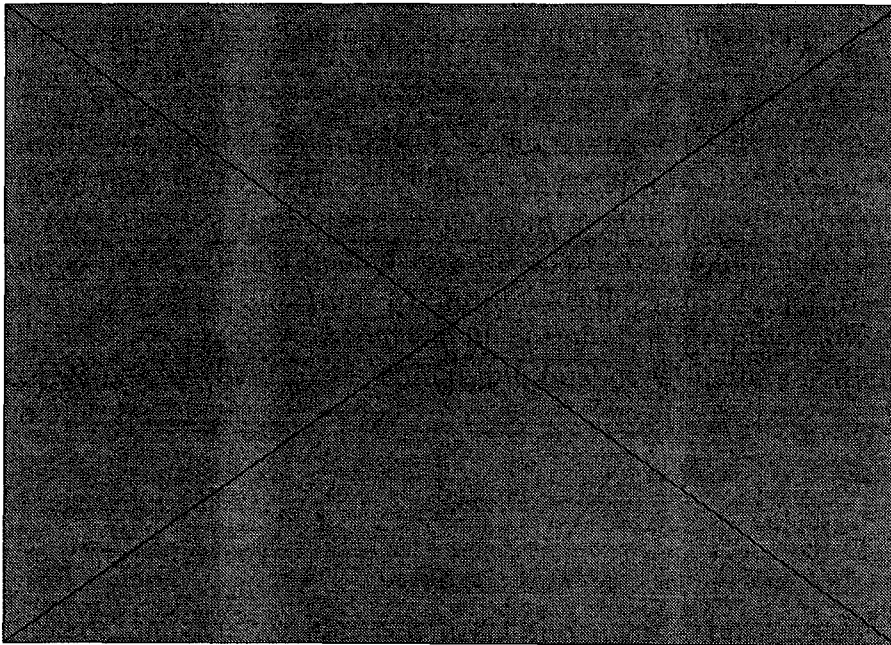
We can combine those opinions in a large variety of ways. Samples based on few nests will likely perform less well than those based on large samples. Moreover, in some years we have no nests at all. To get the largest samples we could combine nests from different years. This runs the risk of combining years where the birds placed their nests in different places because of different water conditions, for instance. To resolve these difficulties, we need to compare and contrast the predictions they produce. This we will do, but first we must explain the final two stages.

Predicting habitat 2: The bush layer

We find that sparrows do not nest near bushes, presumably because of increased predation risk. Using aerial photography, we measured the distance of 52 nests from the nearest bush. Figure 2 shows a sharp increase in nest frequency after 40m from a bush. Therefore, we eliminate classified habitat within 2 pixels (~58 m) of a bush.

Bushes are high in chlorophyll — they are green — compared to the buff tones of the prairie grasses. The satellite images capture these visually obvious features, particularly the cloud-free image from 1994 image. Because of the large spectral differences between bushes and other prairie vegetation, we use the ISODATA (Jensen 1996) algorithm to automatically find signatures corresponding to bushes. Accuracy assessment with aerial photography shows that this algorithm correctly identified pixels containing bushes >5-meters is diameter or clusters of smaller bushes.

Figure 2 – Distance between nests and nearest bush. Few birds nest with 60 meters of a bush.



Predicting habitat 3: eliminating small habitat patches

Because sparrows need enough suitable habitat for a breeding territory, we eliminate patches of habitat smaller than 25 pixels (2 ha) from the predicted area of habitat. We use 25 pixels to be consistent with the territory size used in making signatures.

Stage II: Evaluating the predictions

The evaluation stage has three parts. Any attempt at prediction begs two questions: "of what?" and "by what?" The first answer is simple — bird distributions. It is the second that 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. Ours is the ability to predict distributions in all populations in all years from a sample of nests that will be from only the more accessible populations and only from some of the years. The first stage explores how accurately we can do this.

The second stage is an analysis of the habitat predictions within each of the populations. It links water management decisions to their effects on the habitat and the population.

The third part is a detailed and technical analysis of the errors in our predictions. We defer this to Appendix 1.

Each of these components uses the annual range-wide surveys of the sparrow's abundance and distribution. Tests in the intensive study areas indicate an observer can hear a singing sparrow up to 200 meters away — an area of about 13 hectares. We calculate how much predicted suitable habitat is within a circle of 200-meter radius about the survey point. If the model predictions are good, then the survey should find birds more often in areas where the model predicts more habitat. In a graph of sparrow presence versus amount of habitat predicted (Figure 3a) the curve should be low on the left side (less habitat predicted) and high on the right side (more habitat predicted).

Predicting habitat in years without enough nests

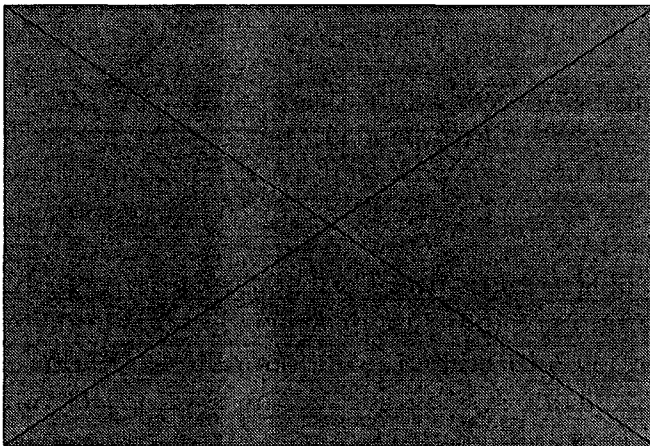
We only have nest locations from 1996 onward, and 1996 and 1997 have too few nests for good results. However, we need to predict habitat from 1992 onwards. An efficient solution would be to use nests from *all available* years on *every* year's imagery. This provides a large sample size and allows predictions in every year. Both ecological and empirical evidence support this approach.

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 posit that the areas in which sparrows nested during the detailed surveys, 1996 through 1999, were also suitable habitat in prior years. Sparrows nest in very similar places each year, so that a nest in 199x would almost certainly be within a territory in 199y.

Figure 3 (b) through (d) shows the empirical results supporting our assumption. These graphs compare nests from 1998, 1999, and from all years on various years' imagery. (We have too few nest locations in 1996 and 1997 to separate them out.)

Ideally, we would get a graph comparable to figure 3a, showing a monotonic 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 the 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, when there would need to be a sharp transition about the threshold. In reality, the graphs are more variable, but the relationship still holds.



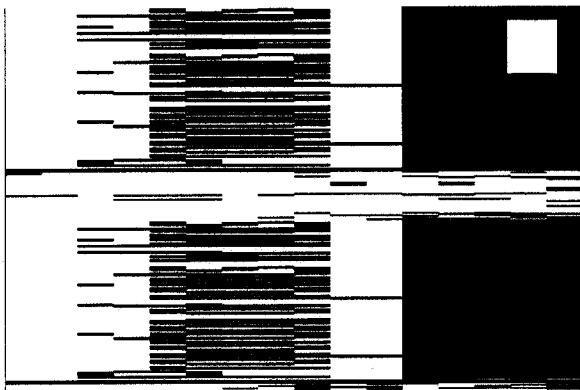
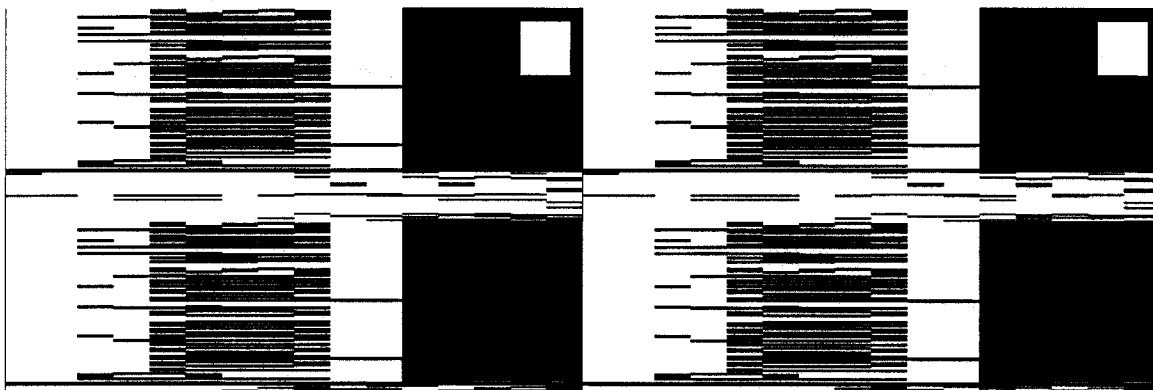


Figure 3 – The proportion of sites surveyed by helicopter where one or more birds were encountered versus the percentage of the area predicted to contain suitable sparrow habitat on the basis of different sets of nests. (a) Ideally, as the model predicts more habitat the survey will find more birds, thus we should see a positive slope. (b-d) In reality, the results have noticeable variability, but do show a definite positive slope. Each line corresponds to a combination of nests (1998, 1999, or all) used as seed pixels and years of imagery analyzed (nest year or non-nest year). All years is a summation of the results from every year's imagery using a given set of nests.



In figure 3b, using 1998 nests to predict where birds should be encountered on 1998 imagery gives a strong, but variable, increase in the proportion of survey points containing birds as the amount of predicted habitat increases, as we expect. When using 1998 nests on non-1998 images a similar pattern occurs. Thus, 1998 nests predict habitat just as well in other years as they do their own. In figure 3c, using 1999 nests on the 1999 image and other years gives a similar result. Thus, 1999 nests work as well. For both 1998 and 1999 images, using all nests produces the same pattern. Figure 3d shows a summation of results from using 1998, 1999, and all nests to map sparrow habitat. Again, none of the curves differs substantially from each other. These results indicate that the year of the nest does 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 predicting habitat in other years. To gain the maximum sample size we use all nests to map habitat in each year. This provides the opinions of the most sparrows' and thus predicts the most habitat.

Habitat analysis

To estimate the total potential habitat, we combine habitat classifications for all years. Looking at the six populations together, we estimate 459 km² held potential habitat in one or more years. Among the populations, A and B have the most potential habitat with 138 km² (30% of the total) and 116 km² (25%) respectively. Population E is third with 82 km² (18%), and C, D, and F have 31 km² (7%), 54 km² (12%) and 38 km² (8%) respectively.

Not all these areas will be suitable habitat each year. In any given year, floods, fires, and other environmental factors reduce the potential habitat, leaving a subset that is currently suitable. Looking at the average amount of this suitable habitat reveals a different pattern than looking at only potential habitat. Overall, the habitat suitable for the birds each year averages 240 km² (52%). Population A averages only 38 km² (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, averages just 20 km² (37%). Populations B and E are relatively constant and have the highest average amount of habitat with 85 km² (73%) and 54 (66%) respectively. Populations C and F average 19 km² (61%) and 23 km² (61%) respectively.

How much of this suitable habitat do the birds occupy?

An important pattern emerges from figure 4. Populations with large year-to-year fluctuations in habitat support fewer birds. After a flood or fire reduces the habitat and then the habitat recovers, it takes time for sparrows to disperse and fully occupy it. Consequently, the more variable the habitat, the less efficiently

sparrows are able to occupy it.

Figure 4 – Area (km^2) occupied by sparrows (columns) and area of suitable habitat (lines). We calculate the occupied area by multiplying the number of birds counted in the survey (table 1) by 8 to estimate the total number of breeding territories, equivalent to breeding males. Each territory is 2 ha or .02 km^2 . The y-axis is a logarithmic scale. 'NS' means there was no survey and 'INC' means the survey was incomplete.

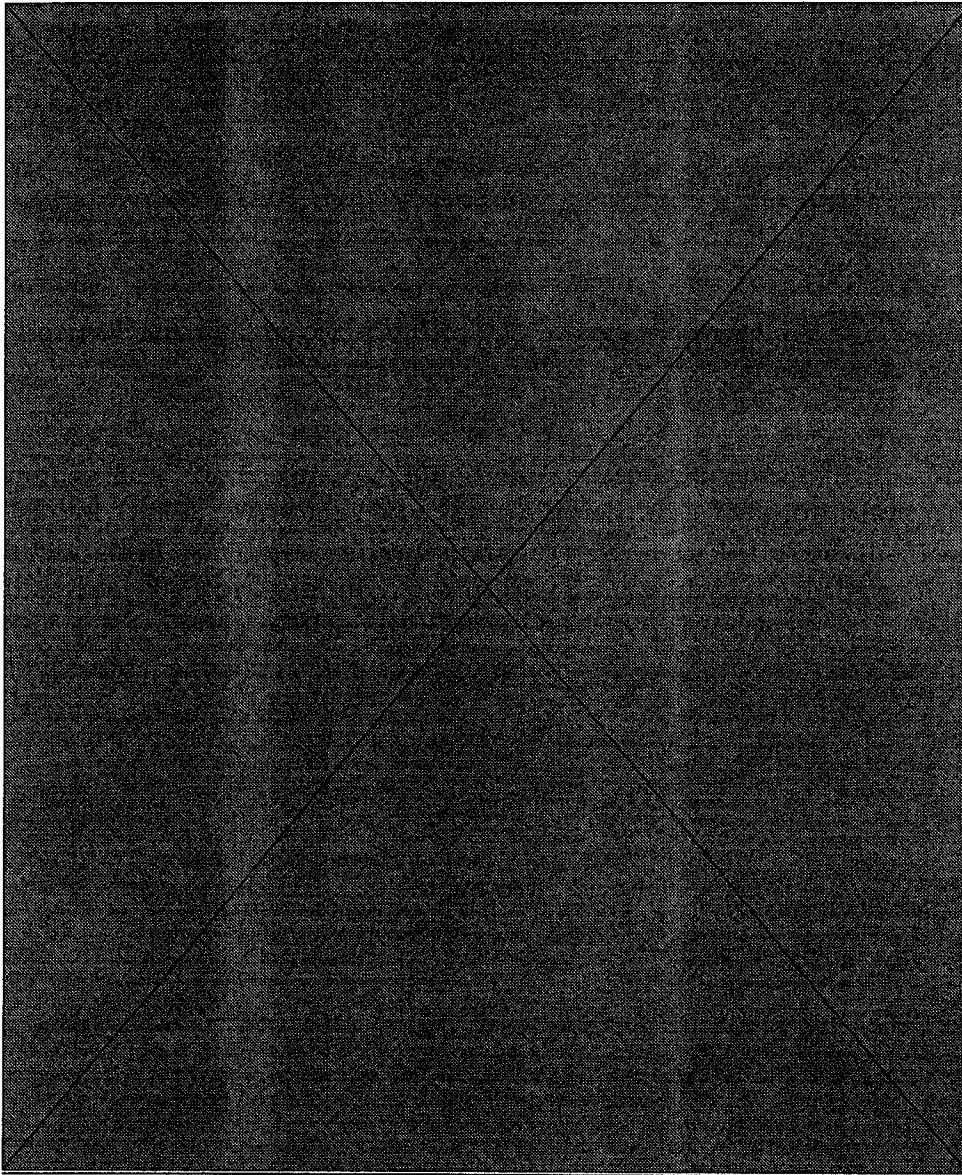


Figure 4 shows these predicted amounts of suitable habitat and their variation

from year to year. It also shows the estimates of the area occupied by sparrows. To calculate these numbers, we take the number of birds heard on the survey in each population (table 1), multiply by eight territories (for the survey counts only one territory in eight — see above) and then by 2 ha per territory, the average size of a territory. For example, in 1992, we counted 146 birds in population A, and estimate the population size as $146 \times 8 = 1168$ territories, that should occupy $2336 \text{ ha} = 23.36 \text{ km}^2$. The predicted suitable habitat for that population in that year was 82 km^2 .

Population A has the largest fluctuations in habitat (figure 4). 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, measurements at the NP205 hydrological monitoring station, located in population A, indicate a lower water level than in 1993. As a result, the habitat rebounds to 58 km^2 , 71% of pre-flood levels. However, most of this habitat was again flooded soon after the image date and sparrow breeding again failed (Nott et al. 1998). The occupied area stayed extremely low at less than 1 km^2 . The 1995 flood reduced the habitat to just 9 km^2 .

In 1996, the water level at NP205 when the 1996 image was taken was $< 4 \text{ cm}$ higher than when the 1994 was taken. 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 dead periphyton covered much of what had been sparrow habitat.

In the following years, the water remained low and a slow recovery of sparrow habitat ensued. This suggests that 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 showed little sign of recovery with occupancy in 1999 of only 4 km^2 of the 60 km^2 available. There is a lag time between habitat recovery and population increases.

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

Population C has a constant amount of habitat except for a decline in 1999. In 1981, this population had 4 km^2 of occupied habitat, but between then and 1992, this dropped to $< 1 \text{ km}^2$. Between 1996 and 1999, the population increased, but decreasing habitat in 1999 may impede further recovery.

Suitable habitat in population D declined from 30 km^2 in 1992 to 3 km^2 in 1993

because of flooding and then steadily recovered until 1996. Since then, the amount habitat has been relatively constant, but the spatial pattern varied. This was most evident in 1999 when the central habitat disappeared and habitat expands around the edges. This population never has shown a high occupancy of habitat, possibly due to variability in the amount of habitat and its location. Only in 1992 and 1999 did the occupancy exceed 1 km².

Population E suffered a small decrease in habitat from the 1993 flood, and the 1995 flood caused a decline from 68 km² in 1994 to 34 km² in 1995. The occupied area stayed relatively low from 1992 to 1996, ranging from 2 to 6 km². This could be due to the effects of flooding in 1993 and 1995. In 1998 and 1999, the occupied area increased to 9 and 8 km² respectively. This higher occupancy may result from the consistent level of habitat since 1996.

Population F appears to have a small, but constant amount of habitat. However, much of this is subject to high fire frequency and as a result, sparrows never occupy most of the habitat.

Conclusions

Water management decisions in southern Florida have resulted in the destruction of habitat of a federally protected species. Flooding during the natural dry seasons of 1993 and 1995 inundated the western population of the Cape Sable seaside sparrow in Everglades National Park. These floodwaters harmed the sparrow both directly and indirectly. First, the floodwaters directly prevented breeding by flooding nests (Curnutt et al. 1998). This direct effect resulted in an order of magnitude decrease in the western population, which was formerly the largest population. Second, successive years of unnatural flooding altered the habitat such that it was no longer suitable for sparrows. Yearly mapping of the habitat using Landsat Thematic Mapper imagery shows that large areas have yet to fully recover 4 years after flooding stopped. This habitat must recover before the population can. Indeed, the western population has yet to show a significant recovery.

Based on the Sweet Home versus Babbitt case, this destruction of habitat constitutes a "take" under the Endangered Species Act. Using satellite imagery, we are able to draw a direct link between this destruction of habitat and the actions of water managers, specifically the opening of the S-12 control structures during the normal dry season. Moreover, we have a methodology for monitoring changes in habitat and quickly evaluating the consequences of management decisions.

Such a tool has potential uses beyond this single species. Ecologists have long struggled with how to precisely map habitats over large areas and quantitatively measure changes. Satellite image analysis provides one answer to this complex

question. With the decreasing cost of computer hardware and satellite imagery, we expect more scientists and government agencies to adopt such an approach in their own work.

Appendix I Error Analysis

The satellite imagery based predictions and the survey results need not always agree, in which case, there is an error. With errors of omission, we encounter birds, but the model fails to predict sufficient habitat. In errors of commission, the model predicts sufficient habitat, but the survey finds no birds.

Figure 3a illustrates the location of the errors on a graph of sparrow presence verses amount of habitat. It suggest we place a threshold, below which we deem there to be insufficient habitat to support a territory and above which birds should be present. Scaled to the area within 200m of the survey point the minimum threshold we might use is 16% (2.0 ha), the area needed for a single breeding territory.

Of the 4645 survey points over 8 years, 663 have held one or more birds. The model successfully predicts that 499 (75%) should hold birds. Some 41 of these 164 errors come from a single population (A) in a single year 1992, a point to which we shall return.

Of the 3982 survey points without sparrows, the model successfully predicts 2484 (62%), should not hold sparrows. There are 1398 errors of commission.

Of course, some of these commission errors may be sites where birds are present, but not detected on the survey. We know from studies presented in the next chapter that birds were likely present at 34 sites in addition to the 165 sites at which they were actually detected in the year 2000 census (see page 103). Scaling this proportion to the previous years suggests that birds should have been present at 800 sites $[= (199/165) * 663]$ 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 without them is 65% accurate.

Even with this correction, this is a substantially smaller percentage than for the prediction of where birds should be. Simply, birds are more often missing from where we think they should be, than present where we think they should not be. The purpose of this Appendix is to ask why there are errors in the predictions and why the difference in the percentages of omission and commission errors.

Error causes

Both omission and commission errors have four potential causes: bird errors, model errors, image errors, and survey errors:

- (2) Birds can make mistakes in their choice of territories, placing them in inappropriate places or not placing them in suitable ones.
- The model can incorrectly predict the habitat.

- Surveyors can make errors when surveying the sparrow population missing birds that are there or recording birds by mistake when they are not.
- The satellite image may not capture an important event affecting the habitat.

We call all these "errors," but they are clearly a mixed bag. The birds' "mistakes," for example, may reflect the limited choices available to them or known to them. An individual bird's view of the available habitat is much smaller than one the satellite sees from hundreds of kilometers out in space. And we have already introduced the survey "errors" by noting that birds are not encountered at sites where they are present. Yet in the next chapter, we demonstrate that these absences are exactly what we expect by chance, given the uncertainties of knowing exactly where the helicopter lands and where in their territories the individual birds are during the survey period. Then there could be unequivocal errors when, for instance, an observer mistakes the very distant song of a red-winged blackbird for this sparrow's song.

So rather than call these categories "bird choices," "expected absences" and "observer errors" we lump them into the catch-all class of "errors." But we must now try to assess their relative frequency and to do this requires a field guide to their distinguishing characteristics.

Omission errors: where the model omits birds from places where they actually occur

Bird errors. Birds can 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 sparrows rarely move more than a few hundred meters between years (Lockwood et al. 1997). 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.

The spatial error is where birds in saturated, productive habitat force other birds into adjacent marginal habitat. A diagnostic of this error is the presence of birds in predicted unsuitable habitat with birds present in the adjacent predicted suitable habitat. Marginal areas will also have a history of fewer birds than the predicted productive areas.

Model errors. Sometimes the model incorrectly predicts that there should be no birds, yet the survey does find birds. Three sets of criteria distinguish these from bird omission errors. (1) The model consistently identifies the area as suitable habitat in the past, we regularly find birds in the past and future, and we see no evidence of fires or floods changing the habitat. (2) Areas surrounded by suitable habitat and consistently having birds are likely model errors. (3) The model eliminates the area because the model identifies it as having too many

bushes, but it consistently has birds.

Survey errors. Survey errors are unlikely in our work. Surveyors only count sparrows if they sing and they are very familiar with the sparrow's song from years of experience and from experience on the intensive plots. In addition, no other bird in the prairie has a similar song. However, very distant songs of red-winged blackbirds and meadowlarks can sometimes fool the inexperienced and we give not guarantees that others who count the sparrows for other projects do not make mistakes.

Image errors. Cloud-free satellite imagery might not always be available during the helicopter survey. So, we remove any survey point that is cloudy in the satellite image before our analyzes. Habitat suitable during the image dates may become unsuitable before the survey, or vice versa, and an error can result. If an area is underwater on the image date, the model will not classify it as suitable. However, if the water recedes before the survey it may become suitable and we will misclassify it. Evidence of fire or flood between the survey date and the image date identifies these errors. All of the images in this study are during or within three weeks of the survey dates. We find no image errors.

Commission errors: where the model predicts birds, but birds are absent

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 appear in one year, and then become occupied by sparrows in future years, confirm this type of bird error. So, too, do areas that had habitat and sparrows in the past, have predicted suitable now, but the birds do not occupy them.

Model errors. In commission model errors, the model predicts there should be birds, but the survey finds none. The absence of sparrows at a survey point and in most adjacent survey points in every year distinguishes these from bird commission errors. We are likely to overestimate model commission errors simply because the sparrow population has only been monitored for a short period.

Survey errors. We have briefly explored these errors above by referring to the detailed discussion in the next chapter. That chapter argues that we should expect there to be a fraction of sites that hold birds but where we do not encounter them. The principal explanation is that the birds move about their territories and so will sometimes be beyond detection distance.

Image errors. If the habitat is suitable during the image dates, but fire or drought

changes it to unsuitable before the survey, we will misclassify it. Evidence of fire or flood between the survey date and the image date identifies these errors. We find no image errors.

Results of Error Analysis

The 164 omission errors

Table 4 lists the classification of errors by year and by type, noting in which population the greatest number occurs.

Temporal bird omission errors have their highest proportions in the flood years of 1993 and 1995 (table 4) and are primarily in population A, 56 of 96. Population B has the second highest absolute number (18) but very few, relative to the number of survey points with birds. Population D has 10 and is the second highest relatively.

Flooding directly causes the high error rates in 1993 and 1995. Most of the errors are in population A, 19 of 25 and 10 of 16 respectively. In both years, opening of the S-12 flood control structures during the breeding season floods potential habitat in the western portion of the park. In population D, flooding causes the 4 errors in 1993. The 5 errors in 1999 are a result of changes in habitat location, possibly due to dry weather that year.

Table 4 – The three types of omission errors each year and the corresponding number of points where birds were encountered.

	bird errors (temporal)	bird errors (spatial)	model errors	total	points with birds
1992	21 (16 in A)	5	42 (41 in A)	68 (59 in A)	164
1993	25 (19 in A)	12	2	39	99
1994	0	4	1	5	60
1995	16 (10 in A)	6	1	23	48
1996	11	3	0	14	75
1998	2	11	0	13	108
1999	21	6	3	30	109
Total	96 (56 in A)	47 (32 in B)	49 (41 in A)	192*	663

* In an early version of this analysis we had a different criterion for the threshold between omission and commission (it corresponded to our requiring that there be 3 hectares of suitable habitat before we predicted birds to be present. The

numbers in this table will be re-calculated in the next revision. However, the general conclusions are unlikely to be changed.

Spatial bird omission errors are almost entirely in populations B and E, 32 and 11 respectively from a total of 47. This is not surprising as these two populations have had most of the birds since 1992 (table 1). We find these bird errors typically along the southern and western edge of population B, and the northern portion of population E. These areas are where there is a sharp division from the dry prairies to wetter slough habitats dominated by sawgrass.

Model omission errors only in populations A and B. Most of these errors, 41 of 49, are in population A in 1992, and most of them are in the western half of the population. The 1981 survey also found birds in this western area. Flooding in 1993 causes these birds to disappear. The most likely explanation for birds being present, but the model failing to classify the habitat, is that the habitat is genuinely different from what we find after the floods. The vegetation records from the 1992 survey support this conclusion. In 1992, 41 (72%) of the error points in population A have sparse sawgrass (*Cladium jamaicensis*) as their primary vegetation. In all of the intensive study sites, muhly grass (*Muhlenbergia filipes*) dominates or it is a mixed prairie with no dominant species. Thus, we can get no spectral signature for the sparse sawgrass habitat type.

If we compare the points that have birds and sparse sawgrass in 1992 to their vegetation in 1999, we find that this area has changed from its pre-flood condition. *C. jamaicensis* now dominates only 18 of the sites and many of those have long hydroperiod species such as *Eleocharis cellulosa*. *E. cellulosa* is the dominant species in 12 other sites. In addition, the average percent ground cover increases from 62.8% to 87.8% ($p < 0.01$). This suggests that flooding has changed the overall vegetation to the detriment of the sparrow. Moreover, the birds we do see in later years do not occur in the western area but only in the eastern half where the model does predict habitat.

Population B has eight errors, but also has 55% of the total survey points with birds. It is also the best-studied population because it has many birds and easy access. Thus, it is the easiest place to identify model errors.

The 1398 commission errors

Table 5 shows the two types of commission errors by year, noting the populations in which the greatest numbers of errors occur.

Bird commission errors are relatively low in the flood years of 1993 and 1995 (table 5). These floods primarily reduce suitable habitat (table 2), and thus bird commission errors, in populations A and D. The highest proportions of bird

commission errors are in dry years after the floods recede, 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 has 0 and 1 errors respectively, indicating an absence of open habitat. In 1994, there is a significant recovery of habitat, but after the 1995 flood, the habitat recovery is much slower. Thereafter, a steady upward trend is evident, going from 1 survey point in 1995 to 46 in 1999.

Table 5 – The two types of commission errors each year and the corresponding number of points where birds were not encountered.

	bird	model	Total	points without birds
1992	126 (37 in B, 36 in E)	135 (88 in A)	261	654
1993	122 (48 in B)	71 (22 in A)	193	754
1994	85 (49 in B)	52 (37 in A)	137	425
1995	71 (20 in D)	54 (19 in F)	125	688
1996	133 (54 in B)	54 (17 in E)	187	403
1998	144 (46 in B)	59 ((20 in F)	203	510
1999	132 ((46 in A)	79 (34 in A, 20 in F)	211	549
Total	813	504 (215 in A, 102 in E)	1317*	3983

* In an early version of this analysis we had a different criterion for the threshold between omission and commission (it corresponded to our requiring that there be 3 hectares of suitable habitat before we predicted birds to be present. The numbers in this table will be re-calculated in the next revision. However, the general conclusions are unlikely to be changed.

The 1993 flood causes a large decrease in open habitat in population D, going from 36 bird commission errors to 6. The 1995 flood effects are less severe with 20 error points, close to the average. From the satellite images, it is clear that while the flood in 1995 was more extensive around population A than the 1993 flood, it was less extensive in the region around population D. This may be due to less pumping of water into Taylor Slough, which flows into population D.

The other populations have a higher elevation, protecting them from flood damage. The low number of bird commission errors in populations B and C in 1995 is due to clouds obscuring the image. The decline in population B from 1996 to 1999 is due to fewer survey points (table 1) and also in 1999 to clouds and smoke.

Model commission errors show both temporal and spatial influences. They are higher in 1992 both in raw number (135) and proportionally (0.21) than any other year. This high error rate is entirely accountable for by population A. In 1992, population A has 88 commission errors whereas the average for other years is only 21.2. 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 they potentially had suitable habitat because of the 1993 and 1995 floods. If the model predicts an area suitable only in 1992 and it has 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 be good habitat and had birds for the last 10 years, and by chance had no birds in 1992. However, all we know is that it has no birds in 1992, and thus it is impossible to rule out model error.

The second explanation is that the sparrows were using the sparse sawgrass habitat in the west rather than the muhly 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 occupy most of the sparse sawgrass habitat before they expanded into the muhly and mixed prairie habitats.

Population E has a high number of model errors concentrated in the center region. The model consistently finds the area suitable but it never has sparrows. However, in 1981 sparrows from the main population did extend farther southwest into this habitat than in 1992 and later years. In addition, a small population of sparrows occurs near the southwestern end of this "mis-classified" 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 and the sparrow population was likely already stressed and suffering higher than average mortality. Then in 1993, flooding eliminates the southwestern sub-population. The combination of the 1989 fire and 1993 flood may have left population E with only a small northern sub-population. Without survey data during this period, it is impossible to confirm this scenario and thus rule out model errors. So this area may be suitable, but sparrows have yet to re-colonize it.

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

Chapter 5.

The 2000 Cape Sable sparrow census

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Introduction

Each year, we survey the Cape Sable sparrow by landing at several hundred survey points then counting the number of birds heard and seen. Previous papers describe the methods in detail and we do not intend to repeat them here. This chapter has two objectives. The first is to present the year 2000 count and the estimated population sizes in the six sub-populations. The second is to respond to the concerns of the AOU committee's report that urged us to evaluate the accuracy of the survey. We did this in two ways. Although our analyses are still preliminary, we conclude that the survey methods are remarkably — and encouragingly — close to what we would expect if the methods were unbiased efficient estimators of the true population size.

The counts

Two surveys were completed in 1999 but one was much later than the other. (The AOU's recommendations were not received in time to do otherwise.) The later survey had fewer birds in sub-populations where reproduction is poor (compatible with the suggestion that birds had abandoned territories after breeding). In the more productive sub-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).

Two surveys were completed in 2000, both within April and May across much the same range of dates, with two different survey crews, but using identical methods. The overall counts were:

Table 1: Actual counts of sparrows in each year in each population

Counts	1981	1992	1993	1994	1995	1996	1997	1998	1999	2000 1st	2000 2nd
A	156	146	24	5	14	24	17	11	25	28	25
B	147	199	154	135	130	118	177	113	128	114	153
C	27	3	0 NS		0	3	3	5	9	7	4
D	25	7	6 NS		0	5	3	3	11	4	1
E	42	37	20 7/inc		22	13	52	57	48	65	44
F	7 0/inc		0 NS		0 1/inc		1	1	1	0	7
Total	404	392	204	147	166	164	253	190	222	218	234

"inc" means incomplete, NS means not surveyed.

Using the correction factor of x 16 to convert these to population estimates that we have used in previous years, we obtain the following estimates:

Table 2: Estimate numbers of sparrows in each year in each population

Population estimates	1981	1992	1993	1994	1995	1996	1997	1998	1999	2000 1st	2000 2nd
A	2496	2336	384	80	224	384	272	176	400	448	400
B	2352	3184	2464	2160	2080	1888	2832	1808	2048	1824	2448
C	432	48	0		0	48	48	80	144	112	64
D	400	112	96		0	80	48	48	176	64	16
E	672	592	320		352	208	832	912	768	1040	704
F	112		0		0		16	16	16	0	112
Total	6464	6272	3264	2352	2656	2624	4048	3040	3552	3488	3744

Not only are the 2000 totals remarkably similar (3488, 3744) but so too are the individual numbers within each sub-population. This implied question about consistency is something to which we shall return.

First, some comments about the population sizes.

Population A has continued to remain at a near-constant level for the last three years. While that level is still less than 20% of its numbers prior to the massive dry-season water releases across the S12s that so severely jeopardized its survival, there is some good news. High water levels threatened to reduce its numbers yet further early in 2000. The efforts to prevent dry season flooding likely saved this population. Simply, it could have been a lot worse.

Populations B and E remain the two most abundant populations, with numbers little changed from previous years. C, D, and F hold few birds. Interestingly, F had a count (7 birds) on the second survey that matched the highest number ever encountered here. The sample sizes are too few to draw any statistical conclusions.

In sum, 2000 was a year much like the last two.

We feel that the AOU committee's concerns about the survey can be distilled into two questions: How repeatable (or consistent) is the survey? And how accurate are the population estimates based on the correction factor of counts $\times 16$?

How repeatable is the survey?

The experience of 1999 illustrates the concern: the numbers on one count were quite different from those of 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. However, were there 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.

Table 3: 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			

There are very many reasons we should *not* expect the surveys to be replicates — and so, by inference, be concerned about the accuracy of the survey results in general. Different observers, variation in the birds' propensity to call across the breeding season, and so on.

Are the data presented above inconsistent with the each survey being a true replicate? Should one be concerned that (for instance) single birds were seen 28 sites on the first survey yet none at the same sites 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 GPS prevent that. (The GPS signal is scrambled to limit its accuracy.) Even if the signal were not scrambled, the birds move within their territories. These are roughly of 2 hectares; at its most compact, a territory might be a circle of 80 meters radius. The correction factor of 16 assumes that all birds within 200 meters will be counted. Yet, a bird could be a mere 41 meters away on one count and at the other end of its territory, 201 meters away — and so out of range — on the next.

This suggests a statistical model for the distribution of sampling outcomes that we have proposed before. It is one for which there is a long history in statistics. If the true density of territories is such that there are λ per sampling area across the entire survey arena, then the distribution of counts of territories will have outcomes 0, 1, 2, ... described by a Poisson distribution with mean λ . For example, suppose the true mean density were to be 1, then there is a 37% chance that no birds will be encountered, a 37% chance that 1 bird will be encountered, then 18% for two, 6% for three, 2% for four.

Previously, we have applied this statistical model to calculate confidence intervals on the single survey estimates. The standard deviation of Poisson outcomes is also λ , and the standard error follows simply.

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 $(0.37 * 0.37 = 0.14)$, 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. And 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 the figure below, we plot the log frequency of those mean values.

The shape — a logarithmic reduction in frequency with increasing abundance is typical of many populations.

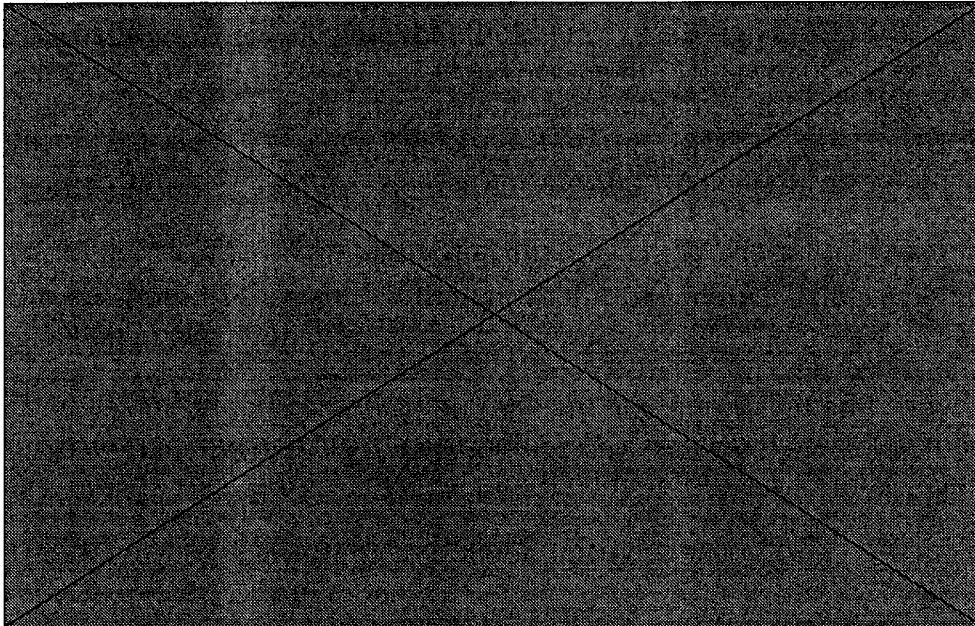


Figure 1:
the frequency of average values of sparrows encountered per survey site (Note the log scale for the frequency)

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 $I = 0, 1, 2, \dots$ and $J = 0, 1, 2, \dots$ when the true density is 0.5, 1.0, ... 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 earlier example.) So we correct for that undercount, by multiplying the frequencies by the constant required to match the observed and expected counts.

This matrix sums to ~199 individuals (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.)

Table 4. 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
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One way to summary 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.

Table 5: 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. The color-coding matches table 4.

Difference	expected	observed
0	30.14	22
1	78.73	84
2	34.85	40
>3	21.64	19

The differences between observed and expected are not significant (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.

How complete is the survey?

In the addendum that follows, Professor Lockwood presents the results of her teams efforts 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 her report contains justifies the decisions we have made in the past. We do not count birds into June, late in the morning, when the wind picks up, and when it is misty (the helicopter cannot land).

Amid the plethora of results she presents 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?

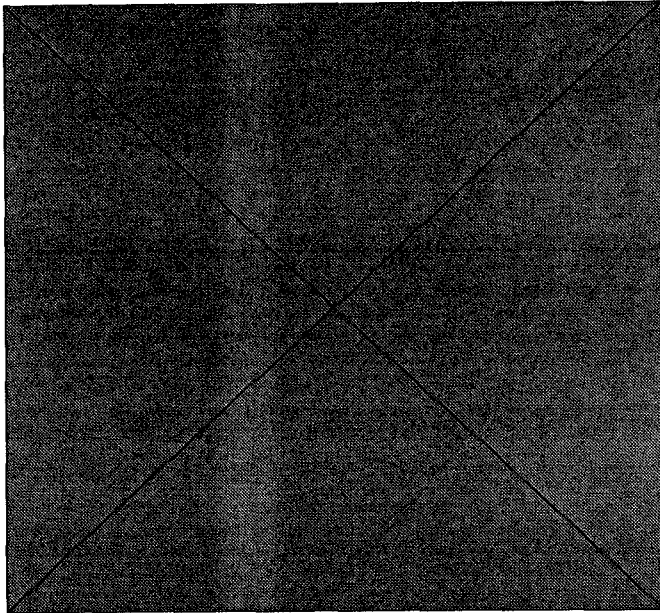
The answers are "no" — and "not that it would matter if the answer were 'yes.'"

The second answer is the easier to explain. Even if the counts were underestimates, none of the inferences we have drawn (and on which Biological Opinions are based) would be altered. The damage done by releasing massive flows of water over the S12s, for instance, reduced the population to a mere 10% of its pre-1993 level. That statement — and the consequences that follow from it — are not changed if we multiplied the actual bird counts by 16 (as we do) or the first number that came into your head multiplied by the square root of e .

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

Lest the niceties of probability density functions be lost on the reader, here is a geometric example.

Figure 2. An hypothetical example of territories (open circles) within a survey radius (stippled.) How many birds will be encountered on average? (Read the text for the answer.)



The small clear circles are territories (80 meter radius) and the larger, stippled circle is the 200 meter detection radius scale appropriately. These territories are packed unreasonably closely and we know that territories are not circular and so cannot be packed thus. But for an illustration, we ask: how many 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 (you guessed?) 63%.

The sarcastic reader will note only that this author clearly learned some tricks for teaching sampling theory during his 7 years on the Statistics Faculty at a major research university. But the example makes the point: an unbiased, efficient survey should detect birds only a fraction of the time and Professor Lockwood's 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 — it requires us to complete the GIS work presently underway. 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 true estimate of the sparrow's total numbers.

An Addendum

Detection probabilities and other results relevant to population estimation.

Julie L. Lockwood

Introduction

The American Ornithologist Union external peer review committee strongly recommended the estimation of sampling variances for the extensive survey results (AOU 1999). As part of this estimation, the review panel recommended calculation of detection probabilities. Detection probability, or the chance that a male sparrow will be recorded 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 estimate protocols to avoid inaccuracies in abundance calculations (Barker and Sauer 199X). In June 1999 we established a series of point count locations within our intensive study plots. Beginning in April of 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.

Since 1981 the abundance of the Cape Sable seaside sparrow has been estimated using an extensive 1km grid of point counts (Curnutt et al. 1998). These count locations are distributed over the known range of the sparrow. The count locations are accessed with the use of helicopters. The observer begins to count the number of sparrows heard singing, or sighted, over a seven-minute interval beginning after the helicopter noise subsides. Surveys are typically conducted from April to early June and occur between sunrise and 10:00am.

Kushlan and Bass (1982) calculated a correction factor of 16 for these point counts. This correction is intended to account for all sparrows present within a 1km² area, males and females. Thus, for every male heard singing it is assumed there are eight others within the 1km cell of that grid location and each of these males have one female mate (Curnutt et al. 1998, Kushlan and Bass 1982). These corrected counts are then summed to provide a range-wide estimate of sparrow abundance.

The correction factor of sixteen is based on the fraction of total area sampled (a) and detection probability (p), such that $ap = 1/16$ (AOU 1999). Below, we

directly calculate p , and variations in p , by conducting fixed-radius point counts within intensive study plots and then comparing these counts to the results from detailed territory mapping (see below for details). The mapping efforts represent the 'true' number of individuals within a 200m radius of the point count location. Once detection probability is calculated, a correction factor can be estimated under all conditions explored (e.g., wind speeds, density groups, and time of day).

Methods

We conducted fixed-radius point counts from 14 April to 17 July 2000. We located point count locations 400m apart within seven 600 X 800m plots. Six plots are within subpopulation B and one plot is within subpopulation E. Counts were made following the procedures described in Kushlan and Bass (1982) and Curnutt et al. (1998). All individuals heard singing, or sighted, were recorded for up to seven minutes 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 has qualitatively similar effects on resident males. When generally disturbed (i.e. when not defending a nest), males will tend to perch atop sawgrass seedheads and sing. We varied our start times across study plots such that all time frames between sunrise and 11:00am were covered. During each count we recorded the observer, visibility, water depth (cm) 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 1).

Table 1. 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 very tops of grasses were moving.
2	Calm wind such that entire stalks of grasses were moving.
3	Moderate wind such that leaves on trees in hammocks were moving.
4	Strong winds such that tree branches in hammocks were moving.

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 three hours. Observers located sparrows using spotting scopes or binoculars and the location of their territories were marked 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 Global Positioning System (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 within a 200m radius of each count location based on these maps.

The total number of marked territories within 200m of a point count station represents the 'true' number of sparrows. The number of individuals detected during each point count is then scaled by this value. This proportion is considered the detection probability. It is possible for the observer to over estimate the number of sparrows within the 200m radius detection zone (e.g., birds not resident within 200m 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 four nominal categories. The first category included start times between 6:00am and 7:00am, the second category included start times between 7:00am and 8:00am, and so on. A final category included all starts after 10:00am. We compared the mean detection probability between these four start times using ANOVA. Similarly, we compared mean detection probability between observers (seven), and months (four) using ANOVA. We looked for changes in detection probability with water level and wind speeds using simple linear regression and ANOVA. Water depth was measured from 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 200m 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.

Results

Seven individuals 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 200m 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 zero and 1.67. On 14 occasions ($14/254 = 5\%$) more birds were detected than were shown on territory maps. Over-estimates occurred throughout the season and start times with no noticeable pattern. On 11 (4%) occasions no birds were detected in areas that contained more than one mapped territory (i.e. a false negative occurred). The vast majority (95%) of errors in detection was under-estimates. Visibility very rarely fell below 200m, twice falling to 150m and once to 60m. Thus, during 99% of the counts it was possible to easily see birds within a 200m radius of the count location. Wind speeds varied between zero and four with a modal Beaufort score of one. The earliest start time was 6:48am and the latest was 10:14am. Most counts (84%) were made between 7:00am and 9:00am.

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

Detection probability varied significantly according to observer, time of season (i.e. month), time of day, sparrow density, and wind speeds. Detection probability ranged from 0.378 ($n=8$) for one observer to 0.683 ($n= 36$) for another. Mean detection probability was significantly different between observers (ANOVA $F = 2.57$, $df = 6$, $P = 0.02$). Time of season (month) also had a statistical influence on detection probability (ANOVA $F = 5.90$, $df = 3$, $P = 0.0007$). 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 10:00am produced the lowest mean detection probabilities (0.30, $n = 4$). Point counts that started at 9:00am and 8:00am 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 am (0.70, $n = 114$). These differences were statistically significant (ANOVA $F = 15.4$, $df = 3$, $P < 0.0001$). Detection probability and wind speed were negatively correlated ($F = 30.05$, $df = 2$, $P < 0.0001$). The correspondence of effects for wind speed and start time is not independent. Wind speed tends to increase as the morning wears on ($F = 43.80$, $df = 3$, $P = < 0.0001$).

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 ($t = 2.50$, $df = 1$, $P = 0.01$).

Discussion

The range of detection probabilities provided here should now be incorporated into an overall estimate of error in the extensive survey. Our results can also be used to increase the accuracy of these population estimates by decreasing detection error. Detection probability can be quite high depending on conditions. An early morning, low wind, count is often better than 60% accurate. 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 time periods before 9:00am and under wind conditions of a Beaufort scale of two or less. 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 9:00am. Thus, discretion in applying this recommendation is necessary, as it may be possible to conduct accurate counts late in the morning on some occasions.

Detection probabilities also tend to vary by observer. The individuals conducting these point counts varied from those with several years of experience to those with none. However, there was no evidence that experienced observers performed better than inexperienced observers. Cape Sable seaside sparrows are relatively easy to recognize in the field as they have a distinctive song and are typically the only sparrows or finches in the area (JLL, pers. obs.). Some variation from observer to observer is to be expected and likely co-varies with the sites or conditions in which the observers are most often confronted (e.g., high density sites).

We could find 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 site 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.

Because sparrows were absent in the western study population (i.e. the Shark

Valley plot) during the 2000 field season (see section II), we can not judge differences across the spatial extent of the sparrow's range. However, 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 pre-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 are present, they are likely to be counted. However, there also appears to be a saturation level beyond which observers have a difficult time distinguishing all resident males. Detection probability dropped to 0.49 in locations that held five or more territories. This leads to the slightly counterintuitive result that the extensive survey is likely to under-estimate the number of males within densely populated areas as compared to sparsely populated areas.

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 50m of the nest and can not be heard given the slightest wind. This is in sharp contrast to departure calls given by other marsh nesting birds (Greenberg, pers. com.). We find that counting females by listening for departure call is not practical in this context.