

1025
Bass

The 1997 Annual Report on the Cape Sable Seaside Sparrow

Overview

Our yearly reports have grown continuously as we accumulate more information on the Cape Sable sparrow. This year's report is a set of several documents that we label "chapters" for convenience. For the first time, four of these are manuscripts that have been (or we hope soon will be) accepted for publication in major international journals. Other chapters are technical, working drafts of material that we will work up for publication at a later date. In some cases, the text is obviously already in journal format and we expect to submit the work soon. In other cases, large gaps exist that reflect our need to collect more data or to further analyze those we have.

We have written these chapters for different audiences. They differ in style and, perplexingly, even in the name we use for the bird. (One journal requires us to call the bird, the Cape Sable Seaside-Sparrow — note capitals and hyphen — a requirement that we do not adopt elsewhere.) The different audiences mean that papers repeat some material. Moreover, they require different levels of numerical precision. For example, a value of 46% might appear as "about half" in another chapter.

The reader should also understand that, by request, we produce this report in late summer and not at the end of the calendar year. This gives interested parties in Florida and elsewhere a chance to appreciate and digest our conclusions well before management decisions need to be made the following year. This constraint also means that we must complete these chapters within less than 8 weeks of ending our field season. When chapters are marked "draft" we mean just that. We solicit and appreciate comments.

Please remember that as our knowledge increases we sometimes change our opinion of the relative importance of the factors that affect the sparrow. This year's report replaces previous ones. Where it conflicts with previous reports, this is the one that should be taken as our latest word. For example: in our 1994 report, we thought that Hurricane Andrew may have caused the precipitous decline in the sparrow's numbers west of Shark River Slough. We now think that this storm was, at worst, only a minor contributor.

New readers

Anyone reading these material for the first time should start with chapters 1, 2, and 3 in that order. These papers cover our work up to the end of the 1996 field season. We have submitted chapters 1 and 2 as a pair of papers we hope the journal will publish back-to-back. They complement each other and there is minimal overlap between them. They deal with the history of the sparrow, our surveys of its numbers, its decline, and four factors — chance, catastrophe, fire, and flood — that have contributed to this decline.

Chapter 3 has been accepted for publication in the *Wilson Bulletin* and it covers the bird's breeding biology. There is some overlap in the introduction of this paper and material that appears earlier.

Chapter 4 is an addendum to chapter 3 that covers the breeding season of 1997. We have become ever more adept at finding nests — and skilled at recruiting individuals who can find nests. The 1997 season greatly expanded our knowledge of the bird's nesting ecology. At the time of writing (August 1997) this report is still very preliminary.

Chapter 5 reports on our work during the non-breeding season. I had asked Ms. Balent and her team to prepare the work for publication, but to include supplemental, supporting materials that would excised by a journal before acceptance. We expect to submit a suitably shortened version of this manuscript in the near future.

Chapter 6 is a paper peripheral to our main efforts. A special symposium of the Zoological Society of London, held in London in September 1996 asked us to consider the interface between ecosystem management and the protection of single endangered species. The work on the sparrow relies heavily on material published in chapters 1, 2, and 3. We include it here for completeness and to share with those interested our views on the wide implications of our research.

The remaining chapters are working documents.

Chapter 7 updates the annual survey.

Chapter 8 reports on the bird's annual survivorship.

Chapter 9 covers a new initiative for this year. It combines satellite imagery and detailed on-the-ground-surveys in the hope of producing a more detailed understand of the bird's habitat requirements. (I will write more about this below.)

For previous readers: highlights of this year's report

What are the new features that readers of previous reports should expect?

Chapter 1 shows that the absences of the birds from the eastern portions of its range are likely to be driven by the high incidence of fires there. These absences are too long to be expected by chance alone, even for sparrow populations (which are highly variable from year-to-year) and peripheral populations (which are even more variable than core populations.)

Chapter 2 confirms the high water levels west of Shark River Slough as the cause of the population's decline there. It shows that managed flows over the S12 structures contribute sufficient water depth during the breeding season to be responsible for the birds' failure to breed.

Chapter 3 defines the length of the nesting season and shows how high water levels in June terminate nesting by greatly increasing nest predation.

Chapter 4 extends the nesting data for 1996 and shows that high water levels at the start of the nesting season also prevent successful nesting. There are differences between sites in nesting success that correlate with water levels.

Chapter 5 finds that birds remain on the sites throughout the year, moving only short distances, and selecting the taller clumps of sawgrass.

Chapter 6 argues that though Everglades National Park and associated areas is one of the largest protected regions in the Americas, it is still too small to be managed by benign neglect. Even at this large size, its constituent species are vulnerable to the vagaries that beset all small populations and processes outside the park drive the key variables of fire and flood.

Chapter 7 finds that the population west of Shark River Slough has not yet recovered in numbers from its losses in 1993.

Chapter 8 presents maximum likelihood estimators of the sparrow's survival. About half the breeding adults survive from one year to the next. There are some tentative indications that survivorship is different from one year to the next and different between sites. Banding efforts in 1997 were much more successful than in previous years. Moreover, in 1997 we banded many more young in the nest. (Nesting observations took precedence in previous years.) These young dispersed greater distances than adults in the months after leaving their nests.

Chapter 9 documents an intensive plant survey designed to uncover the exact habitat choices the birds make. It shows the extent of our surveys, but detailed analyses are not yet available. Satellite images of the plots in all recent years are in hand and we will map banded bird locations, nest locations, and plant data onto these images in the months to come.

Stuart L. Pimm
August 1997

POPULATION DYNAMICS OF THE ENDANGERED CAPE SABLE SEASIDE
SPARROW

John L. Curnutt¹, Audrey L. Mayer¹, Thomas M. Brooks¹, Lisa Manne¹, Oron L. Bass, Jr.², D. Martin Fleming^{3*}, and Stuart L. Pimm^{1*}.

¹ Department of Ecology and Evolutionary Biology, University of Tennessee,
Knoxville, TN 37996-1610, USA;

² South Florida Natural Resources Center, Everglades National Park, 40001
State Road 9336, Homestead, FL 33034-6733, USA

³ Biological Resources Division, USGS, Everglades National Park, Homestead,
FL 33034

* To whom all correspondence should be sent. E-mail: stuartpimm@aol.com

Running head: Cape Sable seaside sparrow population dynamics

Abstract: The Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) has disappeared from its only known breeding areas episodically since its discovery early this century. To determine the complete range and population size of this elusive sparrow, we conducted systematic surveys across its range in the southern Everglades in 1981 and from 1992 to 1996. The sparrow's range is fragmented into six sub-populations, two constantly occupied *core* areas east and west of Shark River Slough and four smaller, intermittently occupied, *peripheral* areas. The sparrow population decreased by 58% between 1992 and 1995, with the near extinction of the western half of the population. The results of the 1996 extensive survey show only a modest increase of 9% from 1995 to 1996.

We review the history of the Cape Sable sparrow and its habitat in this century. We then analyze the effects of chance, hurricanes, and fires on the sparrow's range and numbers. These factors represent the most important natural influences on the persistence of this Endangered sub-species. A fourth factor, hydrology, is largely artificially controlled and is the subject of a companion paper.

Other similar grassland sparrows have populations that vary considerably from year to year. Yet the decline in the western sub-population and the local extinction of some of the peripheral populations cannot be explained by mere demographic vagaries. Hurricanes can extinguish local populations directly and indirectly by causing major changes in vegetation. Hurricane Andrew

passed over the western population and two peripheral populations prior to the particularly poor year of 1993. However, the extended patterns of population change are not consistent with what we expect were the hurricane the most important mechanism.

Fire helps to maintain suitable sparrow habitat, but too frequent fires prevent successful breeding. A previous study suggested that sparrows abandoned areas that had not burned for more than five years. In contrast, we found that sparrows increase in abundance in the absence of fire for at least ten years following fire.

Global extinction remains a distinct possibility for this species because it inhabits such a restricted area. However, under natural conditions, the sparrow population might be expected to exhibit a high level of resiliency that could insure its long-term survival—provided key habitat is preserved. Even in as large a national park as the Everglades, preserving key habitats requires constant vigilance.

Introduction

The Endangered Species Act of 1973 calls for the protection of "species and the ecosystems on which they depend" (National Research Council 1995). The Cape Sable seaside sparrow, (*Ammodramus maritimus mirabilis*), is found entirely within the wetland ecosystems of southern Florida. Moreover, its range falls within the Everglades National Park and the Big Cypress National Preserve, two large areas managed for their biological resources. We will show that despite its protected status within protected ecosystems, the species' future is not secure. Its population is buffeted by a combination of fire, flood, chance, and catastrophe. The first two factors are largely or partly under human control, the last two are natural ones that, nonetheless, might still doom the population in the long-term. We demonstrate that even species within extensive protected ecosystems require our constant vigilance. Moreover, such vigilance informs the management of those ecosystems across a wide landscape.

The Everglades system has undergone extreme anthropogenic modification for more than half a century. Massive hydrologic projects, urbanization, agriculture, introduction of exotic species, and environmental contaminants have all had profound effects on the system and on the species that live in it (Robertson and Frederick 1994). Populations of many species have declined, some to dangerously low levels, and three pineland bird species have suffered local extinctions within the boundaries of Everglades National Park. The

Cape Sable seaside sparrow is in decline. It inhabits marl prairies, which were once abundant throughout southern Florida, but are now greatly reduced (Davis et al. 1994).

In the first section, "History," we review the history of this landscape and of the sparrow. The sparrow was discovered only in this century and, on more than one occasion, disappeared from its only known habitats. Its elusive behavior and sporadic distribution required a large-scale survey to determine its range and numbers. In 1981, Bass and Kushlan (1982) conducted an extensive survey to delimit the sparrow's range. In 1992, we resurrected this survey and have since repeated it annually. The sparrow occurs in six sub-populations, four ephemeral or *peripheral* populations and two persistent *core* populations, one of each side of the main drainage of Shark River Slough. The western core declined by 91% in this period; most of the decline was between 1992 and 1993. These and other details of the sparrow's numbers form the second part of this paper, "The extensive survey".

The next sections of this paper, "Chance," "Hurricanes," and "Fire" explore three factors that affect sparrow numbers:

- Demography and chance local extinction: the highest number of sparrows recorded at any of the four peripheral populations was under 700 individuals. Three of these populations suffered local extinctions between 1992 and 1996. Are these extinction events to be expected for such small populations?

- **Hurricanes:** The Everglades ecosystem has been directly affected by over 80 tropical storms in the last century (Duever et al. 1994). In 1992, Hurricane Andrew provided us with the rare opportunity to compare sparrow data from before and after the event and so to assess the storm's impact.
- **Fire:** Fires burn Everglades prairies regularly (Gunderson and Snyder 1994). We examine the effects of fire frequency and fire season on the distribution and dynamics of the sparrow population. How do sparrow populations respond to fires?

We leave the complex story of managed water levels and their consequences to the sparrow to a companion paper (Nott et al. 1998).

History

The landscape

The pre-drainage Everglades system was inundated for longer periods and over a much greater spatial scale than it is today (Fennema et al. 1994). Then, as now, the primary drainage of overland flow in the southern Everglades was Shark River Slough (Fig. 1). In the pre-drainage system, overland flow occurred across a broader expanse than at present. To the west of Shark River Slough, lay the higher ground of the Big Cypress and, to the east, the Atlantic coastal ridge. Expanses of marl prairie lay between the main drainage of Shark River Slough and these two modest ridges. These prairies are inundated on average from 3 to 7 months per year (Olmsted et al. 1980). With

over 100 plant species, this is the most floristically diverse community in the Everglades (Olmsted and Loope 1984). Historically, there were much greater expanses of marl prairie than at present (Davis 1943). These prairies are the particular ecosystem on which the Cape Sable sparrow depends.

Drainage and development brought major changes in the vegetation and hydrology of the southern Everglades. Currently, nearly all overland flow in the Shark River Slough drainage originates from the four S-12 gated spillways at the northern boundary of Everglades National Park (Fig. 1, Fennema et al. 1994). The east-west distribution of these structures covers about half of the pre-drainage expanse of Shark River Slough. In the past, most overland flow occurred toward the eastern edge of Shark River Slough. The S-12 structures, however, are on the western edge. This artificial hydrology has had the greatest effect on the marl prairies. These prairies naturally remained dry for much of the year. They were inundated seasonally with the overflow from the slough. Western prairies are now subject to the vagaries of water releases from the S-12 structures. Meanwhile, eastern prairies are now flooded less often than under natural conditions and, furthermore, are drained to the east by an extensive network of canals (Fig. 1).

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 (Fig. 1). It ended at the thin line of mangroves along the northeastern shore

of Florida Bay. To the north, the marl prairies extended in a long arm to central Broward County (Davis 1943). This expanse of potential sparrow habitat suffered two major assaults.

Beginning in the late 1940's, the federal government constructed a series of canals. These canals permitted 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 subject to over-drainage. This is thought to contribute to the second assault—woody shrub invasion (including exotic species such as *Melaleuca quinquenervia*).

Davis et al. (1994) report that the spatial coverage of marl prairies in the Everglades system has decreased 24% since pre-drainage. When we consider the unconverted areas that are currently over-drained or fragmented, the total proportion of affected original prairie may be closer to 50%. In sum, the sparrow's habitat is greatly reduced and landscape management practices can make the remaining habitat either too wet or too dry.

The Cape Sable sparrow

The sparrow is 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, not saltwater marshes (Curnutt 1996).

DNA studies have yet to resolve its taxonomic status. In addition to its unique habitat, it is geographically isolated. The nearest subspecies, *A. m.*

peninsulae is 300 km to the north. These facts lead us to concur with the findings of the National Research Council (NRC 1995) in selecting evolutionarily independent populations as the basis for decisions about endangered species. Henceforth, we drop "seaside" from the name and will refer to the Cape Sable sparrow as a "species" for convenience.

Arthur Howell discovered the Cape Sable sparrow on February 18, 1918, in the coastal prairies of Cape Sable, the southwestern tip of Florida (Howell 1919). He found the bird to be "moderately numerous" and later gave the species' range as "an area about six miles in length and about a half mile in breadth" (Howell 1932). By September 2, 1935, the day of the worst recorded hurricane in Florida's history, the sparrow was reported from only one other location. Nicholson (1928) made two sightings in Collier County near Pinecrest (Fig. 1) but he reported the location incorrectly. The belief that the species was restricted to the Cape remained unchallenged. The 1935 hurricane's storm surge covered Cape Sable with 2 to 4 meters of salt water. There were numerous reports of Cape Sable sparrow sightings within its former range over the next few years, but all proved to be cases of mistaken identity. Most were Savannah sparrows (*Passerculus sandwichensis*) and sharp-tailed sparrows (*Ammodramus caudacutus*), both known to winter in southern Florida. Repeated searches along the salt marshes by experienced birders were unsuccessful (Stimson 1956). A single environmental catastrophe had apparently driven the Cape Sable sparrow to extinction.

Two events led to the rediscovery of the Cape Sable sparrow and a more complete knowledge of its range. In 1941, a thorough search of southern Collier County by Anderson (1942) proved Nicholson (1928) was right. In 1943, Davis published an important volume on the landscape and vegetation of southern Florida. Armed with Davis' maps and the knowledge that the Cape Sable sparrow could be found further inland than any other seaside sparrow, Stimson (1944, 1948) set out to find the limits of the species' range. By 1953, Stimson had located three colonies of sparrows in Collier County (Sprunt 1954). In 1955, Stimson (1956) discovered the Cape Sable sparrow in freshwater habitats and extended his search south and east of Collier County to the edge of the Shark River basin. On 7 May 1955 Stimson recorded 56 Cape Sable sparrows along a 40 km loop through the prairies of Everglades National Park west of Shark River Slough. For the next two and a half decades, researchers thought the range of this unique "seaside" sparrow was limited to the prairies west of Shark River Slough (Ochopee to the headwaters of the Broad River; see Fig. 1).

The U. S. Fish and Wildlife Service included the subspecies in the first list of legally Endangered species on March 11, 1967, (32 Federal Register 4001). The restricted range of the Cape Sable sparrow and the fate of the population on Cape Sable were the primary justifications. At this time, nearly 50 years after its discovery, researchers still did not fully understand the range of the Cape Sable sparrow. In 1971 John Ogden found the remains of two partially eaten Cape Sable sparrows in a short-tailed hawk's (*Buteo brachyurus*) nest near

Long Pine Key in Everglades National Park (Ogden 1972). A search of the area uncovered a colony of sparrows near Taylor Slough adjacent to the main park road (Fig. 1). Park visitors had reported Cape Sable sparrows in this area as early as 1957 but the park staff failed to confirm the sightings (Werner 1975).

In 1974 and 1975, Werner (1975) conducted an extensive survey of all potential sparrow habitat. He found sparrows as far north as Grossman Hammock and as far west as the eastern edge of Shark River Slough. It was apparent to Werner (1975) that the original extent of sparrow habitat would have included prairies to the north of Grossman Hammock, indeed, perhaps as far north as Broward county. For the most part, most of the prairies north of Homestead had been converted to agricultural and residential use and a host of exotic plant species populated the remaining fragments.

Werner had rediscovered the sparrows near Fox Lakes (north of Cape Sable) in 1970, but found no birds in 1973. This type of intermittent occupancy also occurred near Ochopee (Werner 1975) and at several other sites (see below). By the close of the 1970's, Werner, Stimson and others had identified the birds' range and also realized that the distribution of birds within it was patchy and temporally dynamic. In the late 1970's, Bass and Kushlan (1982) revisited all of the sites where Werner found birds. Concern over the absence of sparrows in many of these sites prompted the range-wide survey of 1981.

The extensive survey

Methods

Bass and Kushlan (1982) conducted the first extensive Cape Sable sparrow survey in 1981. They estimated the population to be 6600 birds. Bass repeated the survey in 1992 and, with the increasing involvement of others, each year since then. The survey uses a helicopter to drop observers at sites across a 1 km grid that covers all sparrow habitat. Observers record the number of sparrows seen or heard within a 10 minute interval for up to three hours each morning. They also collect data on dominant vegetation, surface water depth, and the presence of trees or shrubs. We take particular care to visit all locations that might hold sparrows and, we do not observe birds at most of the sites we survey (~ 79% of 3760 sites surveyed over all years held no birds). This suggests that we do not miss many (if any) sites that hold birds.

Kushlan and Bass (1982) established a non-random pattern of sampling sites from east to west through the breeding season (mid-March through May). This non-random drop pattern led to a confounding effect of time in the breeding season with location of sample site. We changed to a stratified random sampling method in 1995. We alternated between eastern and western populations among days.

Over the duration of the survey (1981 and 1992 to 1996) we have used eight observers. Whenever possible, we dropped two observers at one site and

compared their observations. From the small number of sites for which this was possible we could not detect any differences between observers. Logistical problems prevented this for all observers and we resorted to an alternative calibration. We compared survey results at adjacent survey sites at the same time on the same day taken by different observers. There were no significant differences between observations made by different observers (one-way ANOVA: $F = 0.74$; $df = 470$; $P = 0.61$).

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

We can compare the number of birds recorded during the helicopter survey with the numbers known on the ground. Our intensive plots range in size between 0.25 and 0.6 km², large enough that we average the four nearest helicopter survey points for our calibration. We have five plots and up to four years of data for each, for a total of 15 separate calibrations.

The ratio of average plot density divided by the average number of birds counted in the four adjacent helicopter survey points yields a correction of 25. This number may seem at odds with the value of 16 proposed by Kushlan and Bass (1983). However, we can and do get zero values during the helicopter survey, but, by design, we pick our study sites to hold birds. The ratio is

strongly right-skewed by occasional small totals of birds counted at the four adjacent survey points. (Theoretically, the ratio could be infinite, if no birds were counted.) Moreover, several study plots were established because of known concentrations of birds. This selection of high density sites drives the correction factor higher than if our sites were more randomly distributed with respect to sparrow numbers.

One way to stabilize the right-skewed values of densities to birds counted is to take their reciprocals and then average these numbers over the 15 calibrations. Re-inverting this average, yields an estimate of the correction factor of 18 — very close to Bass and Kushlan's estimate. Given the uncertainties and likely biases, we feel that the published value of 16 is adequate and that there is no need to change it at this time.

Extensive survey results

In 1981, Bass and Kushlan (1982) found the total sparrow population to exist in six sub-populations; two core populations that held most of the sparrows, and four peripheral populations (Fig. 2a). Core population A inhabited the marl prairies west of Shark River Slough, interlaced between drier shrub-dominated areas, and wetter areas dominated by sawgrass (*Cladium jamaicanese*). It extended into Big Cypress National Reserve, and held an estimated 2688 individuals. (Fig. 2a shows the 168 birds counted: 168×16 (the correction factor) = 2688.) Core population B held 2320 individuals near the center of Everglades National Park. Peripheral sub-population E, just

north of B, held about 700 sparrows, while C and D located along the Park's eastern boundary, held about 400 individuals each. F was the smallest sub-population (at 112). The survey covered a few possible breeding sites on Cape Sable, but found no birds there.

Bass repeated the survey in 1992, exploring many wetter sites in Shark River Slough (and elsewhere) in case the bird was more widely distributed than expected. It was not and the numbers in 1992 closely mirrored those in 1981 (Fig. 2b). (Similarly, in 1996, we searched for possible sparrow habitats in openings among the mangrove-dominated areas to the west of area A. We found no birds in them.)

Population A decreased by 84% from 1992 to 1993—a decline from nearly 2700 birds to just over 400 birds (Fig. 2c). In 1994, technical difficulties led to our visiting only ~25% of population A's sites (Fig. 2d). We counted 5 sparrows at only two sites, yielding an estimated population of 80 sparrows. At these survey sites in 1993, we counted 8 birds at 7 sites. Our inferences about population A in 1994 are limited, but the population may have declined even further. In 1995, the second year for which we have complete survey data for this area after Hurricane Andrew, we found that the population decreased to nearly half of the 1993 abundance (Fig. 2e). In 1996, population A doubled from approximately 224 to 416 but it was still nowhere near 1992 levels (Fig. 2f).

Since 1992, population B has held the majority of the sparrows. (In 1981 area A held more birds). This area showed an *increase* in numbers from 1981 to 1992 of more than 600 birds. While there is some inter-annual variation in population B, it is overall constant.

Population C declined to 11% of its 1981 value by 1992. After an apparent three-year absence, we estimated 48 sparrows in this area in 1996. Population D declined from 1981 to 1992 and was not counted in 1994. We found no birds here in 1995, but estimated the population in 1995 to be 80 birds. Population E decreased little between 1981 and 1992. The southern cluster of birds in this population disappeared in 1993 and we counted only single birds here in 1995 and 1996. Population F became extinct in 1993, and we counted only a single bird in 1996.

Chance

All populations fluctuate from year-to-year (Pimm 1991) and grassland sparrow populations fluctuate considerably (Curnutt et al. 1996). Even so, the one-year decline in population A to 16% of its 1992 level is atypical. For instance, in the extensive, long-term population monitoring of British birds, the most severe one-year decline was caused by the usually harsh winter of early 1963 (Pimm 1991). The most severely affected species — small-bodied insectivores — declined to ~50% of their 1962 levels. The causes of population A's much larger decline clearly require investigation.

More problematic are the other populations. Small, isolated populations typically fluctuate more than larger, more central ones (Curnutt et al. 1996). Local extinctions in such populations are commonplace for abundant, widespread species, and need not elicit special concern. For the Cape Sable sparrow, we should examine every local extinction outlined above and ask whether the event is too large or too frequent to be explained by such normal fluctuations. Only if this is the case, should we view the local extinctions or declines as evidence of factors whose influence we might control.

Methods

Curnutt et al. (1996) used North America Breeding Bird Survey (BBS; Robbins et al. 1986) data to analyze the spatial and temporal population variability of 10 species of grassland sparrows. Our results showed that the ranges of sparrows typically consist of one or more areas of high density and relatively low variability surrounded by peripheral low-density populations that are highly variable. The Cape Sable sparrow population appears to behave in much the same way.

With two assumptions, we can apply the same analyses to our Cape Sable sparrow data. The first is that we wish to estimate the probability that it would be absent from an area for a given length of time *given that its dynamics are typical of other, non-endangered grassland sparrows*. There is little variation among the 10 species of sparrows Curnutt et al. (1996) analyzed

and it is not unreasonable to assume that Cape Sable sparrow dynamics might be comparable.

The second assumption rests in the correspondence of BBS data and the extensive sparrow survey (Bass and Kushlan 1982). Each BBS consists of 50 observation points no closer than 0.8 km from each other where participants recorded all birds heard or seen. Observations for the Cape Sable sparrow survey are similar except for the distance between sites (1 km versus 0.8 km). A failure to observe birds in our survey, as in the BBS, may not mean an actual local extinction, but if not, then the apparent absence represents the numbers falling to some small and comparable level. (Recognizing this possibility, we will not preface each use of the word "absent" by "apparent" for simplicity's sake.)

We determined the probabilities of sparrows being continuously absent from a BBS route for 1 to 12 years—the maximum length of an absence that could appear in our Cape Sable sparrow data. We combined the data for all 10 grassland species and selected all BBS routes that had continuous data from 1970 to 1989. We further selected routes where birds were present the first and last years of record ($n = 284$) to rule out areas where the species might be lost from long-term habitat changes. For each route, we calculated the mean abundance over 20 years and tallied the number of occurrences that a species was absent one year, two consecutive years, three consecutive years, etc. We grouped routes by their mean abundances (in increments of 10) and

determined the rate of occurrence for each length of absence relative to the number of routes in each group. We expressed these rates as proportions to determine probabilities (Fig. 3).

Results

Cape Sable sparrow populations A, B, and E have consistently held sparrows over all survey years (1981, and 1992 through 1996). In contrast, populations D, C, and F have apparently dropped to zero on one or more occasions (Fig. 2). For these areas we can compare the survey results to our probability model to determine if we would expect these absences to be due to chance.

In typical years, there are 70 survey sites within the area of population D, 43 sites in area C and 38 in area F. We assume that these numbers are close enough to the 50 sites of a BBS route that we can make direct comparisons with them. That is, a zero count from one of these areas is equivalent to a zero value in the BBS data set. Survey data for both populations C and D are incomplete for 1994.

We counted 25 birds in population D in 1981; birds were absent for one year (1995) and could also have been missing in 1994. Our model shows that for BBS routes with between 20 and 30 birds counted on average, the probability of a single year absence is 0.15 (Fig. 3.) This is well above the arbitrary 5% probability accepted as significant for most statistical tests. So we should not

consider a one-year absence to be unusual. If there were no birds in D in 1994, then a two year absence would have been highly unusual (Fig. 3).

The area of population C encompasses the upper reaches of Taylor Slough—formerly prime habitat for Cape Sable sparrows. It was here that Werner (1975) conducted much of his work on sparrows and, as late as 1981, sparrows were relatively plentiful (27 birds). This population was absent for either three consecutive years (1993 to 1995) or twice for one year, depending on the unknown value for 1994. In the BBS data, three year absences are unknown for populations that average more than 20 birds, and occur less than 5% of the time for those that average more than 10.

The area of population F holds only 38 sites so we should be cautious in applying the BBS-derived model to the Cape Sable survey data. The area is bounded to the east by agricultural fields and is surrounded by habitat unsuitable for sparrows primarily due to high densities of native and exotic shrubs. We can assume, therefore, that the survey results represent the entire population of the area, and that zero values are comparable to BBS zeros. We counted 7 birds in 1981, two in 1992, and no more until we saw one in 1996. The sparrows could have been absent for a maximum of three consecutive survey years. The probability of a population averaging 7 birds being absent for this length of time is 9%—a low, but not statistically significant probability.

Conclusions

If 1981 represented an average year for its sub-populations, then the likely three year absence of the birds from population C, and the possible two year absence from population D are unusual events. Population F is so small that such absences might occur in roughly one in ten comparable data series. Combined, the declines in these three peripheral populations are sufficiently unlikely to merit our search for unusual events or anthropogenic causes.

Hurricanes

In this century, 80 hurricanes and other tropical storms passed close enough to south Florida to affect the Everglades (Duever et al. 1994). The official hurricane season lasts from June through November with September being the most frequent month of occurrence. Hurricanes could have a variety of affects on sparrows. They normally fall outside of the main sparrow breeding season of March to early June (Lockwood et al. 1997) and thus are unlikely to kill nesting birds. When hurricanes do strike, the high winds could kill birds directly. Hurricanes and tropical storms can drop up to 25 cm of rain. Thus, a storm early in the storm season could result in flooding and the termination of nesting, since most nest are within 15 cm of the ground (Lockwood et al. 1997). Wet storms that occur as late as October or November could prolong a high wet season water table (Duever et al. 1994), consequently delaying the period of "drydown" the following spring. This in turn could delay the onset of sparrow breeding.

We know of two hurricanes that have affected the sparrow. In 1935, a hurricane temporarily flooded Cape Sable with up to 4 m of salt water, and caused the subsequent change in vegetation that made Cape Sable unsuitable for the sparrow. Previous to the hurricane of 1935, the Cape held large expanses of prairie dominated by cordgrass (*Spartina bakerii*) (Holt and Sutton 1926). By the 1970's many of these prairies had converted to mangroves, bare mud flats, and halophytic forbs (e.g., *Batis* sp. and *Borrchia* sp.) as a result of the substrate deposited by the storm (Kushlan et al. 1982).

Werner (1975) and Bass found sparrows on Cape Sable until 1978, but not since (Bass and Kushlan 1982). We speculate that the habitat remaining on the Cape became too small to support a viable population of sparrows. This scenario suggest a hurricane-mediated extinction but in the long-term, through habitat changes, rather than directly because of the storm itself.

In August 1992, hurricane Andrew scored a near direct hit on the Cape Sable Sparrow, its eye and eyewall encompassing almost the bird's entire range (Fig. 2h; Armentano et al. 1995). The strongest winds, those trailing the eye, passed over the southern part of population A, and population E (Pimm et al. 1994). Population B lay to the south of the storm's eye, while populations C, D, and F held few birds in 1992 in any case. Population A declined from an estimated 2608 sparrows in 1992 to 432 in 1993 and population E declined by about 50%.

Andrew's effect was most obvious in hardwood hammocks and pines that stood directly in its path while the prairies of the Everglades—Cape Sable

sparrow habitat—suffered only temporary alteration (Pimm et al. 1994). There is no evidence that hurricanes cause direct mortality of sparrows, although surely the sustained winds of 242 km/hr of Hurricane Andrew were lethal to at least some of them. On the other hand, we could not count the birds in the period following the storm, or indeed, can we count them outside of any breeding season.

Despite the overall declines in areas A and E from 1992 to 1993, the details suggest that Andrew may not be their major cause. In area A, the numbers outside the eye in the north eyewall declined dramatically. The numbers in population B in the southern eyewall did not. The decline in area E was entirely within its southern part. The numbers in the northern part, though also within the storm's eye, actually increased. We might expect population A to recover from a short, sharp mortality were habitat conditions suitable. In fact, it declined further and has remained at low levels since. It is possible, however, that Andrew caused long-term changes in the population or its habitat of which we are simply not aware. In the companion paper (Nott et al. 1998) we present evidence for other causes of population A's decline.

Fire

The prairies of southern Florida are fire-maintained systems. In the absence of fire, they are invaded by hardwood species (Craighead 1971). Nonetheless, in the short-term, fires may be hazardous to the birds and especially their

nest. Within a time frame of a decade, we ask: how does the frequency of fire affect the birds' numbers?

Our discussion of sparrows and fire must be prefaced with an account of the over 350 km² "Ingraham Fire" of May 1989. Its importance lies not only in its unusually large extent (only two larger fires were recorded in Everglades National Park) but also in its location. This fire burned much of the marl prairie east of Shark River Slough—including the area that held the highest numbers of sparrows for all of our extensive surveys (including 1981). This begs the question: Are sparrow densities in this area high because of this fire or in spite of it? To address this question we will separate the Ingraham fire area from the rest of the data in the following analyses.

Methods

We obtained the dates and spatial extent of fires in Everglades National Park from July 1982 to April 1996. We converted these data to 1 Km grids to match the 450 sparrow survey sites. Thus, each site has one sparrow survey point (with up to 5 years of data: one for each year the site was surveyed) and an average of 3.9 fire data points (with as many records as there were fires at each point). We limited the influence of factors other than fire by including only those sparrow survey sites that would likely hold sparrows.

First, consider only the areas east of Shark River Slough. Unlike the prairies to the west, this area has not been extensively flooded for the last four years

(Nott et al. 1998). We also limited our analyses to sites that held sparrows at some time over the period of record. This way, we eliminate sites that may be avoided by sparrows for various other reasons. Another confounding effect is the depth of surface water at the time a site is surveyed for sparrows.

Sparrows restrict their breeding activity (including singing) at high surface water levels (Werner 1975, Lockwood et al., ¹⁹⁹⁷~~in press~~). Thus, we include in our analyses only those sparrow survey sites that had <1 cm of surface water present at the time of the survey. After we imposed these limitations our data consisted of 227 sites.

For each site, and for each of the sparrow surveys, we determined the frequency of fires and the number of days since the most recent fire. For example, site A may have experienced fires in 1989, 1991 and late-1994. Here, the fire frequency would be two for the 1992 through 1994 sparrow surveys and three for the 1995 and 1996 surveys. Similarly, we would refer to the 1991 fire as the most recent one in this site for the sparrow surveys up to 1994, and the 1994 fire as most recent for the remaining sparrow surveys. The fire data begin 10 years before our first survey (1992), so when calculating fire frequency for each survey year we counted only those fires that occurred up to 10 years previous to the survey.

Finally, we assigned each fire to either the wet season (June 1 to October 31) or the dry season (November 1 to May 31).

We use the results of these analyses to answer three questions: (1) Is there a threshold of fire frequency that precludes the establishment of sparrow populations?; (2) How long does it take for burned areas to reach peak sparrow densities?; and, (3) Does the season of the burn affect differences in sparrow re-colonization?

Results

Timing of fire

There are three sources of fire in Everglades National Park: lightning strikes, unplanned human ignition (including arson), and prescribed management burning. Prescribed burns occur throughout the year, with a slightly higher proportion occurring from November through March (Herndon and Taylor 1986). These fires are usually small and account for a small proportion of the fire activity in the park. Unplanned human-caused fires have been the most numerous and have burned the most area. These fires occur predominantly around the perimeter of the park, especially in the north-east corner near urban areas (Fig. 2g). The timing and frequency of lightning-caused and human-caused fires are highly divergent (Gunderson and Snyder 1994). Lightning-strike fires are most numerous from March to September, with a peak in July. Human-induced fires (non-prescribed) occur mostly in the dry season from December through May, with a peak in April and May.

For sparrows, the importance of this seasonal distinction lies in the differential effects of wet and dry season fires on the availability of breeding areas. Prairie fires in wet months tend to leave behind a mosaic of burned and unburned patches, while in the dry season burning is still patchy, but much more complete (Taylor 1983). Prairie burned in the dry season would have recovered, at most, only 5 or 6 months before the sparrow breeding season resumes. This might prohibit breeding in the area of the burn. Taylor (1983) showed that, after a fire, prairie vegetation growing over deep soil recovered (i.e., attained pre-fire levels of live biomass) in just two years while shallow-soiled prairies did not recover for at least four years. Sparrows show the same pattern of response—occupying deep-soiled prairies more quickly after fire than they do shallow-soiled prairies (Taylor 1983). Extensive dry-season fires could greatly reduce resiliency of the sparrow population by diminishing the extent of the most productive breeding areas.

We have data on 31 dry-season fires that occurred in Everglades National Park from 1982 to 1996. Seventeen of these were in the northeast corner of the park—where sparrows have been sporadic for well over a decade. Six occurred in the prairies east of Shark River Slough where the sparrows are most numerous (sub-populations B and E; Fig. 2). Four of these six fires were less than 1 km² in extent and the remaining two between 1km² and 2 km². Overall, sparrow numbers were lower at sites which had a dry-season fire as their most recent fire occurrence (*t*-test: $t = 2.28$, $P = 0.02$). This statistic, however, is not sufficient to explain the effects of dry-season burns on

sparrows for the following reasons. First, there have been very few dry-season fires in the area we are analyzing. While this may be good for sparrows, it makes appropriate comparisons of effects difficult. Second, to properly determine the effects of fire season on birds we need long-term continuous data on sparrow numbers at controlled sites to compare with the burned sites. Unfortunately, we do not have such data. There is an obvious need for a long-term study of the effects of seasonal fires on sparrows.

Fire frequency

Fig. 2g shows that the number of fires recorded at all sites ranged from 1 to 12 ($\bar{x} = 3.59$; $SE = 0.06$). For those sites that held sparrows over the period of record, fire frequency ranged from 1 to 7 ($\bar{x} = 2.97$; $SE = 0.06$) (Fig. 4).

Mean sparrow numbers were highest where there was one or two fires over the previous ten year period (Fig. 4). Sparrows were found at lower numbers at sites with fire frequencies of three to six, and were absent from sites that burned seven or more times. The different responses of sparrows to fire frequencies are significant (ANOVA: $F = 6.62$ $DF = 433$; $P < 0.001$), and the highest two values were significantly different from the others. There was only a slightly higher fire frequency at sites that burned in the Ingraham fire compared to those that did not. However, this difference was negated when we removed the Ingraham fire itself from the data.

Other authors (Werner 1975, Taylor 1983, Kushlan et al. 1982) have suggested that otherwise suitable prairies that burn too frequently would not hold sparrows, but they failed to quantify this effect. We did not find sparrows at sites that burned more than six times in ten years. Sparrows were found, albeit at low numbers, at sites that burned four, five, or even six times over the same period. This translates to one fire every 1.6 to 2.5 years.

This apparently Phoenix-like behavior of sparrows can best be explained by considering the nature of fire in Everglades prairies. Even the most intense and extensive fires do not completely denude large tracts of prairies. Fires invariably leave behind a mosaic of unburned patches which could support sparrow populations for a time. Taylor (1983) observed crowding of sparrows in unburned patches during the first year after a fire. By the second year, sparrow densities in the patches declined and sparrows were observed in the adjacent prairie that had by then recovered somewhat from the fire.

Sparrow numbers after a fire

Werner (1975) and Taylor (1983) observed that the sparrows avoided recently burned prairies. Werner (1975) reported that, after avoiding the prairies for up to one year post-fire, sparrow numbers increased annually until four years after a burn. While our extensive sparrow survey is not designed to monitor sparrow and fire interactions we have, over the years, sampled sites that had recently burned. Our results match Werner and Taylor's observations (Fig. 5).

After four years, Werner argued that the sparrow numbers declined, avoiding the area by the sixth year post-fire. Werner (1975) cited an increase in the proportion of dead plant biomass as the probable cause of the decline. Results from our analyses contradict these findings. We found a significant positive relationship between time since fire and sparrow numbers for up to 10 years post-fire ($R^2 = 0.15$; $F = 6.79$, $P = 0.01$) (Fig. 5) and no evidence for a decline.

Sparrows, fire frequency, and time

Werner (1975) suggested that sparrows increase in density up to three or four years after a fire then decline in numbers and will abandon a site after the sixth post-fire year. These observations, led him to suggested that optimum sparrow habitat could be maintained if prairies were burned every four or five years. Taylor (1983) conducted the only other study of the effects of fire on the Cape Sable sparrow. Like Werner (1975), he found sparrow numbers increased from one to four years post-fire, but his data for longer periods were either lacking or inconclusive. Taylor (1983) did, however, report sparrows breeding at sites that had last burned 10 to 12 years previously.

Our analyses include data collected across a much greater spatial and temporal scale than those of Werner (1975) or Taylor (1983). Our results suggest that, on the scale of decades, frequent fires are detrimental to sparrows. We suggest that the decline of the Taylor Slough sparrow population described by Werner (1975) occurred over a very small part of the sparrow's range and had local causes (see Nott et al. 1998). Our five intensive study sites were within the

Ingraham burn of 1989, yet all held dense populations of sparrows in 1997, with no noticeable reductions in numbers since the sites establishment in 1993 to 1995 (Lockwood et al. ¹⁹⁹⁷ ~~in press~~; Pimm et al. in preparation).

Craighead (1971) proposed that fire exclusion would cause prairies to be invaded by hardwood species. Thus, the complete absence of fires in prairies would eventually render them unsuitable for sparrows. To date, we do not know just how long prairie will remain free of hardwoods in the complete absence of fire.

In sum, frequent fires are harmful to the sparrow. We have not found a fire interval so long that it would harm the birds, though we cannot yet evaluate Craighead's suggestion. The very frequent burns along the north-eastern edge of the sparrow's range (populations C, F) are thus the likely the cause of its decline there. Whether these burns are just a consequence of unplanned human ignition in the area or further exacerbated by the over-draining of these prairies remains to be investigated.

The Future of the Cape Sable Sparrow

Any small-bodied, short-lived vertebrate whose numbers are below 3,000 individuals is in danger of becoming extinct—the Cape Sable sparrow deserves its Endangered status under U. S. law. Our collective goal should be to not let this species disappear. The question then becomes what can we do about it? Our results suggest that the Cape Sable sparrow has been subject to

two separate fates in recent years—one more devastating than the other. The population west of Shark River Slough has all but disappeared in an alarmingly short period of time. In our companion paper, we indict the artificial water regimes that have left the prairies in that area submerged for long periods. The sparrow populations on the east side of the slough have fared better, though the north-eastern populations are likely small because of too frequent fires. What does this mean for the future of the sparrow?

Very small populations of sparrows become locally extinct—and then return. All three peripheral populations that experienced local extinctions had birds in 1996. It is too soon to say whether these populations will increase or disappear again. Either way, the re-colonization of isolated patches of habitat implies that the global population is productive enough to maintain its range provided its habitat remains suitable.

Hurricanes have little effect on mainland populations of sparrows. Hurricane Andrew was a severe storm that caused untold damage to a number of natural and human systems. Yet, there is no evidence that the storm, in itself, had any deleterious effects on the sparrow population. Hurricanes do little direct damage to dry-prairie. Storm surges, associated with coastal areas, could drastically change habitat, but the interior of southern Florida is safe from these events.

Longer intervals between fires mean more sparrows—at least until hardwoods invade the prairies. Fire is ultimately necessary for the

maintenance of sparrow habitat, but sparrow numbers increase in the absence of fire for at least ten years (the limit of our data). Frequent burning of prairies would result in a decrease in the ability of the sparrow population to recover. Finally, large infrequent fires are not necessarily a threat to the future of the sparrow. The Ingraham fire of 1989 swept across most of the area of population B and apparently had little long-term effect on the population of sparrows.

The well-being of the prairies of population B is critical to the survival of the Cape Sable sparrow. This 200 km² area currently holds the vast majority of them. It is primarily muhly grass (*Muhlenbergia filipes*) and mixed-species prairie. After a fire, sparrows can reach high densities here in as few as three years. Population B will be the primary source of sparrows that colonize other areas.

This paper does not directly address the major cause of the sparrow's decline: the changes to water levels. It is the consequences of these changes that we now turn in the companion paper that follows this one. As we shall see, too much water can flood the birds, too little can lead to the prairies being so dry that they are vulnerable to fires we have discussed here.

Acknowledgments

This project is funded by the National Biological Service, the National Park Service, the Fish and Wildlife Service, the Army Corps of Engineers and by a Pew Scholarship in Conservation and the Environment awarded to S. L. Pimm. We thank the Americorps volunteers Tabby Fenn, Alison Hayden, Laura McMahon, Barron Moody, Sarah Richart, Debbie Rosenthal, Mervin Stringer III, and Jan Yacabucci for their invaluable help and for the Americorps program for their support: We also extend our gratitude Karla Balent and Ester Stanton. We also thank Tom Armentano for reviewing this manuscript.

Literature Cited

- Anderson, W. 1942. Rediscovery of Cape Sable Sparrow in Collier County. Florida Naturalist 16:12.
- Armentano, T. V., R. F. Doren, W. J. Platt, and Troy Mullins. 1995. Effects of Hurricane Andrew on coastal and interior forests of southern Florida: Overview and synthesis. Journal of coastal Research Special Issue No. 21: 111-144
- Bass, O. L., Jr., and J. A. Kushlan. 1982. Status of the Cape Sable Sparrow. Report T-672, South Florida Research Center, Everglades National Park. Homestead, Florida. 41 pp.
- Craighead, F. C., Sr. 1971. The trees of South Florida. University of Miami Press. Coral Gables.
- Curnutt, J. L. 1996. Cape Sable Seaside Sparrow. Pages 137-143 in J. A. Rodgers, Jr., H. W. Kale, II, and H. T. Smith, editors. Rare and Endangered Biota of Florida, Volume V. Birds. University Presses of Florida, Gainesville.
- Curnutt, J. L., S. L. Pimm, and B. Maurer. 1996. Population variability of sparrows in space and time. Oikos 76: 131-144.
- Davis, J. H., Jr. 1943. The natural features of southern Florida, especially the vegetation, and the Everglades. Florida Geological Survey Geological Bulletin No. 25.

Davis, S. M., L. H. Gunderson, W. A. Park, J. R. Richardson, and J. E. Mattson.

1994. Landscape dimension, composition and function in a changing Everglades ecosystem. Pages 419-444 in S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida.

Duever, M. J., J. F. Meeder, L. C. Meeder, and J. M. McCollom. 1994. The

climate of south Florida and its role in shaping the Everglades ecosystem. Pages 225-248 in S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida.

Fennema, R. J., C. J. Neidrauer, R. A. Johnson, T. K. MacVicar, and W. A.

Perkins. 1994. A computer model to simulate natural Everglades hydrology. Pages 249-290 in S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida.

Gunderson, L. H. and J. R. Snyder. 1994. Fire patterns in the southern

Everglades. Pages 291-305 in S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida.

- Hernden, A. and D. L. Taylor. 1986. Response of a *Muhlenbergia* prairie to repeated burning: changes in above-ground biomass. South Florida Research Center Report SFRC-86/05.
- Holt, E. G. and G. M. Sutton. 1926. Notes on birds observed in southern Florida. *Annals Carnegie Museum* 16: 435-436.
- Howell, A. H. 1919. Description of a new seaside sparrow from Florida. *Auk* 36: 86-87.
- Howell, A. H. 1932. *Florida Bird Life*. Coward-McCann, Inc. New York.
- Kushlan, J. A. and O. L. Bass, Jr. 1983 Habitat use and distribution of the Cape Sable seaside sparrow. Pages 139-146 in T. L. Quay, J. B. Funderburg, Jr., D. S. Lee, E. F. Potter, and C. S. Robbins, editors. *Occasional Papers of the North Carolina Biological Survey, 1983-5*. Raleigh, North Carolina.
- Kushlan, J. A., O. L. Bass, Jr., L. L. Loope, W. B. Robertson, Jr., P. C. Rosendahl, and D. L. Taylor. 1982. Cape Sable Sparrow management plan. South Florida Research Center Report M-660. 37 pp.
- 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: xx-xx. (issue 4: December)
- National Research Council, 1995. *Science and the Endangered Species Act*. National Academy Press, Washington DC.

- Nicholson, D. J. 1928. Nesting habits of seaside sparrows in Florida. *Wilson Bulletin* 40: 234-237.
- Nott, M.P., O L. Bass, Jr., D. M. Fleming, S. E. Killeffer, N. Fraley, L. Manne, J. L. Curnutt, T. M. Brooks, and S.L. Pimm 1998. Water levels, rapid vegetational changes, and the Endangered Cape Sable seaside sparrow. *Conservation Biology* (under review).
- Ogden, J. C. 1972. Florida region. *American Birds* 26: 852.
- Olmsted, I. C., L. L. Loope, and R. E. Rintz. 1980. A survey and baseline analysis of aspects of the vegetation of Taylor Slough, Everglades National Park. South Florida Research Center Technical Report T-586, Everglades National Park, Homestead, Florida.
- Olmsted, I. C. and L. L. Loope, 1984. Plant communities of Everglades National Park. In P. J. Gleason, editor. *Environments of South Florida: Present and Past II*. Miami Geological Soc. Memoir II.
- Pimm, S. L. 1991. *The Balance of Nature? Ecological issues in the conservation of species and communities*. University of Chicago Press, Chicago.
- Pimm, S. L., Davis, G. E., Loope, L., Roman, C. T. Smith, T. J. III, and J. T. Tilmant. 1994. Hurricane Andrew. *Bioscience* 44: 224-229.

- Robbins, C. S., D. Bystrak, and P. H. Giesler. 1986. The Breeding Bird Survey: Its first fifteen years, 1965-1979. Resource Publication 157, US Department of the Interior, Fish and Wildlife Service, Washington, DC.
- Robertson, W. B., Jr. and P. C. Frederick. 1994. The faunal chapters: Contexts, syntheses, and departures. Pages 709 - 737 in S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida.
- Sprunt, A., Jr. 1954. Florida Bird Life. Coward-McCann, Inc. New York.
- Stimpson, L. A. 1944. Rediscovery of the Cape Sable seaside sparrow confirmed. Florida Naturalist 17: 31-32.
- Stimson, L. A. 1948. Cape Sable sparrow still in Collier County. Florida Naturalist 21: 68-69.
- Stimson, L. A. 1956. The Cape Sable seaside sparrow: its former and present distribution. Auk 73: 489-502.
- Taylor, D. L. 1983. Fire management and the Cape Sable sparrow. Pages 147-152 in The Seaside Sparrow, its biology and management. North Carolina Biological Survey and North Carolina State Museum.

Werner, H. W. 1975. The biology of the Cape Sable Sparrow. Report to U. S. Fish and Wildlife Service. Everglades National Park, Homestead, Florida. 215 pp.

Werner, H. W. 1978. Cape Sable Seaside Sparrow. Pages 19-20 in H. W. Kale, II, editor. Rare and Endangered Biota of Florida, Vol. 2: birds. University Presses of Florida, Gainesville.

Figure Legends

Figure 1. A map of southern Florida showing location names referred to in text and the flow-path of Shark River Slough. Under natural conditions, the flow would be the light-grey shaded area, plus the darker grey to the east. Currently with water releases from S12 water-control structures, the darker grey area to the east receives little water and that water flows through the darker grey area to the west. Solid black lines are the boundaries of Everglades National Park, large dashes are the county boundaries. Small dashes show canals and the levees that accompany them. The canal running southwards from the eastern S12 spillway is the L67 extension that restricts the water flow into the north eastern portion of Shark River Slough.

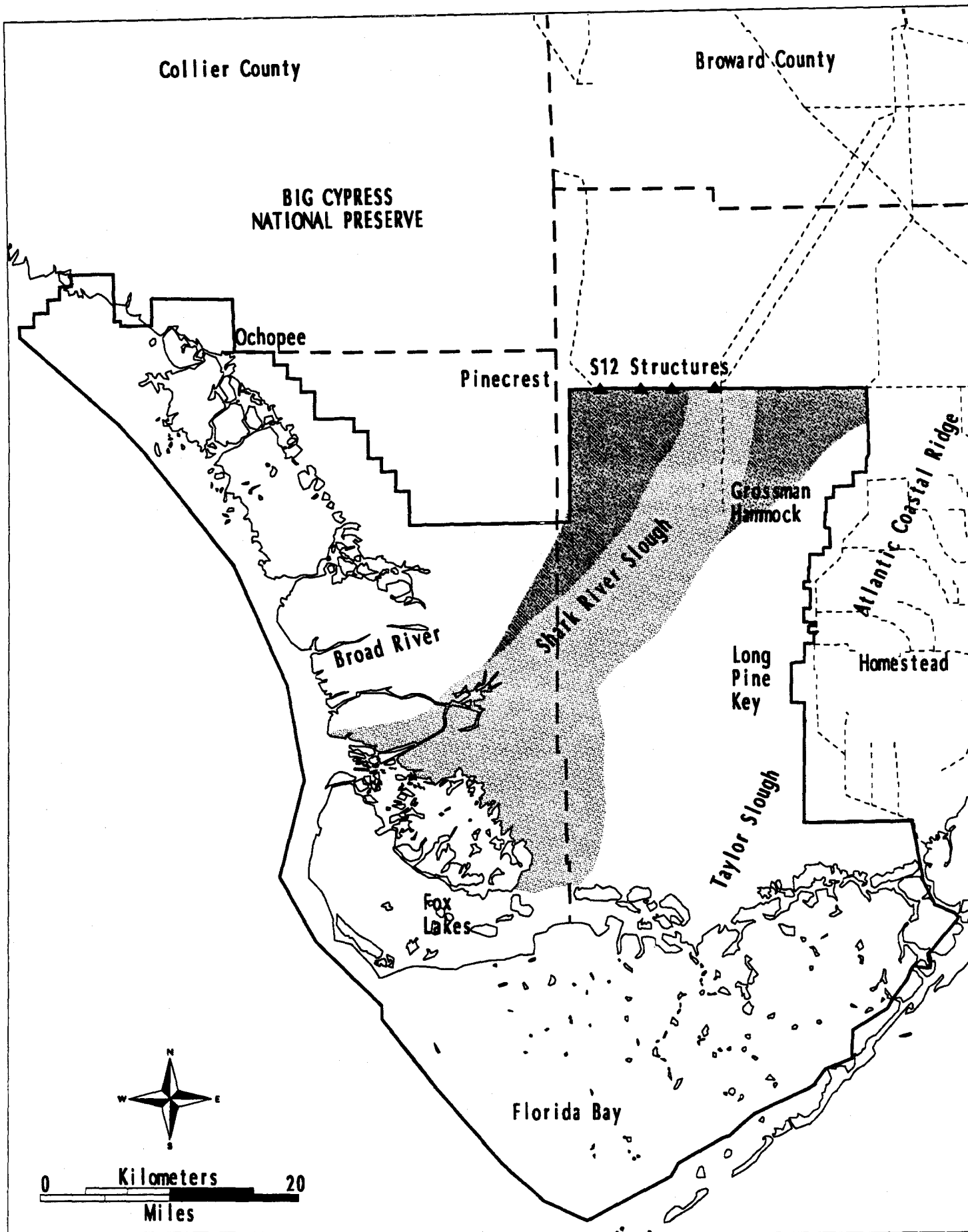
Figure 2. Parts (a) through (f) the numbers of sparrows counted in years 1981 and 1992 through 1996. In part (a) the letters refer to the six subpopulations to which the text refers. The gap between eastern and western populations is the wetter areas of Shark River Slough, that between the eastern populations is a pine-dominated habitat that the birds also do not occupy. Part (g) shows the number of years in which areas were burned from 1982 to April 1996. Within the sparrow's range, the areas in the north and east (populations C and F) endure particularly high fire frequencies. Part (h) shows the path of the eye

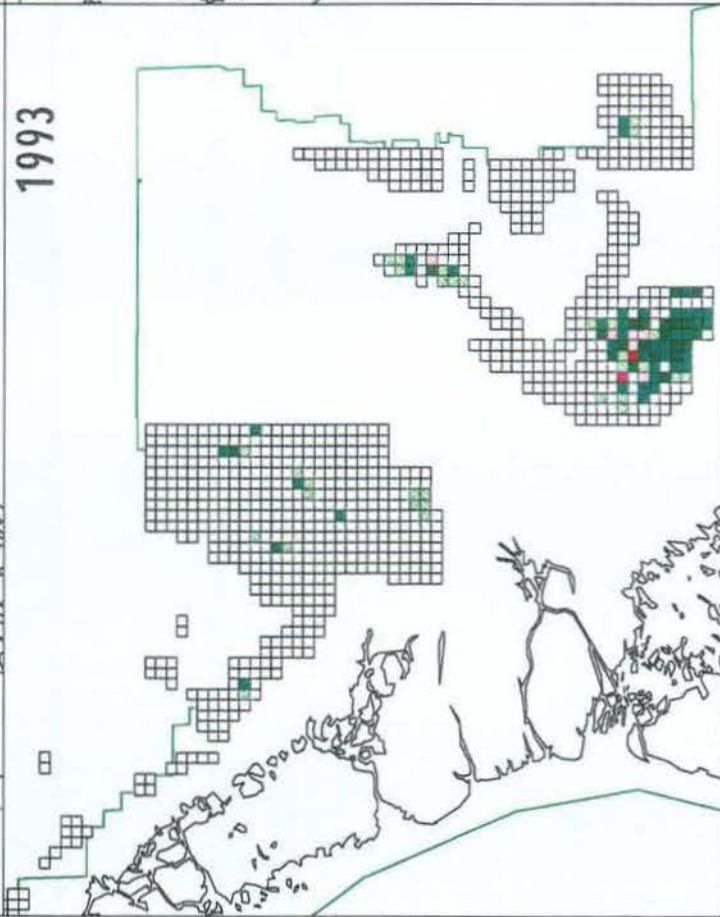
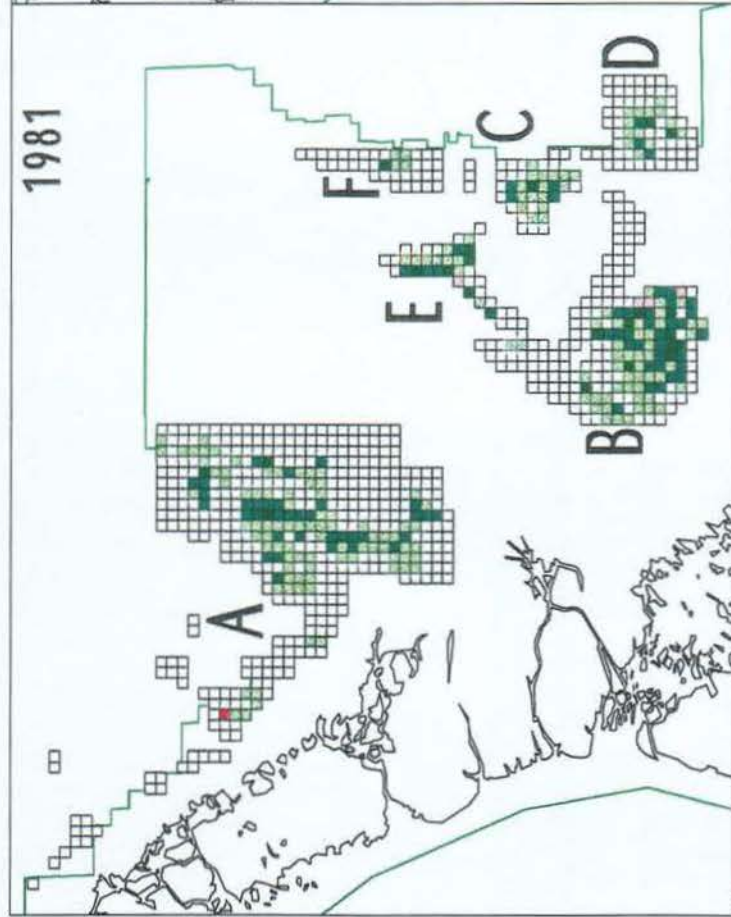
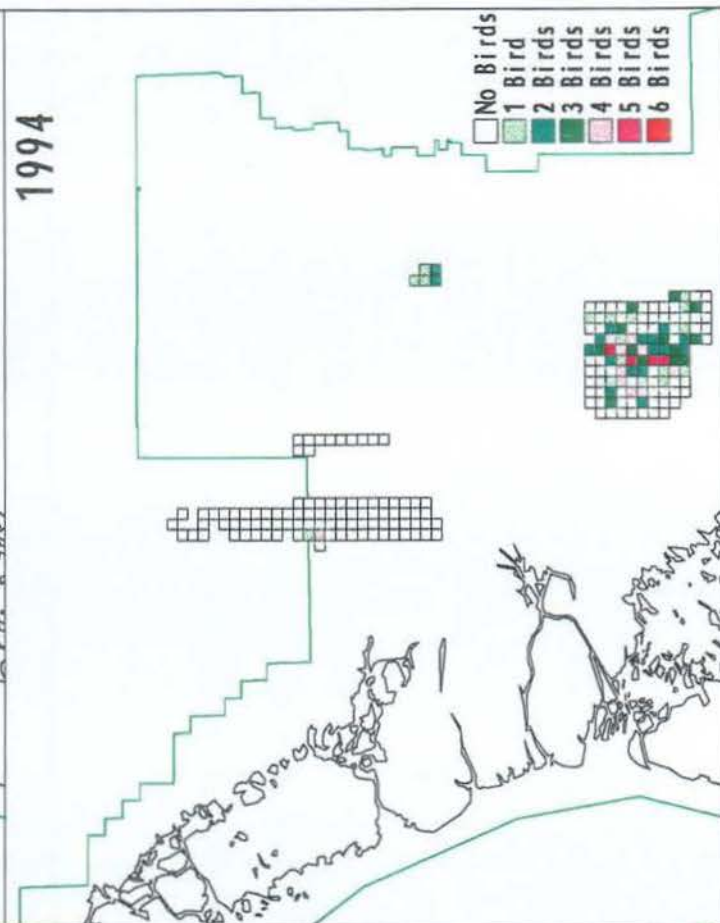
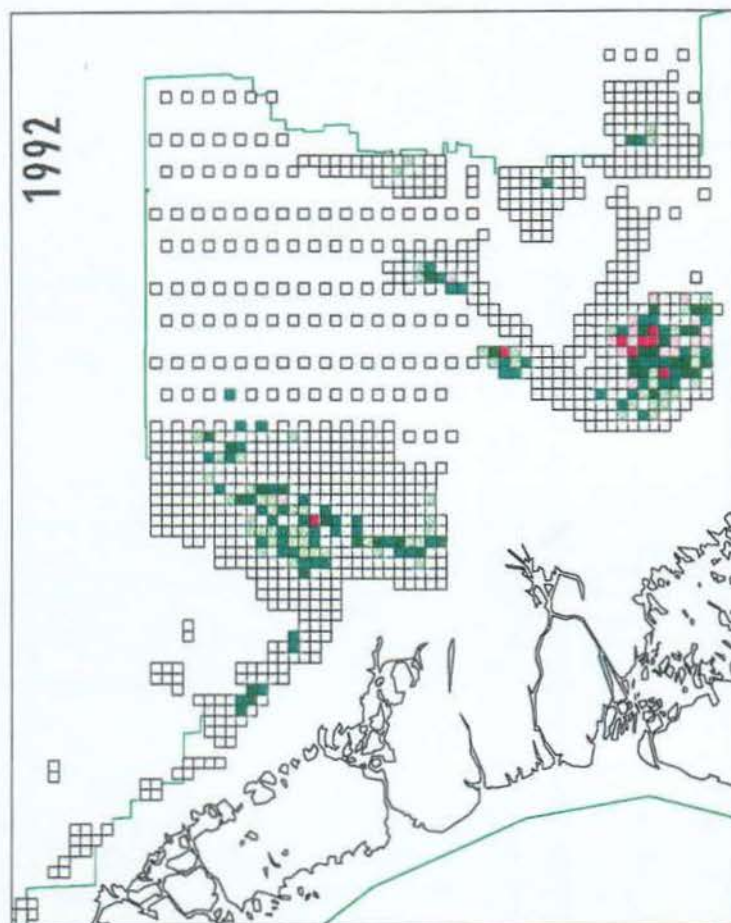
and eyewall of Hurricane Andrew in 1992. The strongest winds tailed the eye.

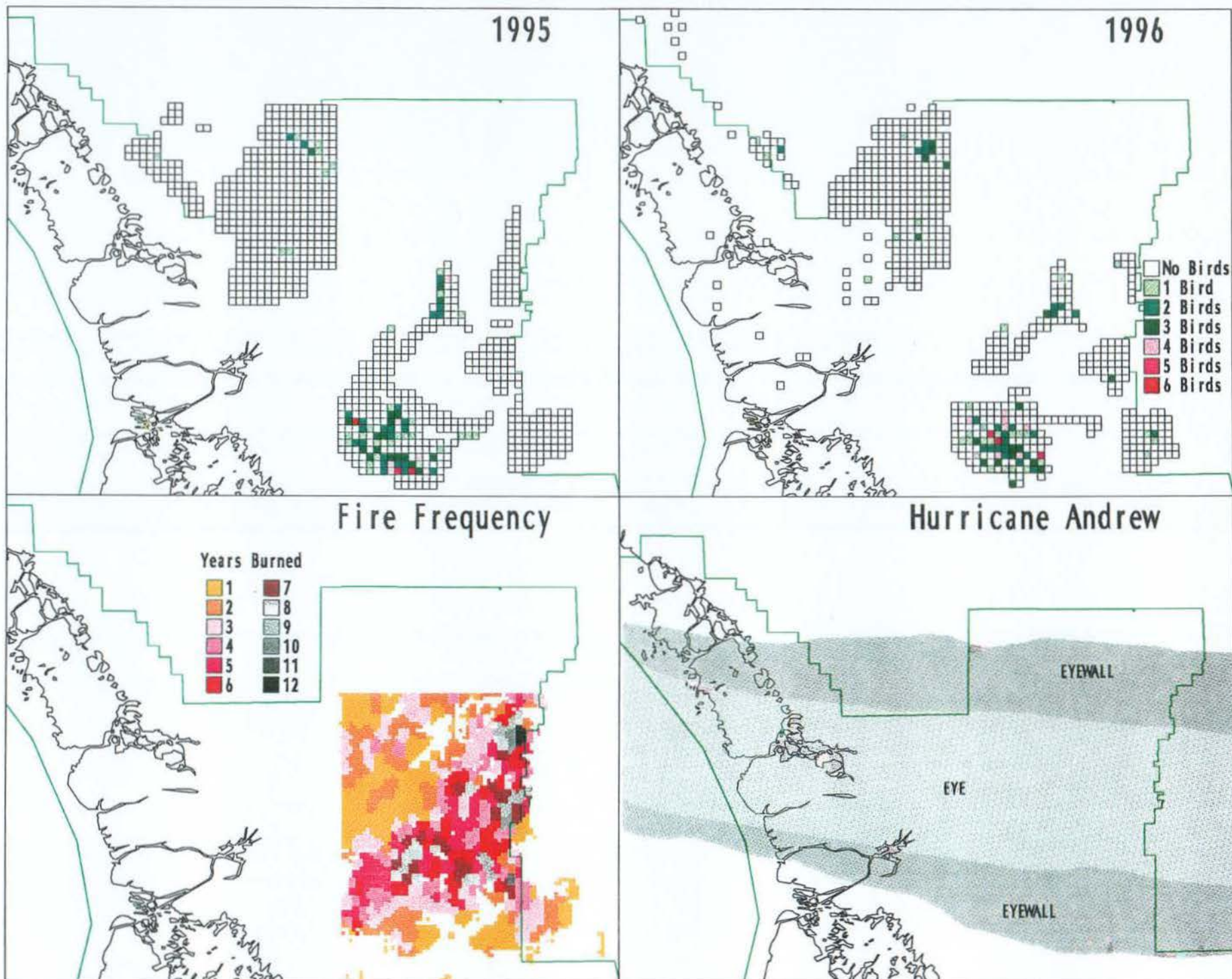
Figure 3. The frequency of occurrence of consecutive zero counts of ten species of grassland sparrows on BBS routes for different overall mean

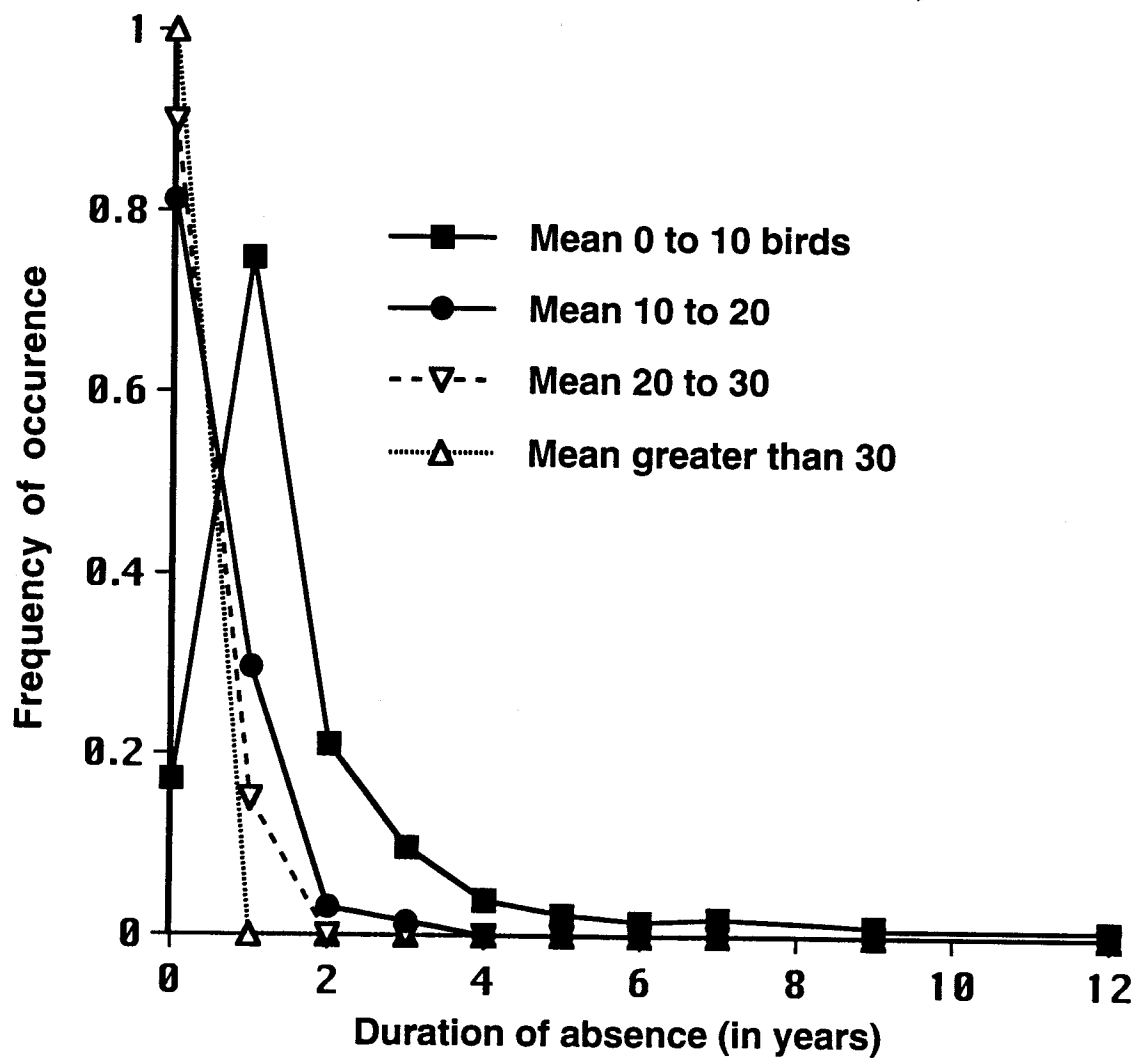
Figure 4. The mean number of Cape Sable sparrows per sampling site declines with increasing fire frequency over 10 years for all sites east of Shark River Slough dominated by muhly grass. Error bars represent ± 2 standard errors.

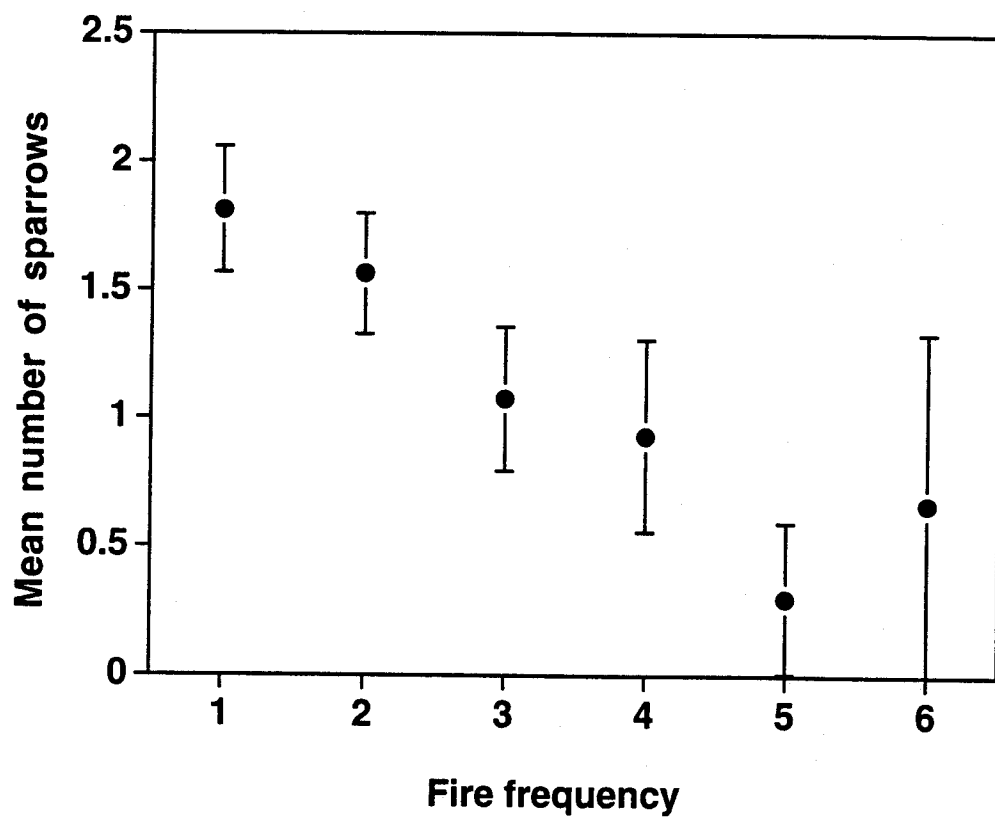
Figure 5. The relationship between the mean number of Cape Sable sparrows recorded at each site and the number of days since the most recent fire at each site ($R^2 = 0.15$; $F = 6.79$, $P = 0.01$)

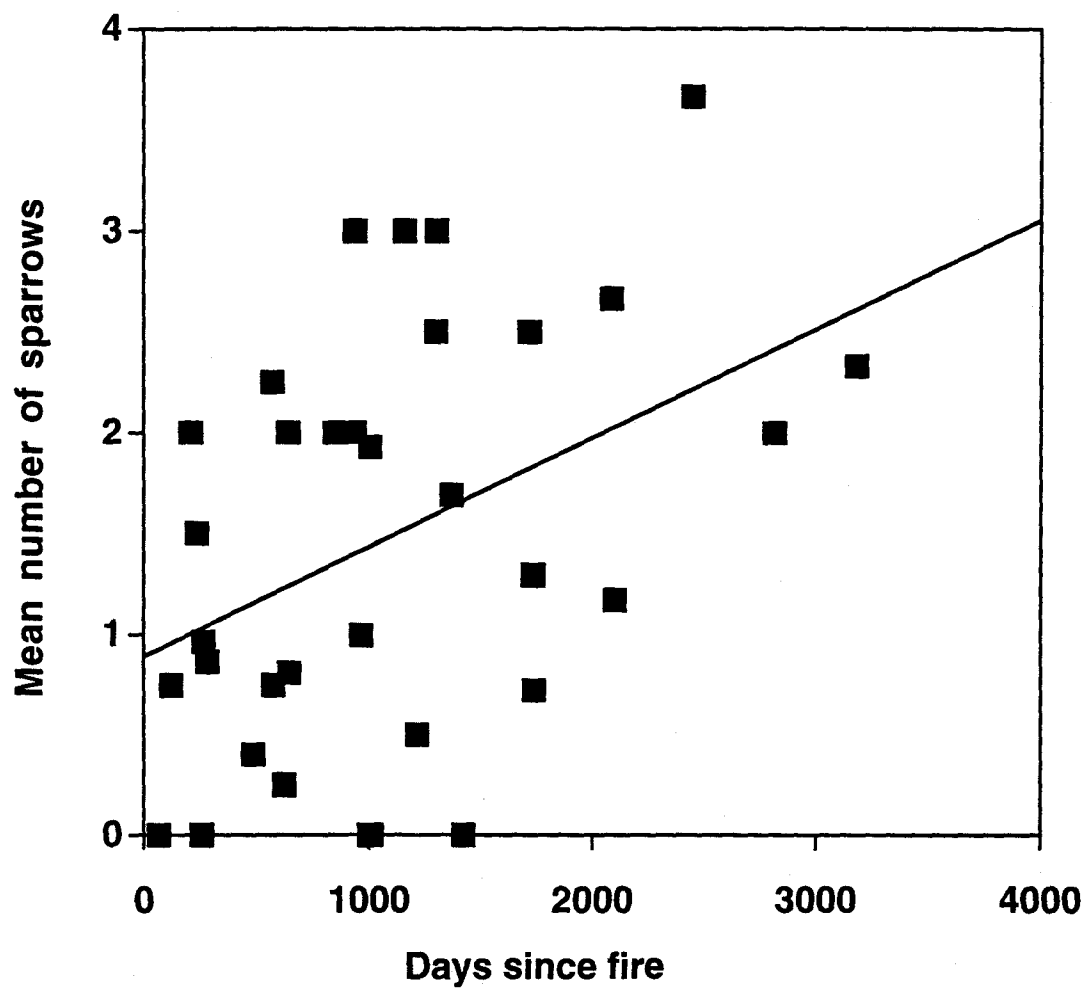












WATER LEVELS, RAPID VEGETATIONAL CHANGES, AND THE
ENDANGERED CAPE SABLE SEASIDE SPARROW

M. Philip Nott¹, Oron L. Bass, Jr.², D. Martin Fleming,³ Stephen E. Killeffer¹,
Nancy Fraley¹, Lisa Manne¹, John L. Curnutt¹, Thomas M. Brooks¹, Robert
Powell¹, and Stuart L. Pimm^{1*}

¹Department of Ecology and Evolutionary Biology
The University of Tennessee
Knoxville, Tennessee 37996

²South Florida Natural Resources Center
Everglades National Park
Homestead, Florida 33034

³Biological Resources Division, USGS,
Everglades National Park
Homestead, Florida 33034

*To whom all correspondence should be addressed. E-mail

StuartPimm@aol.com

Abstract

The legally Endangered Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) is restricted to short-hydroperiod, marl prairie within Florida's Everglades National Park and Big Cypress National Preserve. Marl prairies are typified by dense, mixed stands of graminoid species usually below 1 m in height, naturally inundated by freshwater for three to seven months annually. Water levels affect the birds directly, by flooding their nests, and indirectly by altering the habitat on which they depend. Managed redistribution of water flows flooded nearly half of the sparrow's geographical range during several consecutive breeding seasons starting in 1993. Furthermore, these high water levels rapidly changed plant communities, so jeopardizing the sparrow's survival by reducing the availability of nesting habitat.

Introduction

The Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) is found only in freshwater, marl prairies of the Everglades of south Florida (Bass and Kushlan 1982, Kushlan and Bass 1983). In a companion paper (Curnutt et al. 1998) we review the history of this species and the ecosystems on which it depends. In 1992, the population numbered about 6600 individuals in six subpopulations. The subpopulation to the west of the area's main drainage — Shark River Slough — declined from an estimated 2700 birds in 1992 to only 400 birds in 1993. The population has remained at low numbers ever since. A smaller, but well-studied population of over 430 birds along Taylor Slough declined to fewer than 50 in 1992 and birds have been seen only sporadically since then. Only one populations of ~2000 birds, east of Shark River Slough has remained more or less constant. Here we explore the immediate and longer term consequences of altered water levels to these declines.

The geographic range of the sparrow is bounded to the north by a large impounded marsh (Water Conservation Area 3A), to the east by agricultural land, to the south and west by mangroves, and to the northwest by mixed cypress and pine forests (Gunderson 1994). Shark River Slough is the central flowway through the southern Everglades and it is flooded most of the year. Marl prairies, flooded from three to seven months each year flank the eastern and western edges of this slough and provide the sparrow its preferred

habitat. Taylor Slough is a much smaller drainage in the east of the sparrow's range.

Historically, water flowed over a wide path across the entire width of Shark River Slough. A system of ridges west of Shark River protected the higher elevation marl prairies to their west from flooding. The construction of a system of levees created the Water Conservation Area 3A (WC3A) impoundment in the mid 1960's. Four gated spillways (S12A - S12D) control the release of water from WC3A into Shark River Slough. These structures constrict the flowpath primarily to the western portion of the slough.

Another levee (L67-extension) prevents water from these spillways from flowing to the east (see Fig. 1 in Curnutt et al. 1998). S12A allows released water to flow behind the protective ridges and directly into the western prairies. The resulting redistribution of flows causes deeper water levels within the western portion of Shark River Slough than occurred historically. It also extends the period these western prairies are flooded (Van Lent 1996).

Taylor Slough is a much smaller drainage that flows roughly southwards to Florida Bay. The agricultural and urban areas to its east are drained by an extensive network of canals (see Fig 1 in Curnutt et al. 1998). Towards the southern end of these areas a pumping station S332 started operation in 1980.

We explore two effects of changing water levels on the sparrows. The first is the immediate and direct consequences of high water during the breeding

season. The second is the longer-term, indirect consequences of changed vegetation.

The sparrow only breeds during the dry period (normally, mid-March through mid-June) when the water table can be as low as 1m below the surface. They breed until the onset of summer rains and may nest into July (Werner 1975, Lockwood et al. 1997). On our extensive surveys in 1981 and from 1992 to 1997, we did not find singing birds when water levels exceed 10cm. It is reasonable to assume that even if the birds are present, they will not establish territories.

Detailed studies of the birds' breeding success shows that all active nests are lost to predators when water levels rise above 10cm (Lockwood et al. 1997). In any case, nests are built 10-20 cm above the base of the grass tussocks (Werner 1975, Lockwood et al. 1997). Water levels above these heights flood the nests and so restrict the breeding habitat.

Vegetational changes follow prolonged flooding and these changes alter the bird's habitat. We shall show that changes between prairies with plants characteristic of short versus long periods of flooding (*hydroperiods*) occur over a span of just a few years. Sparrows only occupy short-hydroperiod prairies, so inundation deprives them of their habitat.

Part 1. The direct consequences of high water levels.

The differences in water levels between 1992 and 1995 are self-evident in the satellite images of the area taken during the birds' breeding season of April and May (Fig. 1). In 1992, large areas of dry prairie are visible as pink regions in the images on either side of the main drainage of Shark River Slough. In 1995, in contrast, the area west of the slough is blue, indicating it was covered in water. The years 1993 and 1995 were broadly similar while 1994 and 1996 were only slightly drier.

Within these images, lies the essence of our story: one year of high water (1993) was responsible for greatly reducing the sparrow's numbers west of Shark River Slough. Three more wet years kept the numbers low. There may have been sparrows in the area in 1993, but unless they sing we cannot find them. We do know, however, that the annual survival of territory holding males is about 50% (Pimm et al. in preparation). Four years without breeding and we would expect there to be few individuals that lived to see the relatively dry year of 1997.

Although the overall story is obvious from Fig. 1, there are details. It is on these details of the sparrow population to the west of Shark River Slough that we shall focus in this section of the paper. We first document the detailed temporal changes at two water level monitoring stations, then spatially extend the information at these two points. As a final step, we ask what factors drive the water levels.

Temporal changes

The South Florida Natural Resources Center provides us three sources of information about water. First, there is a rainfall monitoring station situated close to the S12A spillway at the northeastern corner of the survey area. Second, there are daily water release data for the S12A structure. Finally there are two hydrological monitoring index stations, NP205 and P34, at the northeast and southwest edges of the bird's western subpopulation respectively (Fig. 1, Fig. 2a). NP205 station lies on the ridge that separates Shark River Slough from the western prairies. This gauge is ~7.5km south and downstream of S12A. The ground elevation of NP205 is ~180cm above mean sea level (MSL). P34 station is ~60cm above MSL.

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

The temporal trends in mean breeding season water levels at NP205 and P34 over the period 1976-1996 are very tightly correlated. The exceptions are the dry years 1977, 1989, 1990, and 1991, when the water levels in P34 remained

relatively high. P34's much lower elevation means that it cannot dry down to the levels seen at NP205. (P34 levels cannot drop below sea level (-60cm MSL). With this caveat, we find the water levels to be so similar, that we conclude that the water levels are even across the survey area. Henceforth, we will consider the levels at NP205 to adequately represent water levels for the entire study area.

Fig. 3a shows that daily NP205 water levels varied considerably among years. Between 1975 and 1978, the water table was permanently 50-200 cm below ground level all year round. The 1980's were generally much wetter. During the four year period 1989-92, the dry period lasted 2 months during the first half of the year. Since, NP205 water levels have remained above ground level for most of the time. There were two short dry periods during 1994 and 1996.

We calculated how many days would be dry during each breeding season — defined as March 15th and 90 days thereafter (Fig 3b). Lockwood et al. (1997) suggest ~40 days as the minimum dry period within which one breeding cycle can occur. A 60 day period allows for the initiation of second clutches and an 80 day period allows for the fledglings of the second clutch to leave the nest.

The four wettest breeding seasons are 1984, 1987, 1993, and 1995. Other than these, only two years (1980, 1983) were wetter than 1994 and 1996. The period starting in 1988 until 1992 was a dry one, comparable to the four years ending in 1979.

Intepreting these numbers as sparrow breeding opportunities, we see that from 1993 to 1996 high water levels left little opportunity for sparrows to breed at the elevation of NP205 (Fig. 3b). The window of breeding opportunity also lasted less than 40 days in 1980, 1983, 1984, 1986, and 1987. In all but two of the remaining years (1982 and 1988), the breeding opportunity lasted more than 60 days allowing for the potential of second clutches.

In the years of the extensive sparrow survey (see Curnutt et al. 1998), 1981 and 1992 were dry years and sparrows were abundant. The survey years 1993 to 1996, were initially wet, and remained too wet for breeding to occur. The sharp decline in sparrow numbers from 1992 to 1993 corresponded to a change from four drier than average years to four unusually wet ones.

Spatial patterns

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

During the 1995 sparrow survey, we measured the water depth at 284 census sites within the western survey area. That we could do this across the entire area is itself testimony to that year's high water levels. For each of sites we calculated the mean water depth from measurements taken at six random

points. We expressed these as elevations relative to the NP205 water level for the survey date. Finally, we constructed a sparse landscape matrix at a 500m x 500m resolution. Alternate cells contained no data, but we estimated their values by taking the average value of neighboring cells. Fig. 4a shows the results. The sites differ by about 1m in elevation and a higher elevation ridge runs north to south along the eastern edge of the area.

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

Figs 4d, e, and f show the results of this process for three sample years. In the dry year of 1992, 56% of the total area was dry enough to support one brood, and a further 39% of the area was dry enough to allow two breeding attempts. In contrast, in 1995, no part of this area was dry long enough to allow the birds to attempt even one brood.

Table 1 summarizes the predictions of available habitat for the 20 years for which we have hydrological data. The years 1993 and 1995 were the worst years on record in terms of the available breeding habitat for the sparrow. Only 1983 and 1984 were worse than 1994 and 1996. The four years from 1993

were exceptionally poor in terms of the area of available breeding habitat. These spatial results exactly match those based on the point record of NP205.

The elevational distribution of the survey sites is strongly right-skewed (Fig.5). Most of the landscape lies between 180 and 210 cm above MSL. Sparrows were differentially distributed across this gradient in our survey years. In the dry years of 1981 and 1992, the sparrows were widespread but mainly inhabited elevations of 170 to 210 cm MSL. Since 1993, the elevational distribution of sparrows has narrowed and is now restricted to higher elevations above 200 cm MSL. The sparrows may have been eliminated from low lying areas or, sensibly, moved to higher ground — as do seaside sparrows in saltmarshes, when habitat is flooded (Post 1974).

The causes of water levels

Predicting the average water levels at NP205 during the sparrow's breeding season is not simple. At least three factors may be responsible. The first is the initial height of the water. The higher the water level, the faster one might expect it to drain away. Greater rainfall and the managed flow of water of the S12 structures would increase the average water level. As expected, we find evidence for all three these effects; what is important is their relative contributions.

Table 1 shows the mean breeding season level — the average water depth for the 90 days starting on March 15th. The fall in water level is this average

value minus the March 15th value. Fig. 7a shows that when the mid-March level is highest, the water falls the most ($p < 0.01$). (In this plot, large falls in level are shown as negative values.)

We take the residuals about this relationship. Fig. 7b shows that the water level falls less than expected when there is more rain ($p < 0.02$, one tailed test). Interestingly, the regression coefficient is 1.8 — meaning that 1cm of rain creates 1.8 cm of flooding. As estimated, this suggests that the water at NP205 is driven partly by water flows from elsewhere. The coefficient also suggests that the roughly 10 cm range in rainfall over the 20 years of the study would contribute a ~18 cm range in waterlevels at NP205, when corrected for other factors.

Finally, Fig. 7c plots the residual fall in water levels (given both the mid-March level and the rainfall) against the managed flow over the S12s.

Positive residuals characterized all but the two smallest flows of the 11 years in which such flows occurred. Conservatively, we restrict the analysis to the years in which such flows occurred. Water levels dropped less when the flows were greatest ($p < 0.01$).

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

Stated simply, our analysis shows that the managed flows over the S12s contribute to the inundation of this endangered species' nesting habitat. The largest residual water level coincides with the largest release over S12 in 1993 and the year when the sparrow population in this area plummeted. In 1993, the flows added over 22 cm of water to the water level. Had the water levels been 22 cm lower, then roughly half the area would have been dry enough, long enough, to allow nesting pairs to complete one brood.

Part 2: the effects of water levels on vegetation type

The results of our extensive surveys (Curnutt et al. 1998) show that the sparrow is found almost exclusively in prairies dominated by muhly grass (*Muhlenbergia filipes*), and those mixed prairies with no dominant grass species. Mixed prairies are often diverse and include muhly, sawgrass (*Cladium jamaicense*), and black-top sedge (*Schoenus nigricans*). The sparrow avoids prairies dominated by sawgrass and spikerush (*Eleocharis spp.*) that have longer hydroperiods. We now show that prolonged flooding has altered the vegetation in two areas in ways that will inhibit the birds' use of them. These changes were quite rapid but they have longer term consequences to the sparrow than the ephemeral flooding.

The history of Taylor Slough

After the western subpopulation, the largest decline of the sparrow has been in the Taylor Slough drainage (see Fig. 2 in Curnutt et al. 1998). In Taylor

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

We can compare the floral composition of Taylor Slough in 1995 and 1996 to that of Werner's study in 1975 (Table 2). Just as Werner recorded, we found muhly grass and sawgrass to be the dominant species in this area. However, in the 21 years between our surveys, the relative dominance of these two species has switched. The area has changed from a diverse, muhly-dominated prairie to a less-diverse, sawgrass-dominated prairie.

Further support for these changes comes from a detailed vegetation study of Taylor Slough by Armentano et al. (1997). Across ten plots in their transect T1 (Fig. 2a), muhly cover averaged 61% in 1980 but only 9% in 1995. Armentano et al. suggest that the changes may not have happened gradually. In transect T2 (placed within both Werner and Curnutt's study plot) muhly increased in abundance from 35% cover in 1980 to 54% in the dry year of 1992. By 1995, its cover had declined to only 25%.

The conversion of this area from a muhly grass to a sawgrass-dominated prairie indicates a lengthening of the hydroperiod. The placement of a pumping station (S-332) at the boundary of Everglades National Park and Taylor Slough in July 1980 altered the hydrology of the downstream drainage of the slough. Interestingly, Kushlan et al. (1982) correctly predicted a change from muhly grass to sawgrass dominance in the plant community directly downstream of the station. Fig. 8 shows the number of days the water level at the monitoring station at Taylor Slough bridge was above ground level for the 90 days following March 15th. The area was typically dry for most of the sparrows breeding seasons up until 1992. Almost certainly as a consequence of increased pumping from S332, the area since 1993 has been much wetter than the 20 years prior to the pump's operation.

This is not the whole story, however. The sparrow population has also declined dramatically in the *upstream* portions of S332. By 1981, it was apparent that the northern reaches of the Taylor Slough drainage were experiencing shortened hydroperiods as a result of the dredging of the L-31(W) canal (Kushlan et al. 1982). (These are areas F and almost all of area C in Curnutt et al.'s study; see their Fig. 2.) Whether this drying also increased the frequency of fires to an extent detrimental to the sparrow (see Curnutt et al.), we do not know. What seems clear is that the annual or biennial fires were too frequent to supports large sparrow populations in what would otherwise have been suitable habitat. In sum, it seems that in Taylor Slough,

the sparrow has declined through a combination of making some of its habitat too wet and some of it too dry.

Vegetation changes west of Shark River Slough

We return to the population west of Shark River Slough that experienced a precipitous decline in 1993 from which it has not recovered. Could changes in vegetation similar to those in Taylor Slough be responsible for preventing the species' recovery there?

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

Figs 4 c and d show the changes took place between 1981 and 1992 and between 1992 and 1996. There are three sources for these changes. The first are errors of classification. Bass collected all the 1981 and 1992 data and carefully trained one other observer (Manne) in 1996 to assist him in order to

minimize classification errors. The second source stems from the inherent difficulty of locating the exact 1981 survey sites (found by dead reckoning) with the GPS system available in 1992 and 1996. In this area, patches of mixed prairie are small and intermingled with the sawgrass. The helicopter might easily land in mixed prairie one year and sawgrass the next at what appear to be the same site, but what, in fact are sites ~100 m apart. Even between 1992 and 1996, errors in the GPS readings (on the order of 50m) could account for some classification errors. The final source of changes are those that really took place. These latter must be sufficiently numerous and directed to be convincing.

Counting each survey point as being statistically independent shows that more sites initially counted as the wetter, sawgrass-dominated in 1981 were counted as being the drier, mixed prairies in 1992 (96) than vice versa (59); 100 and 74 remained unchanged in the drier and wetter categories respectively ($\chi^2 = 12$, $p < 0.01$). Table 1 shows that the year 1992 was not only a dry one, but followed three other dry years. Between 1992 and 1996 the pattern was reversed. Some 103 sites changed from dry to wet, while only 39 changed from wet to dry; 77 remained dry and 39 remained wet ($\chi^2 = 5$, $p < 0.05$). The years 1993 to 1996 were exceptional wet ones.

The patterns of change (Fig 4c,d) show a finely structured mix of sites that did and did not change during the two comparisons. Between 1981 and 1992 sites that remained dry or which became dry lay along the higher elevation north

to south ridge. Areas in the northwest appeared to dry consistently too. Sites that became wetter were in the lower, south-east corner. In 1996, the sites in the northwest were consistently classified as being drier than in 1992. Only the highest sites remained dry.

The change in one site is not necessarily statistically independent of the change in another site 1km away — if it were these broad geographical trends would not be obvious. This makes our χ^2 values more significant than they are. Nonetheless, most sites do change and the fine mixing of the vegetation and slight differences in elevation makes the changes largely independent. A more formal removal of the effects of temporal and spatial autocorrelation by applying a modified Mantel technique (Mantel 1967, Fortin and Gurevitch 1993) reveals the same qualitative conclusions (Nott in preparation).

The causes of vegetational changes

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

We propose the following mechanism for the change to sawgrass domination. Increased production and changes in the periphyton result from increasing water levels and longer hydroperiods (Browder 1994), or from nutrient enrichment (McCormick and O'Dell, 1996). Normally submerged,

periphyton mats can become floating mats and shade out submerged macrophytes (Van Meter-Kasanof, 1973). Field observations suggest that as heavy floating periphyton mats dry they can flatten and selectively kill the above-ground portion of *Muhlenbergia* and other vulnerable species. In contrast, sawgrass can penetrate this thick mat. An area of several square kilometers once dominated by mixed prairie was covered in such a thick mat after the waters receded in 1996. It no longer held the breeding population of the sparrow that it once had. Indeed, there would have been few places to place their nests had they been there.

Discussion

High water levels west of Shark River Slough are largely a consequence of managed flows from upstream areas to the north of Everglades National Park. In 1993, record flows across the spillways, added over 20cm depth of water to the area and the sparrow population declined precipitously. Relatively high water levels in 1994 to 1996 kept the population low. Moreover, the vegetation has changed from being a mixed prairie to one of mostly sawgrass. The sparrows avoid sawgrass-dominated sites. In the east, in Taylor Slough, a pumping station increased water levels and similarly changed the vegetation from muhly- to sawgrass-dominated and so caused the population to decline.

In the companion paper (Curnutt et al. 1998) we show that the sparrow's eastern populations appear to have been harmed by high fire frequencies,

which in turn may be a consequence of water levels that are too low. The Cape Sable sparrow requires conditions that are "just right" — neither too dry or too wet.

The local implications for the management of the species are obvious. The west needs to avoid unusually long periods of flooding, and the east needs more flooding. It is almost certainly not accidental that such changes in water management would restore the hydrological patterns to something much closer to their original state. As anticipated by the 1973 Endangered Species Act, management of this endangered sparrow requires our protecting the ecosystems on which it depends. Indeed, the requirement of the sparrow's survival informs such ecosystem management.

The global implications are also obvious. Everglades National Park is among the largest two dozen national parks within subtropical North America, Central America and South America (Mayer and Pimm 1997). Yet Everglades National Park is in a sense too small: changes outside its boundaries severely impact large areas within it. Simply, even parks as large as Everglades National Park will not retain their biological resources without constant vigilance.

Acknowledgements

We thank the National Biological Survey, Army Corps of Engineers, and National Park Service for their financial support and the Pew Charitable Trust for a fellowship to SLP. We thank Julie Lockwood, Audrey Mayer, and Gareth Russell for their help and William Robertson, Jr., Larry Harris, Tom Armentano, David Bush, Robert Fennema, Thomas van Lent and George Schardt for suggestions and support. We thank the Americorps volunteers Tabby Fenn, Alison Hayden, Laura McMahon, Barron Moody, Sarah Richart, Debbie Rosenthal, Mervin Stringer III, and Jan Yacabucci for their invaluable help and for the Americorps program for their support: We also extend our gratitude Karla Balent and Ester Stanton.

References

- Armentano, T.V., R. F. Doren, W. J. Platt and T. Mullins. 1995. Effects of Hurricane Andrew on Coastal and Interior Forests of Southern Florida: Overview and Synthesis. *Journal of Coastal Research*, Special Issue No. 21: 111-144.
- Bass, O. L., Jr., and J. A. Kushlan. 1982. Status of the Cape Sable Sparrow. Report T-672, South Florida Research Center, Everglades Natl. Park. Homestead, Fla. 41 pp.
- Browder, J. A., P. J. Gleason and D. R. Swift. 1994. Pp. 379-418 in *Everglades: The ecosystem and its restoration* (S. M. Davis and J. C. Ogden, eds.). St. Lucie Press, Delray Beach, FL.
- Curnutt, J. L., M. P. Nott, A. Mayer, T. M. Brooks, L. Manne, Oron L. Bass, Jr., D. Martin Fleming and S. L. Pimm. 1998. Population dynamics of the endangered Cape Sable seaside sparrow. *Conservation Biology* (companion paper).
- Fortin, M.-J and J. Gurevitch. 1993. Mantel tests: spatial structure in field experiments. Pages xxx-xxx in *Design and analysis of ecological experiments* (S. M. Scheiner and J. Gurevitch, eds.). Chapman and Hall, New York.
- Gunderson, L. H. 1994. Vegetation of the Everglades : Determinants of community composition. Pages xxx-xxx in *Everglades: The ecosystem and its*

restoration (S. M. Davis and J. C. Ogden, eds.). St. Lucie Press, Delray Beach, FL.

Kushlan, J. A., O. L. Bass, Jr., L. L. Loope, W. B. Robertson, Jr., P. C. Rosendahl, and D. L. Taylor. 1982. Cape Sable Sparrow management plan. South Florida Research Center Report M-660, Everglades National Park, Homestead, Fl. 37 pp.

Lockwood, J. L., K. H. Fenn, J. L. Curnutt, A. Mayer and D. Rosenthal. 1997. Natural History of the Cape Sable Seaside Sparrow. (Wilson Bulletin December.

Mantel, N., 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27:209-220.

McCormick, P. V., and M. B. O'Dell. 1996. Quantifying periphyton responses to phosphorous in the Florida Everglades: A synoptic experimental approach. *Journal of the North American Botanical Society* (in press).

Post, W. 1974. Functional analysis of space-related behavior in the Seaside Sparrow. *Ecology* 55: 564-575.

Van Lent, T. 1996. An analysis of hydrologic conditions in western Shark River Slough. Report prepared for the National Park Service, Everglades National Park, Homestead, FL.

Van Meter-Kasanof, N. 1973. Ecology of the microalgae of the Florida Everglades. Part I. Environment and some aspects of freshwater periphyton. 1959 to 1963. *Nova Hedwigia*, 24: 619-664.

Werner, H. W. 1975. The biology of the Cape Sable Sparrow. Report to U. S. Fish and Wildlife Service, Frank M. Chapman Memorial Fund, The International Council for Bird Preservation and U.S. National Park Service, Homestead, Fl. 215 pp.

Figure Legends

Figure 1. Satellite images of southern Florida in 1992 and 1995. In 1992, the areas to the west of the main drainage of Shark River Slough were dry. In 1995 (and from 1993 onwards) they were flooded. The boxed areas show two areas mapped in greater detail in Fig. 2. In the western box, the two labelled points are water monitoring stations.

Figure 2. (left hand side): information that will appear as an overlay to figure 1. Details of the Taylor Slough study area (for location see figure 1). The smaller rectangle is Werner's study site (see text for details).

Figure 3. Annual and breeding season trends in NP205 water level, a) daily levels relative to ground level, b) Annual estimates of the duration of the dry periods during the breeding season. Values above 40 days represent years when breeding was possible. Values above 60 days would allow for a second brood to be started.

Figure 4. Maps of features in the area west of Shark River slough. (a) The height of the terrain; scale at right is cm above mean sea level (MSL). (b) and (c) Changes in the classification of the vegetation between 1981 and 1992 and between 1992 and 1996 respectively. Key: open squares: no change from "dry," grey squares, change from "wet" to "dry", open triangles, no change from "wet," black diamonds, change from "dry" to "wet". The text defines the vegetation of "wet" and "dry" areas. (d), (e) and (f). The areas that were dry

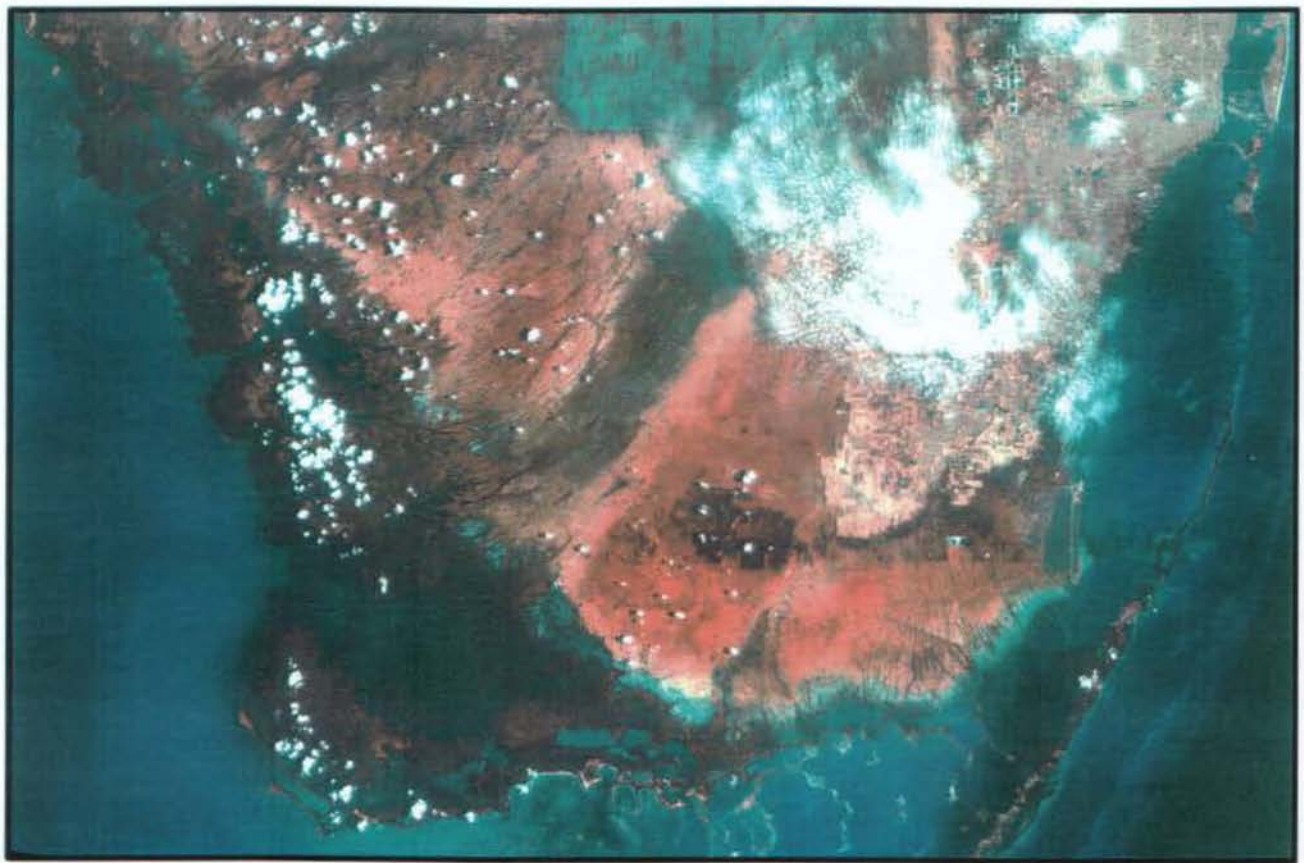
for varying numbers of days (scale in days). Numbers on figures show the percentage of the area that would support one or two broods.

Figure 5. Elevational distribution of survey sites. Open bars represent the total number of sites surveyed at each elevation (right hand axis). Within each bar the increasingly darker bars represent the number of survey sites occupied at each elevation in each survey year (left hand axis).

Figure 6. The fall in water levels at NP205 during the sparrow's breeding season in terms of the mid-March level (a), the rainfall (b) and the water released over the S12A spillway (c).

Figure 7. The number of dry days at the Taylor Slough bridge water monitoring station during the breeding season. 1981 was the first season after the installation of pumping station S332 upstream.

A Dry Year in South Florida

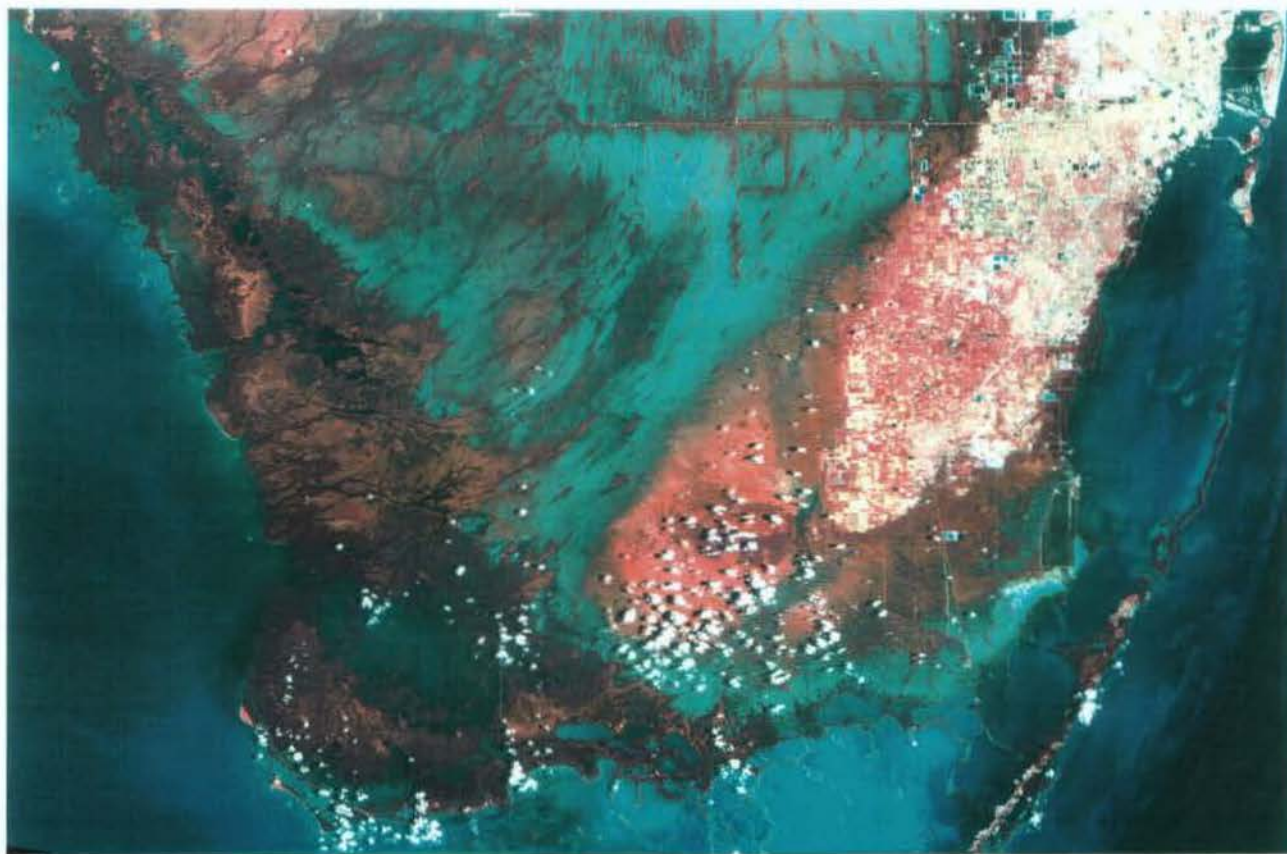


tami92.map

Landsat 5 Thematic Mapper Image
13 May 1992

Band 5 = Red Band 3 = Green Band 2 = Blue

A Wet Year in South Florida



tamiami95.map

Landsat 5 Thematic Mapper Image
6 May 1995

Band 5 = Red Band 3 = Green Band 2 = Blue

NP205

P34

T5

S-332

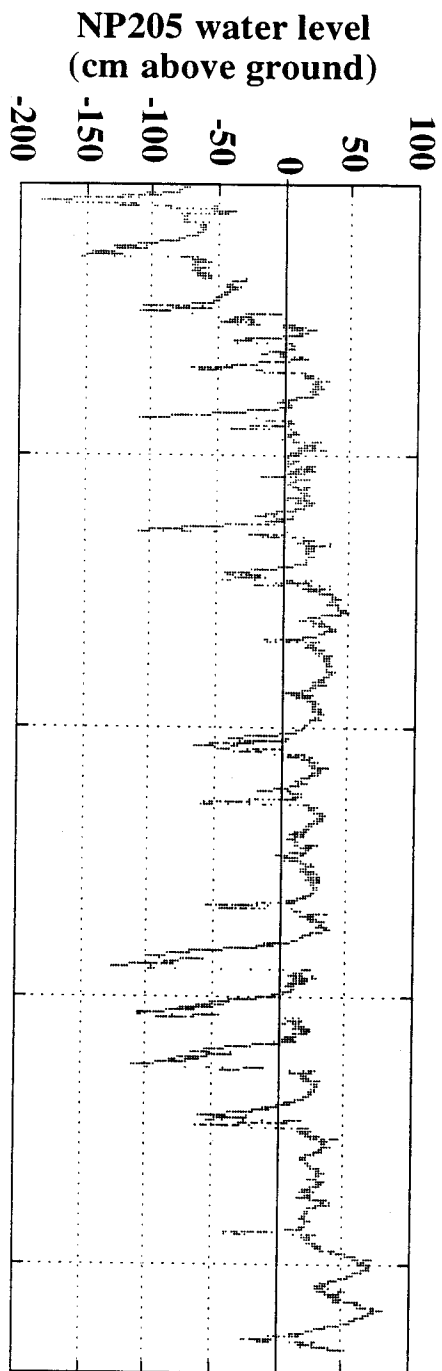
T1

T2

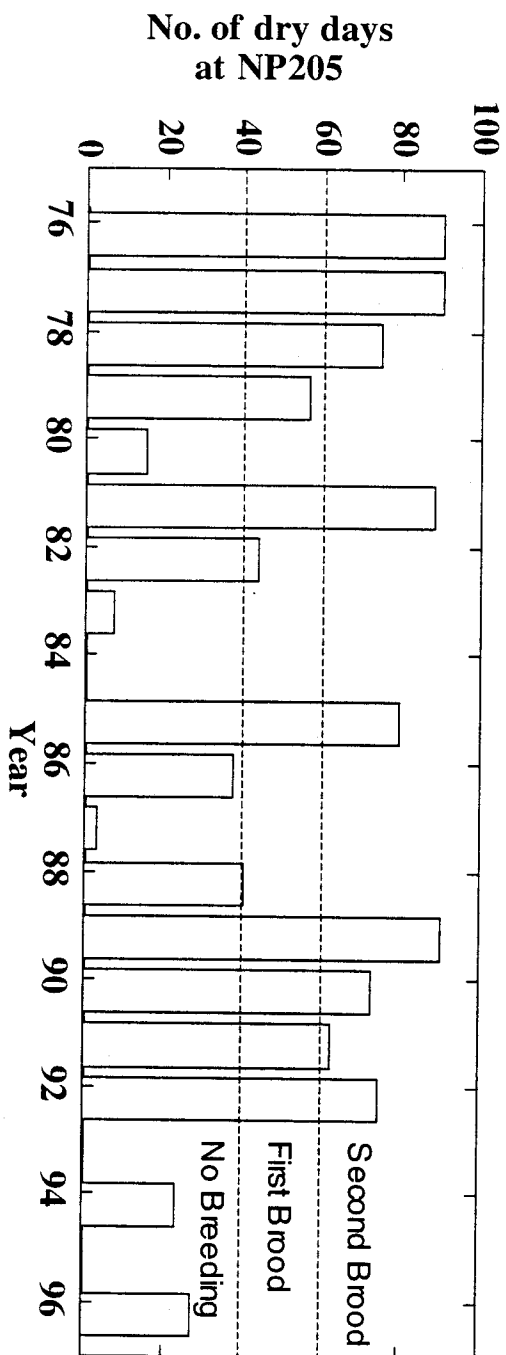
Taylor
Slough
Bridge

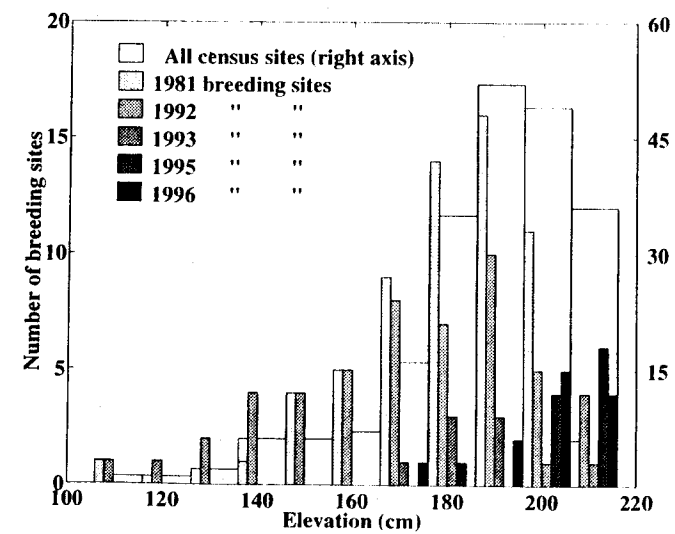
T3

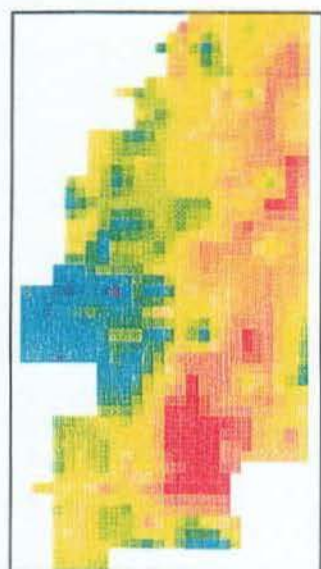
a)



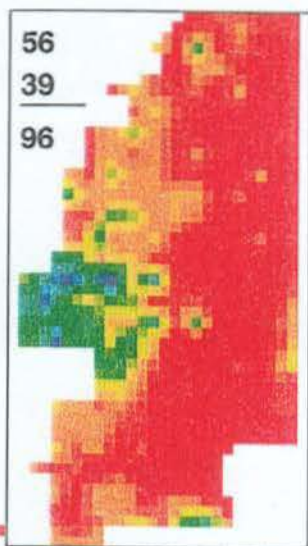
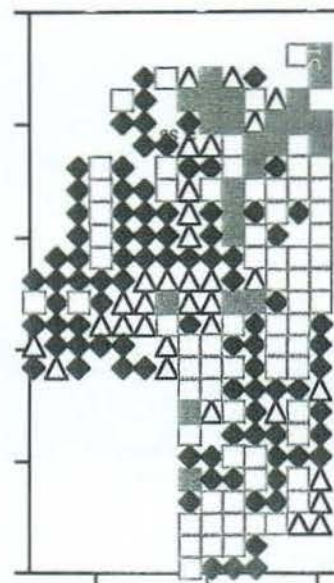
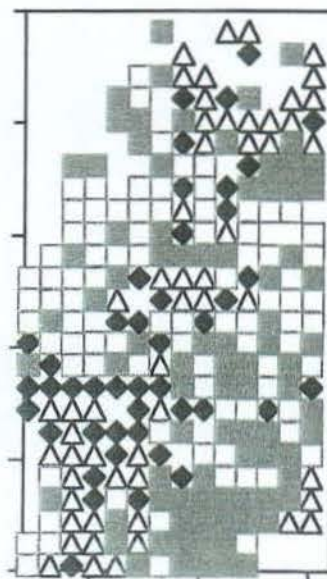
b)





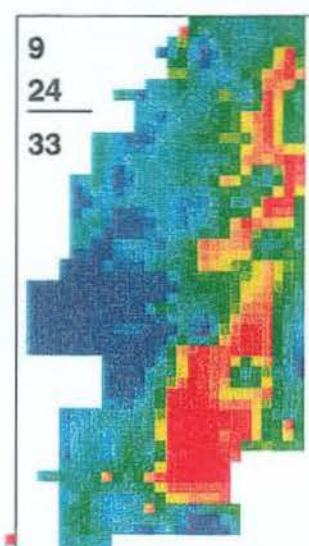
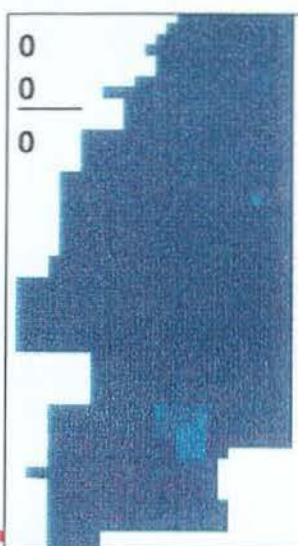


200
180
160
140
120



80
60
40
20
0

II
I
Tot



1992

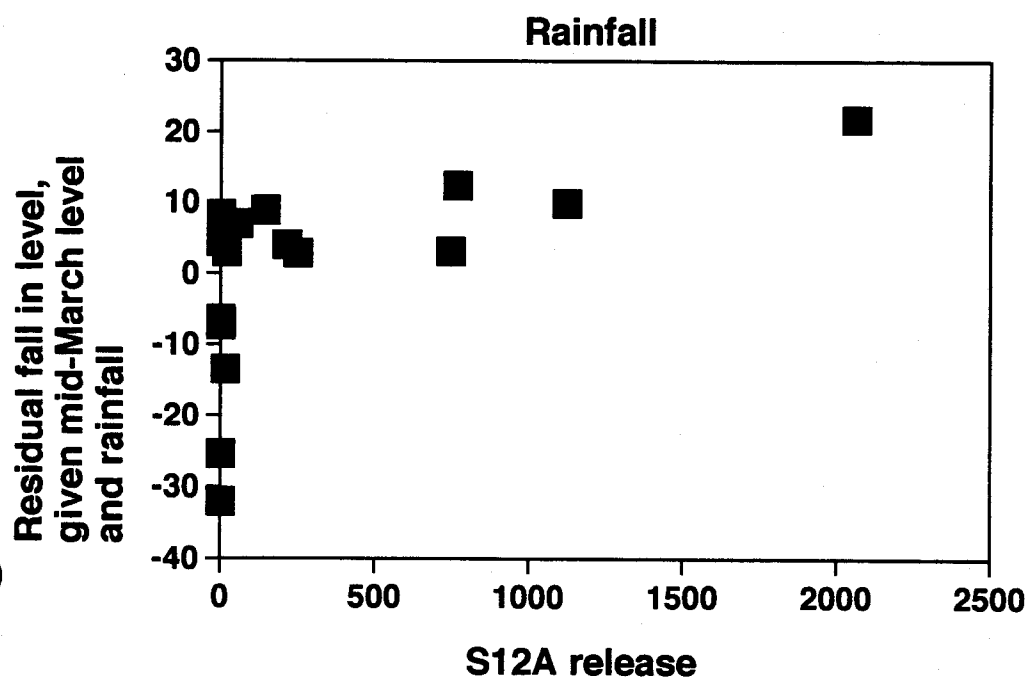
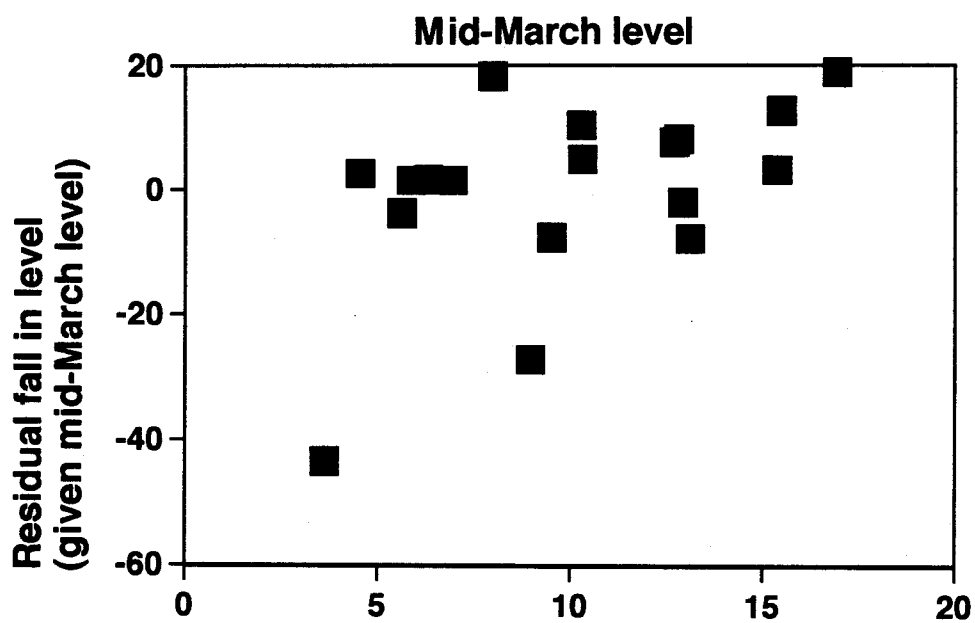
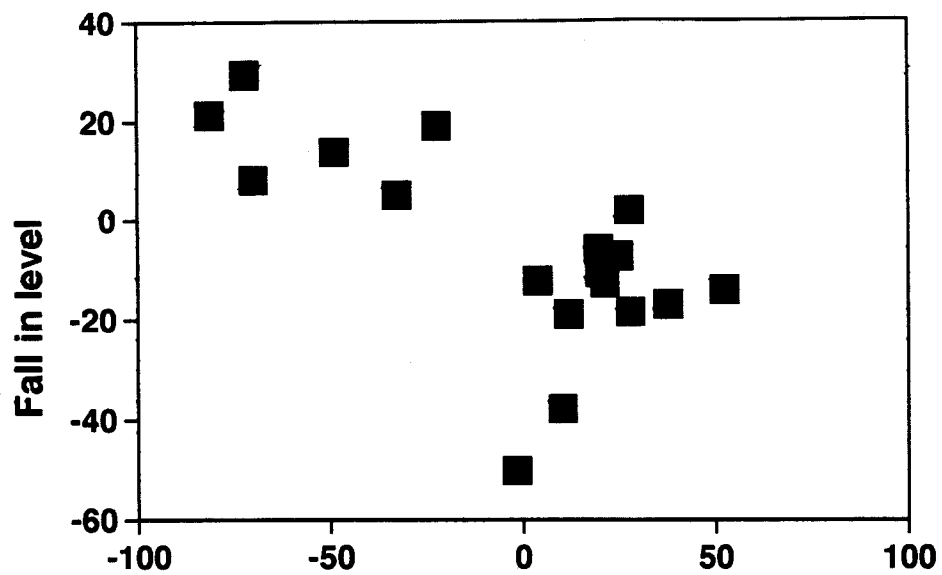
1995

1996

56
39
96

0
0
0

9
24
33



Dry days

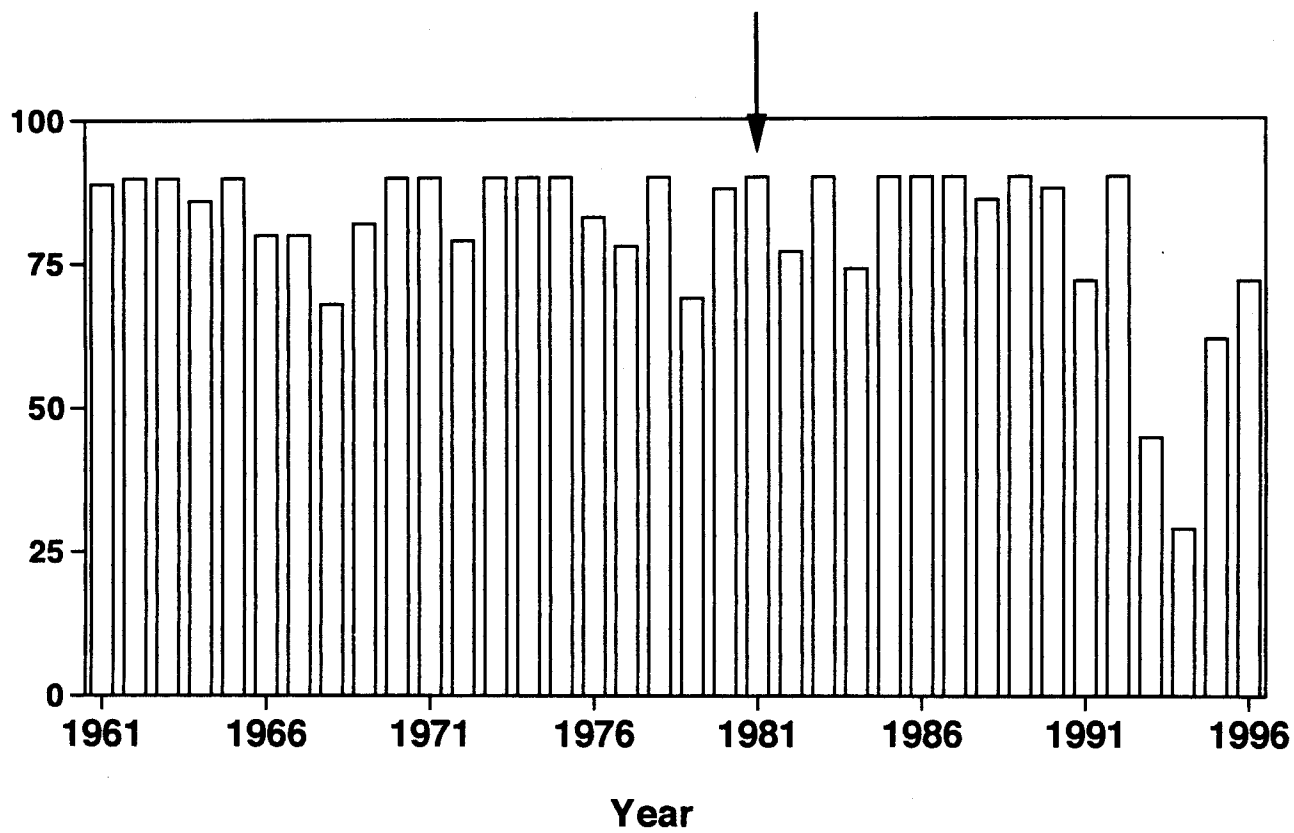


Table 1 Water levels at NP205 and associated statistics

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

Table 2. A comparison of the vegetation of Taylor Slough between the years 1975 (from Werner 1975), 1995 and 1996. We determined species dominance for the 1995 and 1996 data by scaling percentage coverage measurements per square meter to percentage coverage of all live plants after Werner's method.

Parameter	1975	1995/1996
Square meters sampled (N)	50	16
Mean No. of species / square meter	9.9	4.1
Muhly dominance by % cover	82%	21%
Sawgrass dominance by % cover	14%	77%

LIFE HISTORY OF THE ENDANGERED CAPE SABLE SEASIDE-SPARROW

JULIE L. LOCKWOOD^{1*}, KATHERINE H. FENN², JOHN L. CURNUTT¹, DEBORAH
ROSENTHAL³, KARLA L. BALENT¹ AND AUDREY L. MAYER¹

¹ Dept. of Ecology and Evolutionary Biology, Univ. of Tennessee, Knoxville,
Tennessee 37996.

² South Florida Natural Resource Center, Everglades National Park, 40001
State Road 9336, Homestead, Florida 33034.

³ 340 SE Lilly Avenue, Corvallis, Oregon 97333.

*Corresponding author address: Dept. of Ecology and Evolutionary Biology,
Univ. of Tennessee, 569 Dabney Hall, Knoxville, Tennessee 37996. Phone:
(423) 974-1982. E-mail: TCJ@utkux.utk.edu.

RRH: *Lockwood et al.* • CAPE SABLE SEASIDE-SPARROWS

LRH: THE WILSON BULLETIN • Vol. 109, No. 4, December 1997

ABSTRACT. – Cape Sable Seaside-Sparrows (*Ammodramus maritimus mirabilis*), breeding within eastern Everglades National Park, were philopatric and moved only short distances between clutches. Incubation required 12 days, nestlings fledged at 9.2 days, and fledgling care ranged from eight to 20 days. The total nest cycle encompassed 34–44 days. Nestlings were fed spiders and insects, primarily Orthoptera, Lepidoptera, and Odonata. Diet varied between years and study sites. With the onset of summer rains, predation rate increased and nest success decreased. Breeding activity diminished throughout June coinciding with rising water in nest areas. Our results indicated that the lack of breeding habitat and the onset of summer flooding limit the breeding potential of *A. m. mirabilis*. Received 19 October 1996 accepted 5 December 1996.

In 1967, the Cape Sable Seaside-Sparrow (*Ammodramus maritimus mirabilis*), was classified as endangered (32 Federal Register 4001, 1967). Since 1992, its population has declined by more than 50% (Pimm et al. 1996). Its secretive habits, and the general inaccessibility of its preferred habitat, have long discouraged a comprehensive study of its breeding cycle and diet. Here we describe a two-year investigation of the biology of the species within eastern Everglades National Park. In particular, we provide information on nestling diet, nest cycle duration, nest success and non-breeding activity. From these data an accurate population model will be developed as an essential step in updating and implementing a recovery management scheme.

Howell (1919) discovered *A. m. mirabilis* in the sparse salt marsh prairies of Cape Sable. Ignorance of the south Florida interior led to the assumption that the sparrow's entire range fell within the Cape (Howell 1932). The September 1935 hurricane severely altered the landscape of Cape Sable causing the sparrow to disappear along with the prairies it inhabited (Pimm et al. 1996). Subsequent sightings of *A. m. mirabilis* were sporadic and unreliable until L. A. Stimson's search in 1955. Surprisingly, he identified several 'colonies' within freshwater marshes of the everglades (Stimson 1956). These sightings comprised the only known range of *A. m. mirabilis* until extensive surveys in 1981.

The 1981 surveys indicated that Cape Sable Seaside-Sparrows prefer short-hydroperiod freshwater prairies (Bass and Kushlan 1982, Kushlan and Bass 1983). Subsequent, range-wide breeding surveys defined two core areas that accounted for over 70% of all individuals (Pimm et al. 1996). One lies east, and the other lies west, of Shark River Slough (Fig. 1). Five areas of

lower density and intermittent occupancy adjoin these locations to the east. Since 1993, the western population has declined sharply while the eastern core population has remained nearly constant (Pimm et al. 1996).

STUDY AREA AND METHODS

We established six study sites (30–60 ha) east of Shark River Slough (Fig. 1). Water inundates all sites from July to December, but recedes through most of the sparrow's breeding season (March through June). Muhly grass (*Muhlenbergia filipes*) and sawgrass (*Cladium jamaicense*) dominate the vegetation. Muhly-dominated, or marl, prairies are the most speciose plant communities in the everglades (Olmstead et al. 1980). Frequent fires and a characteristic hydroperiod maintain the vegetative structure (Kushlan et al. 1982).

We made systematic nest searches and behavioral observations from late March through mid-August in 1995, and from early March through the end of July in 1996. Study area visits averaged one per week. We also made opportunistic observations from August 1995 until February 1996 within the Dogleg and Alligator Hammock sites (Fig. 1). We recorded the location, time, behavior and all intraspecific interactions of individuals within each study area. We marked nests and monitored them until fledging or failure. During brief visits on alternate days we recorded egg numbers, hatching and fledging dates, and predation events. Daily, we observed what prey items were brought to the young, how often, and by which parent. We recorded the depth of surface water once per week at fixed stations within our study areas.

Observations of morning and late afternoon feedings averaged five hours per nest each week. We photographed adult sparrows holding prey

items within 5–10 m of the nest. Comparing these photographs to observer notes corroborated identification of prey. We were unable to classify 25% of the prey items. Most unidentifiable prey items we estimated were less than half the sparrow beak length.

We sampled the insect communities in our plots using standard sweep-net protocols (see Pimm et al. 1995 for description of methods). To measure this population's relative use of prey orders, we compared prey available (sweep net samples) to prey taken (feeding observations) using the formula: $\text{Relative use} = (\% \text{ taken} - \% \text{ available} / \% \text{ available})$. We divided relative use data into three periods: 25 March to 10 April, 11 April to 25 April, 26 April to 10 May 1996. By dividing the number of prey taken in one period by the total number of prey taken for all periods, we calculated the percent taken. We used the same formula to calculate the percent available. We interpreted relative use as: under-represented ($< \text{zero}$), neutral ($\approx \text{zero}$), or over-represented ($> \text{zero}$).

Using Chi-square contingency tables, we compared proportional representation among prey taxa between years (1995, 1996) and sites (Dogleg, OIHN, and OIHS). Our analyses included only those orders that incorporated more than 5% of the total number of individuals in either sweep net or feeding samples. We did not include two sites for which prey observations were minimal.

Schaub et al. (1992) provided the method of estimating predation rate that we employed. This method calculates predation rate by dividing the number of apparent predation events by the total number of days that nests contained eggs or young. We assumed predation when clutches disappeared between observations or when we found direct evidence — such as broken

eggshells or destroyed nests. The rate calculation gives equal weight to all methods of predation detection.

RESULTS

Breeding season duration. – In 1995 the first nest (found 18 April) held nestlings 5–6 days old. In 1996, we found a nest in which the first egg was laid on 27 March. We estimated that nest building began around mid-March. Werner (1975) observed flightless fledglings as early as 2 April indicating that these nests were built in late February. Thus, it appears the onset of nesting only varies by a few weeks annually.

Cessation time may vary by as much as a month or more, however. Werner (1975) reported observing eggs as late as 7 July, 1974 and nestlings as late as 26 July, 1974. The next year (1975) he reported that nesting ceased in early July concurrent with the onset of summer rains. In our study, the latest nesting activity occurred in mid-May 1995 and late June 1996, also concurrent with the onset of summer flooding.

Nest success. – Searches during the 1995 and 1996 breeding seasons yielded 24 nests. Four of five 1995 nests, and 13 of 19 1996 nests, were first clutches. We positively identified four second clutch attempts in 1996 and none in 1995. One nest in 1995 and two in 1996 coincided with known second clutches. A nest found with eggs in late June 1996 was a positively identified third clutch.

Using the Mayfield method (Mayfield 1975) we calculated a hatching success rate of 88% ($N = 14$, 28 young from 32 eggs) – a rate common for Seaside Sparrows (Post and Greenlaw 1994). This population laid an average of 3.2 eggs per nest ($N = 14$, range = 2–4, mode = 3,4). This is consistent with

the clutches found by Werner (1975) at Taylor Slough but, somewhat smaller than northern populations of Seaside Sparrows (Post et al. 1983, Post and Greenlaw 1994). Each nest on average contained three nestlings (range, 2–4, $N = 14$).

Werner (1975) calculated a crude nest success rate (i.e., the number of fledglings resulting from a known number of eggs) of 62% ($N = 16$). In our study, 15 young fledged from 26 first-clutch eggs. None of eight second-clutch eggs hatched. The sole third clutch of two eggs was abandoned. Overall, we found 36 eggs from which 15 young fledged ($N = 14$). This gives a crude success rate of 42% which is below that reported by Werner (1975).

Breaking down nest success using the methods of Mayfield (1975) and Johnson (1979) more accurately reflected annual productivity. The probability of success for a Cape Sable Seaside-Sparrow nest through 12 days of incubation (see below) was 0.61 ($SE = 0.02$, $N = 13$, 75 nest-days with 3 losses). The probability of success for a nest through the 9 days of nestling care was 0.75 ($SE = 0.02$, $N = 18$, 125 nest-days, 4 losses). Multiplying these with the 0.88 probability of hatching gave the probability of an egg successfully producing a fledgling equal to 0.40. Thus, only 40% of all eggs laid will contribute to the total population annually.

In 1996, water directly influenced the success of two nests. The first, found on 6 June with four eggs, hatched three young on 8 June. When water flooded the bottom of the nest on 12 June all nestlings disappeared. The water level was 15 cm deep, a depth 1 cm above the bottom of the nest. The second nest, discovered on 20 June with two eggs, flooded two days later and incubation ceased. Here, the water level was 23 cm deep, again 1 cm above the bottom of the nest.

Predation accounted for 78% of all losses of young or eggs. In the first five weeks of the breeding season, a nest succumbed to predators on less than 3% of all the days when eggs or nestlings were present (Fig. 2). Beginning in late May, this rate reached 13%. Thirteen nests were first clutches. Only two of the other six nests (i.e., second and third attempts) successfully fledged young.

The presence of surface water corresponded with the late season increase in predation rate. To show this, we calculated success rate in a comparable way to predation rate. We divided the number of hatching or fledging events by the number of days nests held young or eggs. The two rates intersect in early June. June 1 marked the beginning of consistent coverage of all study sites with surface water (Fig. 2).

Kushlan et al. (1982) suggested that rice rats (*Orzymus palustris*) and snakes principally threaten nests. Post (1981) indicated that rice rats, fish crows (*Corvus brachyrhynchos*) and raccoons (*Procyon lotor*) threatened Seaside Sparrow populations in northern Florida. As we have never directly observed any predation events, we cannot speculate on what advantages the presence of surface water may afford predators.

Phenology. – We followed one nest throughout egg laying and incubation. A complete nest found on 22 March did not contain its first egg until 27 March. The female laid the second, and final egg, on 29 March. She then incubated the eggs for 12 days. This is the first direct observation of Cape Sable Seaside-Sparrow incubation length. An incubation period of 12 days is consistent with other populations of Seaside Sparrows (Post and Greenlaw 1994). It is unclear how common it is for *A. m. mirabilis* females to lay every other day. Post and Greenlaw (1994) indicated that most races of Seaside

Sparrow lay one egg per day. Since the average number of eggs laid for this population is 3.2, the number of days devoted to egg laying is likely an equivalent 3 or 4 days.

Nestlings fledged after an average of 9.2 days in the nest ($N = 15$). For two to three days, they remained sheltered under vegetation 5 to 10 meters from the nest. Observations of fledgling-adult interactions were sporadic. We observed adults feeding juveniles eight days after fledging and Werner (1975) observed adults feeding juveniles up to 20 days after fledging.

Totaling these numbers, we estimated the nest cycle of *A. m. mirabilis* to be 34 to 44 days. This number varies according to the number of eggs laid and the length of post-fledging care (Fig. 3). Since nesting appears to began in mid-March, a pair that successfully triple brooded (at least 44 days times 3) would maintain breeding activity into early August. This schedule falls within the observations of Werner (1975) and those reported in Post and Greenlaw (1994).

Nestling diet. – Six orders of Insecta and one order of Araneida composed the observed nestling diet. Males brought food to nestlings in 52%, and females in 48%, of all visits ($N = 251$). Feedings occurred approximately every 16 minutes ($N = 1242$) and adults commonly carried more than one insect per trip (average = 1.35; $SD = 0.56$, $N = 260$). Since adults often carried only the abdomens of Odonata and Orthoptera, we suspected that they either ate or discarded all other parts before arriving at the nest. Post and Greenlaw (1985) and Greenlaw (1992) reported that adults of other races presented macerated, or mucous-bound, food items to nestlings.

Nestling diet included Lepidoptera, Orthoptera, and Odonata to a greater extent than expected by their availability in 1996 (Fig. 4). Conversely, it

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

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

Nestling diet data from 1996 also evinced differences among sites ($\chi^2 = 31.5$, $df = 8$, $P < 0.001$). Odonata were absent from nestling diets at OIHN despite their presence at all other sites (Fig. 6). Lepidoptera were absent from Dogleg, but common at OIHN. Orthoptera had equal representation at each site, as did an unidentified (but distinct) species.

Seasonal and yearly movements. – Male Cape Sable Seaside-Sparrows exhibited a high degree of philopatry – a common trait in all Seaside Sparrow races (Post 1974, Post and Greenlaw 1994). In 1996, three males nested an average of 40 meters away from their 1995 nests. Second clutch nests ranged eight to 95 m from the site of the first clutch nest. Sparrows never re-used nests. After nest destruction, we observed males attending a nest within the

same territory. Since very few females have been banded, we do not know if the re-nest attempts by these males included the same females as well.

Observations of where *A. m. mirabilis* spends the wet-season (post-breeding) are less detailed. Werner (1975) suggested that rising surface water ended the nesting season but, provided no further information. Breeding behavior ceased in two of our study areas when surface water reached the average height of nests above the ground (14 cm). Adults remained within established territories and defended juveniles until surface water appeared. Afterwards, observations of females became rare and some males disappeared. Those males that remained moved into vacant neighboring territories or into taller, denser vegetation. They continued to sing and defend juveniles. Although juveniles tended to associate with a particular male, we observed a group of seven with two banded males outside any territory. Water levels peaked at 18 cm in late June with a subsequent dry-down occurring in mid-July (down to 4 cm). Breeding activity however, never resumed. We observed sparrows around tree islands and sawgrass sways from late June into July (B. Moody and T. Brooks pers. com.). Males sang sporadically in open prairies throughout the remainder of the winter.

DISCUSSION

The Cape Sable Seaside-Sparrow is a dietary generalist. We detected significant differences in nestling diet between years and sites. In addition, *A. m. mirabilis* shifted the importance of prey items in its diet with their availability. This reflects the patchy distribution typical of insects and the opportunistic nature of sparrow foraging (Post and Greenlaw 1994).

Cape Sable Seaside-Sparrows rely on Orthoptera and Lepidoptera much like all other races (Post et al. 1983, Merriam 1983). The absence of Diptera and other mud-dwelling insects from the nestling diet is consistent with Seaside Sparrow populations studied in northern Florida (Post et al. 1983). This behavior contrasts that of sparrows inhabiting salt marshes in the northern parts of the species' range (Merriam 1983). Southern races, including *A. m. mirabilis*, depend less on open mud flats (Post and Greenlaw 1994, Quay et al. 1983). There are few, if any, expansive mud flats within our study areas. Cape Sable Seaside-Sparrows appear unique among the Seaside Sparrow races in their use of Odonata. This is not surprising since this is the only race to inhabit freshwater marshes.

Breeding consistently begins in March and potentially continues into early August. The sparrow may fledge three broods given suitable conditions. Since *A. m. mirabilis* is a breeding habitat specialist (Pimm et al. 1996), consistently available habitat will increase sparrow breeding potential.

Two factors, each working at different temporal scales, limit the sparrow's reproductive potential however. The first, which we do not address here, is the dynamic nature of sparrow breeding habitat. Long-term hydrologic conditions and fire may rapidly change vegetative composition of marl prairies (Pimm et al. 1996). A philopatric male may find his territory unsuitable for breeding from one year to the next. Second, the onset of summer rains limit the breeding season, as the flooding of two nests demonstrates. The initiation of the wet season varies. Thus, with a series of 'good years' (those with delayed summer rains) sparrow populations may increase considerably. Conversely, with a series of 'bad years' (those in which

summer rains begin early) Cape Sable Seaside-Sparrow populations may decrease substantially.

We still lack a complete knowledge of *A. m. mirabilis* wet season dispersal and habitat requirements. In other races, individuals moved to sheltered areas consisting of tall smooth cordgrass (*Spartina alterniflora*) after the breeding season (Post and Greenlaw 1994). The higher concentrations of insects (Post et al. 1983) and seeds in cordgrass presumably attracted individuals (Post and Greenlaw 1994). The same may be true for sawgrass sways in everglades freshwater prairies. In addition, the unique south Florida climate may or may not produce novel wet season (or over-wintering) adaptations.

The next step in formulating a reasonable recovery strategy is linking the known aspects of sparrow breeding biology to this temporally variable environment. Population models of the Cape Sable Seaside-Sparrow, even spatially explicit ones, must incorporate stochastic environmental factors. When this information is available, results from population models will be applicable to management schemes.

ACKNOWLEDGMENTS

We thank the following individuals for considerable help in the field: Thomas Brooks, Gareth Russell, Phil Nott, Jan Yacabucci, Laura McMahon, Ester Stanton, Barron Moody, Stuart Pimm and Stephanie Pimm. Sonny Bass and Marty Fleming contributed invaluable advice. Grants from the National Park Service, the National Biological Survey, the United States Fish and Wildlife Service, the Pew Charitable Trusts and the South Florida Water Management District to Stuart Pimm funded this project. The Americorp

program funded several of the individuals involved. We thank Jon Greenlaw for editorial advice.

LITERATURE CITED

- BASS, O., JR. AND J. KUSHLAN. 1982. Status of the Cape Sable Sparrow. South Florida Research Center Report T- 672, Everglades National Park, Homestead, Florida.
- GREENLAW, J. 1992. Seaside Sparrow, *Ammodramus maritimus*. Pp. 211-232 in Migratory nongame birds of management concern in the northeast. (K. Schneider and D. Pence, eds.). U.S. Dept. of Interior, Fish and Wildlife Service, Newton Corner, Massachusetts.
- AND W. POST. 1985. Evolution of monogamy in Seaside Sparrows, *Ammodramus maritimus*: tests of hypotheses. Anim. Behav. 33:373-383.
- HOWELL, A. 1932. Florida bird life. Coward-McCann, Inc., New York, New York.
- . 1919. Description of a new seaside sparrow from Florida. Auk 36:86-87.
- JOHNSON, D. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651-661.
- KUSHLAN, J. AND O. BASS, JR. 1983. Habitat use and distribution of the Cape Sable Sparrow. Pp. 139-146 in The seaside sparrow, its biology and management (T. Quay, J. Funderburg, Jr., D. Lee, E. Potter and C. Robbins, eds.). Occas. Papers of the North Carolina Biol. Survey 1983-5, Raleigh, North Carolina.

- , O. BASS JR., L. LOOPE, W. ROBERTSON JR., P. ROSENDAHL, AND D. TAYLOR. 1982. Cape Sable Sparrow management plan. South Florida Research Center Report M-660, Everglades National Park, Homestead, Florida.
- MAYFIELD, H. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87:456-466.
- MERRIAM, T. 1983. Food habits of nestling Seaside Sparrows in unaltered and ditched salt marshes on Long Island, New York. Pp. 115-122 in *The seaside sparrow, its biology and management* (T. Quay, J. Funderburg, Jr., D. Lee, E. Potter and C. Robbins, eds.). Occas. Papers of the North Carolina Biol. Survey 1983-5, Raleigh, North Carolina.
- OLMSTEAD, I., L. LOOPE, AND R. RINTZ. 1980. A survey and baseline analysis of aspects of the vegetation of Taylor Slough. South Florida Research Center Report T-515, Everglades National Park, Homestead, Florida.
- PIMM, S., J. CURNUTT, J. LOCKWOOD, L. MANNE, A. MAYER, M. NOTT, AND K. BALENT. 1996. Population ecology of the Cape Sable Sparrow (*Ammodramus maritimus mirabilis*): Annual report, 1996. NBS/NPS, Everglades National Park, Homestead, Florida.
- , T. BROOKS, J. CURNUTT, J. LOCKWOOD, L. MANNE, A. MAYER, M. NOTT, K. BALENT, AND G. RUSSELL. 1995. Population ecology of the Cape Sable Sparrow (*Ammodramus maritimus mirabilis*): Annual report, 1995. NBS/NPS, Everglades National Park, Homestead, Florida.
- POST, W. 1981. The influence of rice rats (*Oryzomys palustris*) on the habitat use of the Seaside Sparrow, *Ammodramus maritimus*. *Behav. Ecol. Sociobiol.* 9:35-40.

- AND J. GREENLAW. 1994. Seaside Sparrow. Pp. 1–28 in *The birds of North America*. No. 127 (A. Poole and F. Gill, eds). American Ornithologists Union, The Academy of Natural Sciences of Philadelphia.
- , —, T. MERRIAM, AND L. WOOD. 1983. Comparative ecology of northern and southern populations of the Seaside Sparrow. Pp. 123–136 in *The seaside sparrow, its biology and management* (T. Quay, J. Funderburg, Jr., D. Lee, E. Potter and C. Robbins, eds.). Occas. Papers of the North Carolina Biol. Survey 1983-5, Raleigh, North Carolina.
- QUAY, T., J. FUNDERBURG JR., D. LEE, E. POTTER, AND C. ROBBINS. 1983. The seaside sparrow, its biology and management. Occas. Papers of the North Carolina Biol. Survey 1983-5, Raleigh, North Carolina.
- SCHAUB, R., R. MUMME, AND G. WOOLFENDEN. 1992. Predation on the eggs and nestlings of Florida Scrub Jays. *Auk* 109:585–593.
- STIMSON, L. 1956. The Cape Sable Seaside Sparrow: Its former and present distribution. *Auk* 73:489-502.
- WERNER, H. 1975. The biology of the Cape Sable Sparrow. Report to the U.S. Fish and Wildlife Service. Everglades National Park, Homestead, Florida.
- AND G. WOOLFENDEN. 1983. The Cape Sable Sparrow: its habitat, habits, and history. Pp. 55–75 in *The seaside sparrow, its biology and management* (T. Quay, J. Funderburg, Jr., D. Lee, E. Potter and C. Robbins, eds.). Occas. Papers of the North Carolina Biol. Survey 1983-5, Raleigh, North Carolina.

FIGURE LEGENDS

FIG. 1. All study sites were located within eastern Everglades National Park. Each are incorporated within a sub-population of the Cape Sable sparrow, southeast of Shark River Slough.

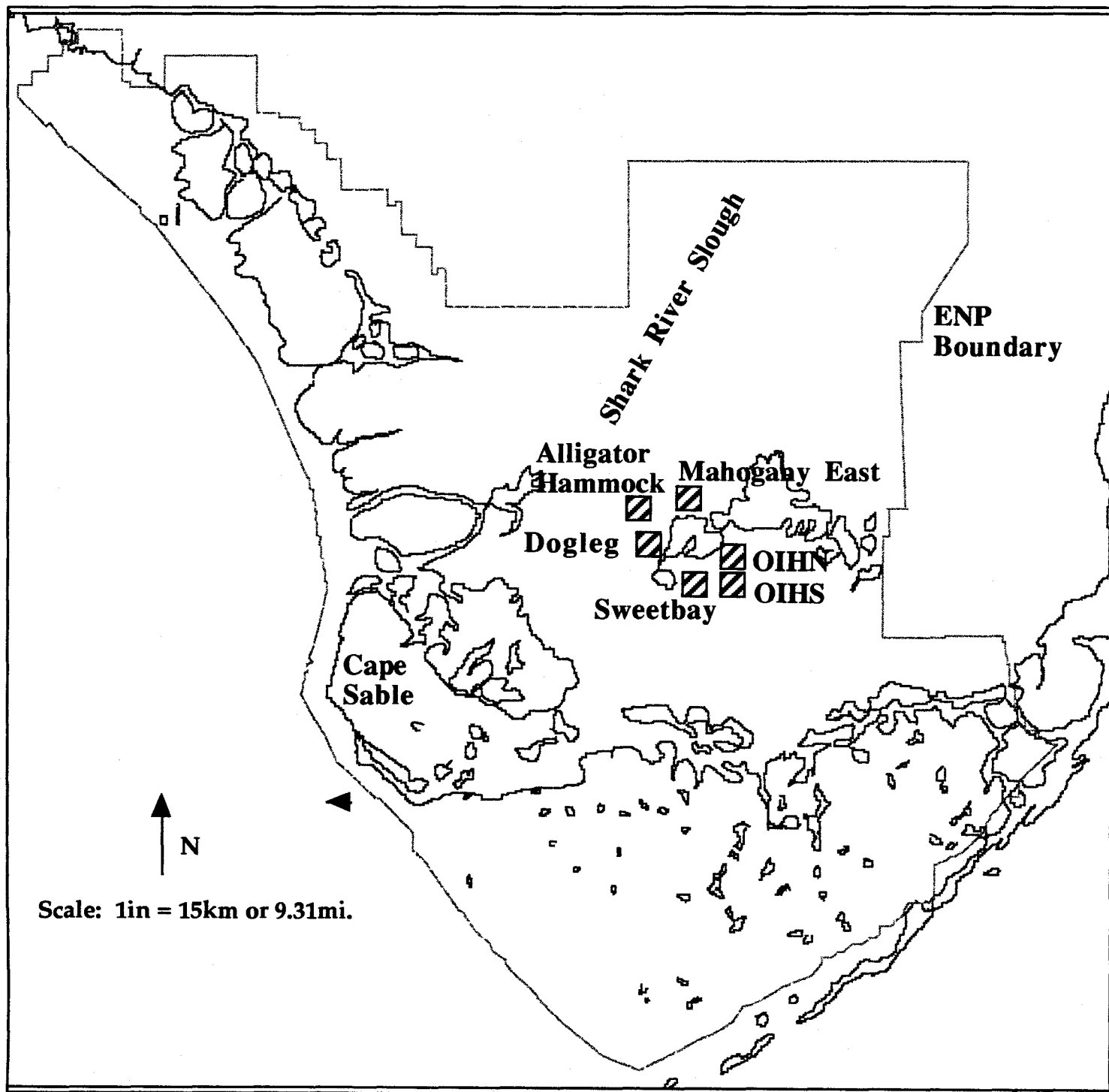
FIG. 2. Predation and success rate for 1996 nests. An increase in nest predation, a decrease in nest success, and the appearance of surface water coincided around June 1, 1996.

FIG. 3. Cape Sable sparrow nest cycle duration encompasses at the most 49 days. Thirty-five of those days can be accounted for through previous observations. The remaining 14 are devoted to courtship, nest building and other activities (e.g., fledgling care, independent feeding).

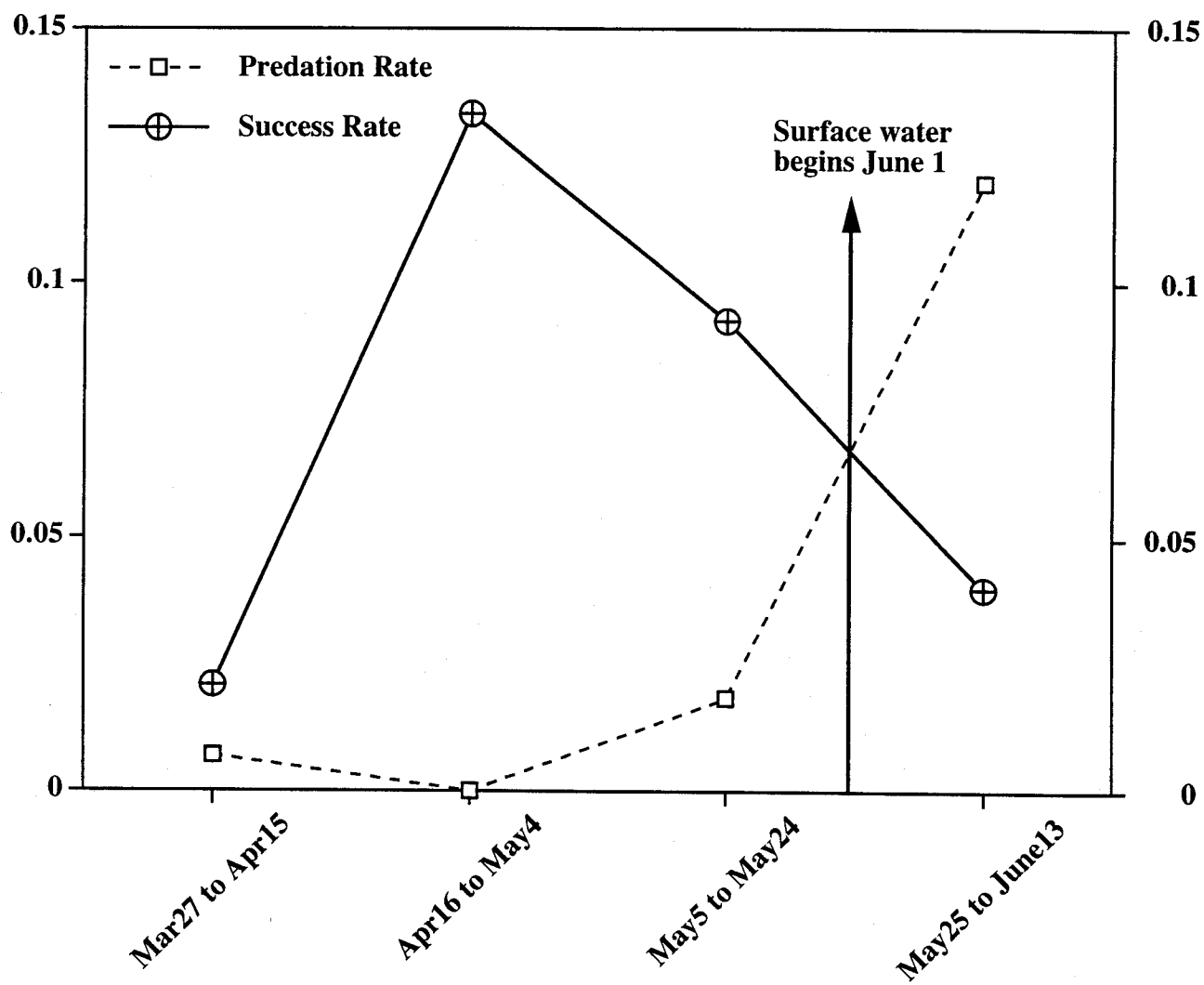
FIG. 4. Relative use of prey items in nestling diet. Availability based on sweep net samples. Prey use based on observations made on 1996 nests.

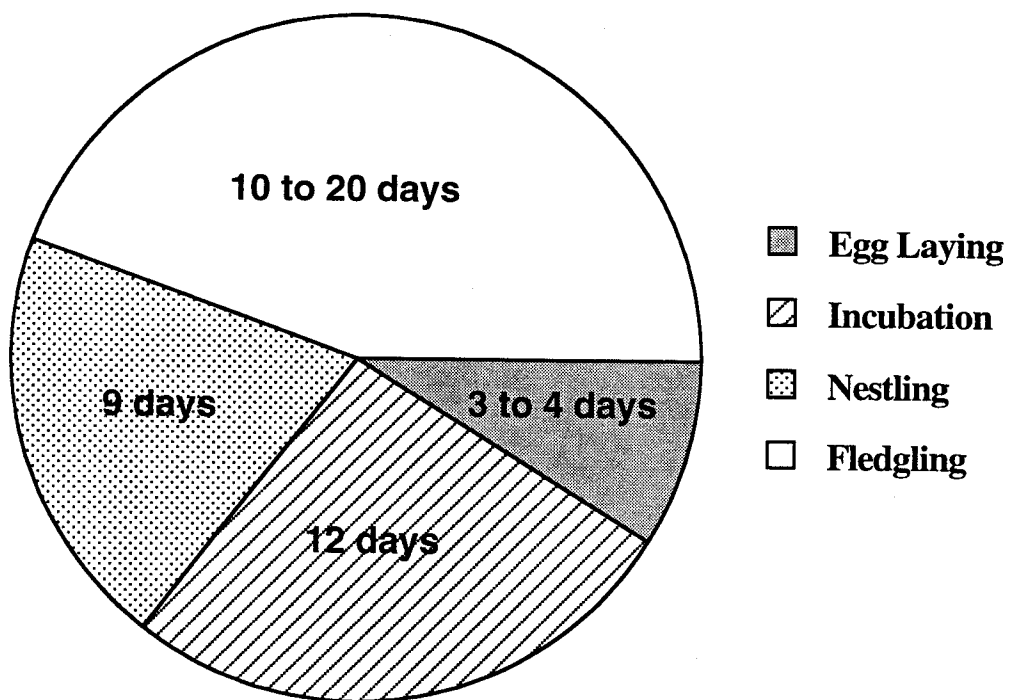
FIG. 5. Composition of nestling diet by insect order. Data collected from first clutch nests in 1995 and 1996. S = significant difference between years.

FIG. 6. Between-site differences in composition of nestling diet. S = significant difference between sites.

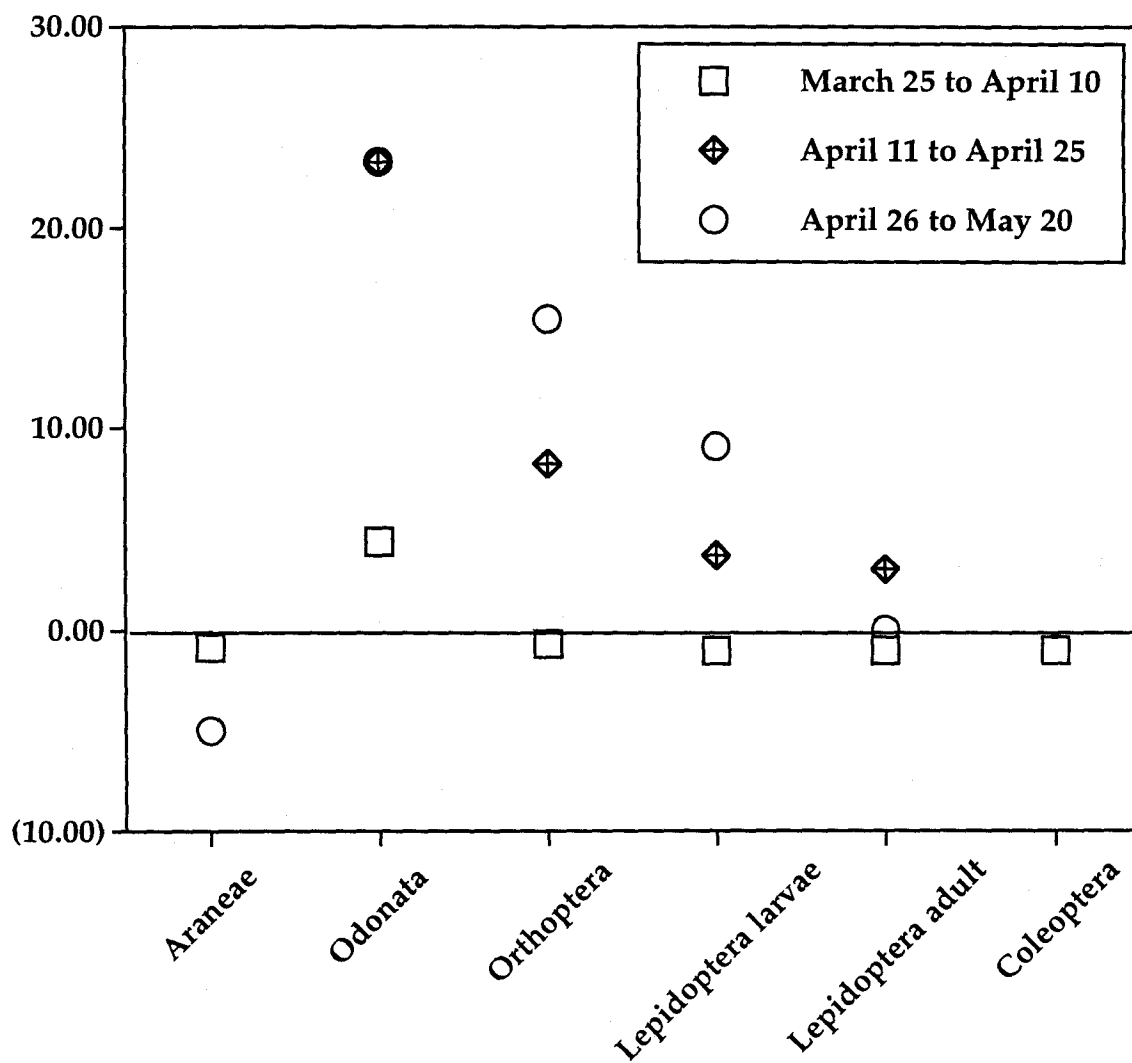


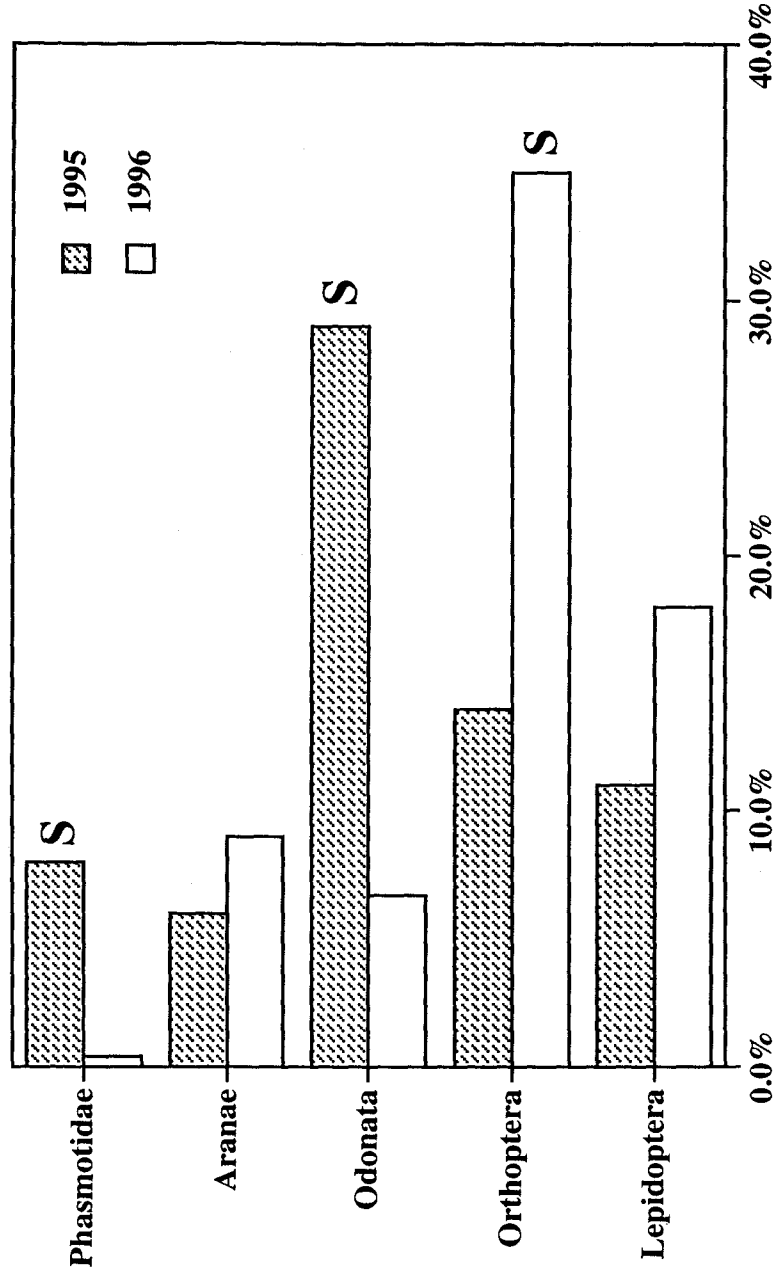
Rate

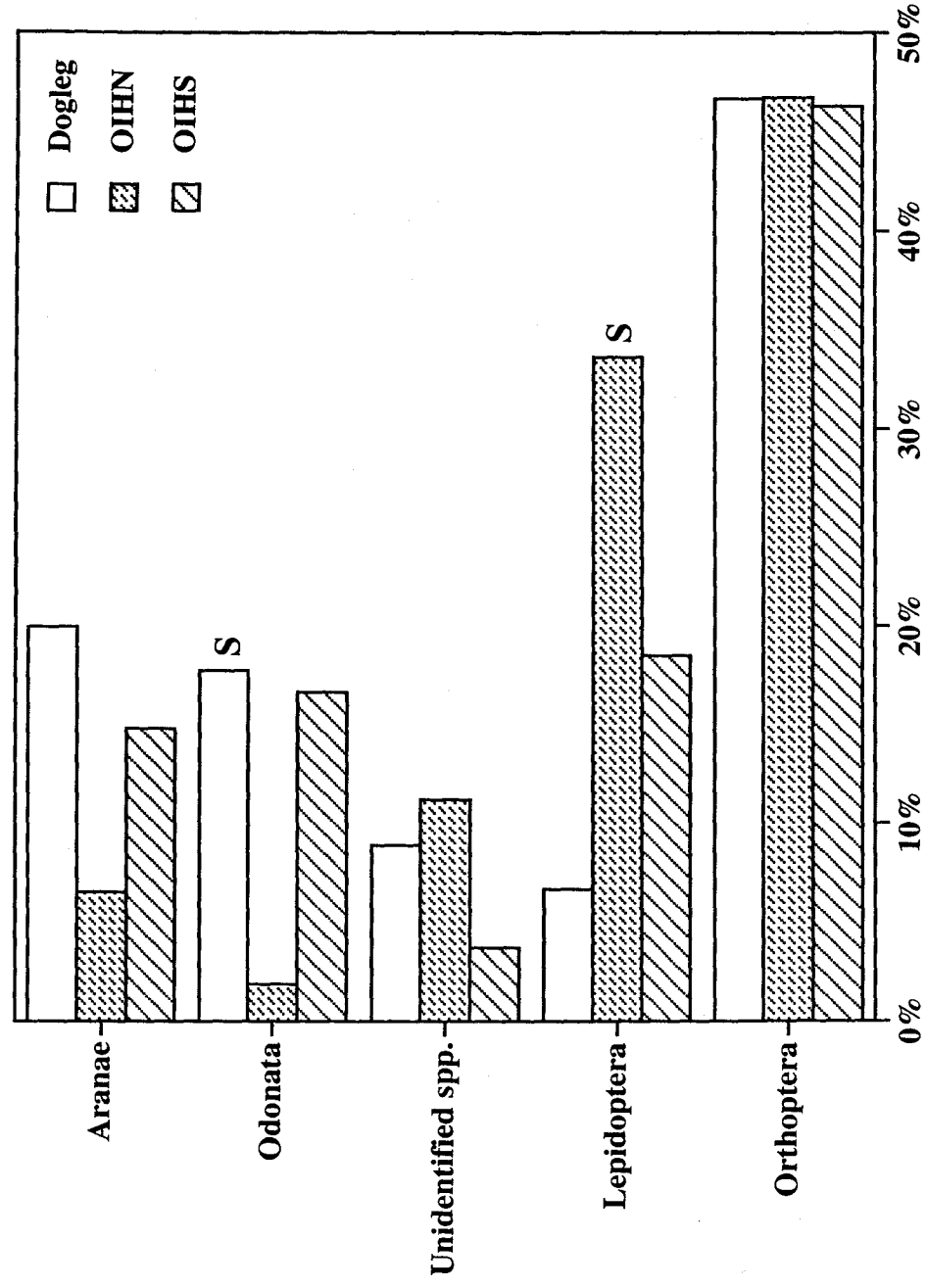




Relative Use







DRAFT – results and conclusions subject to change with increased data or future analyses.

Cape Sable Seaside Sparrow Breeding Report Addendum

DRAFT – results and conclusions subject to change with increased data or future analyses.

Introduction

Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*) populations have experienced tremendous declines within some areas of Everglades National Park. Nott et al. (in review) and Curnutt et al. (in review) attribute most of this reduction to loss of suitable breeding habitat. We know from Werner (1975) the range of habitats in which sparrows breed. We know roughly what habitat types support higher densities of sparrows (O'Meara and Marion 1985, Schroeder and Armbruster 1985, Nott et al. in review, Pimm et al. 1996, Kushlan and Bass 1982). Presumably, within this range of habitats, less suitable habitat should manifest low, or no, breeding success. If so, we can link ecosystem processes (such as hydroperiod and fire frequency) to habitat changes that promote sparrow population declines.

First, however, we must determine how variable sparrow breeding success and nesting habitat preferences may be. Part I provides preliminary data on the variability of breeding success through time and space. Part II provides preliminary data on the variability of nesting habitat and nest site preferences. From this preliminary information we can direct future work toward characterizing 'good' and 'bad' breeding habitat and determining the effects of flood and fire management on each.

Descriptions of study sites

Our analyses included eight study plots within Everglades National Park (Figure 1). All plots are approximately 1 ^{km²} ~~ha~~ in area and support breeding

DRAFT – results and conclusions subject to change with increased data or future analyses.

individuals (Curnutt et al. in review). Seven of six study plots fall within the eastern 'core' sub-population (B) which has varied little in sparrow density since 1981. In six of these seven plots we have banded birds since 1994 and monitored nesting since 1995. The remaining plot, Far East, we established in 1997. Four of these six plots are along the Main Park Road. The remaining three are at the end of Old Ingraham Highway (Figure 1).

The western sub-population (B) experienced a 85% loss of individuals between 1992 and 1993 and continues to slowly decline (Nott et al. in review). Nott et al. (in review) estimate that surface water inundated this area well into the breeding season at least two of the past five years. Consequently, sparrows continue to occupy only small pockets of habitat in higher elevations. In 1997, we established a study plot (Shark Valley) within one of those pockets. We include this plot in our analyses to provide information on the breeding success and nest sites characters within this struggling population.

Parkwide monitoring agencies measure elevation and hydroperiod at scales too large to distinguish our plots. Thus, we independently charted characteristic elevation and hydroperiod of our plots. In early June 1997 (well after the summer rains began) we measured water depth from water surface to ground level at a series of 30 random points within each study plot and underneath all nests. We then compared our measurements to water depth above mean sea level (MSL) recorded at nearby Everglades National Park monitoring stations. By simply subtracting our water depth measurements

DRAFT – results and conclusions subject to change with increased data or future analyses.

from those gathered at the monitoring station, we obtained approximate ground elevation at each point.

Elevational distribution at each plot we compared to all other plots using a Student's t-test. The plots fall into three distinct elevational groups. The Shark Valley plot has the highest mean elevation of 101 cm MSL (sd=7.5). The three plots located at the end of Old Ingraham Highway constitute a group with mean elevation of 67 cm MSL (sd=12.6). The lowest plots fall along the Main Park Road with a elevational mean of 42 cm MSL (sd=8.9).

Water depths from 1997 show that each elevational group (i.e. the Ingraham plots, Main Park Road plots and Shark Valley plot) experienced differing durations of surface water during the breeding months (Figure 2). The zero level in Figure 2 represents mean ground level taken for each of the three elevation groups. The mean deviation from ground level is plotted through the breeding season providing a graph of approximate surface water depth. Thus, when water depth is within 10 cm of the zero line, surface water is present on at least some portion of the plots (plots have a standard deviation in elevation from 8 to 12 cm). Only when water level drops down to approximately 10 cm below ground level is the entire plot likely to be dry (i.e. without measurable surface water).

Figure 2 indicates that during the 1997 breeding season the Ingraham Road plots experienced nearly 40 dry days, all during the peak of the breeding season (April to early May). Although the plots along Main Park Road experienced only 10 dry days in early May they were mostly dry during peak

DRAFT – results and conclusions subject to change with increased data or future analyses.

breeding weeks. The Shark Valley plot experienced no dry days within the 1997 breeding season. Water depths reached approximate ground level the first week of June – well past the peak weeks of the sparrow breeding season.

Thus, our 7 study plots can be grouped by elevation and hydroperiod. The Shark Valley (SV) plot, while being the highest in elevation, experiences the longest hydroperiod. The plots along Main Park Road (MPR), while being the lowest in elevation, experience moderate surface water depths throughout the breeding season. The Ingraham Highway (ING) plots are by far the driest having the highest mean elevation among the eastern sub-population plots.

DRAFT – results and conclusions subject to change with increased data or future analyses.

Part I. Breeding success of Cape Sable Seaside Sparrow through time and space. By: Katherine H. Fenn, Julie L. Lockwood, David Okines and Jeffrey R. Duncan.

Methods

We searched for nests from early March to mid June in 1996 and 1997. Every two to three days we recorded the number of eggs and young. When a nest failed, we recorded its condition and collected any evidence of predation. We calculated predation rate (Schaub et al. 1992, Lockwood et al. in press). and success rate for each stage of the nest cycle (Mayfield 1975). Success rate we calculated by year, clutch and elevation/hydroperiod group (i.e. MPR, ING, and SV). We compared water depth to predation rate using a simple linear regression.

Results

We found 19 nests in 1996 and 33 nests in 1997 for a total of 52 (appendix A). Forty were first clutches, 11 were second and one was a third clutch. Hatching success was 96% (131 hatched/137 laid). The success probability for the incubation stage was 49% (156 exposure days, 9 losses), and the probability of nests surviving the nestling stage was 79% (233 exposure days, 6 losses). Multiplying these probabilities gives a two year nest success estimate of 37% (Figure 3).

Second clutches were less successful than first. They had an incubation stage success rate of 30% (21 exposure days, 2 losses), a nestling stage success rate of 55% (47 exposure days, 3 losses) and a hatch rate of 96% (27 hatched/28

DRAFT – results and conclusions subject to change with increased data or future analyses.

laid). Thus, only 16% of all second clutch eggs resulted in fledglings. First clutch nests had an incubation stage success rate of 53% (135 exposure days, 7 losses), a nestling stage success rate of 87% (186 exposure days, 3 losses), and a hatch rate of 95% (104 hatched/109 laid). First clutch eggs had a 43% chance of successfully producing a fledgling.

Overall success dropped nearly 10% from 1996 to 1997 (Figure 3).

Lockwood et al. (in press) report a hatching success of 88%, a probability of a nest surviving the incubation stage of 61%, and a probability of a nest surviving the nestling stage of 75%. This yields an overall success rate of 40%. The 33 nests found in 1997 yielded hatching success rate of 97% (84 hatched/87 laid). Incubation stage success was 38% (90 exposure days, 7 losses), and nestling stage success was 88% (142 exposure days, 2 losses). Thus, in the 1997 breeding season an egg had a 32% chance of resulting in a fledgling.

We evaluated breeding success within the MPR (22 nests) and ING groups (26 nests). In the MPR group, the probability that an egg laid would result in a fledgling was 56%. In the ING group the probability was 26% (Figure 4). The ING group success rate during incubation was 32%. The MPR group had an incubation success rate of 80%. Few nests failed during the nestling stage. Success rate was 73% in the ING group and 84% in MPR. Thus, nests that survive the incubation stage have an excellent chance of fledging.

DRAFT – results and conclusions subject to change with increased data or future analyses.

Flooding and predation caused most nest failures. (We review the risk of flooding in Part II.) We have never directly observed nest predation, however evidence suggests that rats depredated three nests and snakes depredated two. Rats left their feces among egg shells or nestling bits. Snakes bored holes through the bottom of the nest removing its contents, but not destroying the nest itself. No nests were excessively dishelved or destroyed. We often observed red-winged blackbirds (*Agelaius phoeniceus*), northern harrier hawks (*Circus cyaneus*), red-shouldered hawks (*Buteo lineatus*) and crows (*Corvus spp.*) within our study plots but, we do not know their role in nest predation.

Lockwood et al (in press) demonstrated that plots covered in surface water experienced higher predation rates in 1996. If we review predation rates in 1996 and 1997, we see peaks, early and late in the breeding season (Figure 5). In late March 12%, and in late May 6%, of all active nests were lost to predation. (Nests failed the first weeks of June due to flooding.) Since surface water collects at the beginning of the rainy season, concurrent with these peaks in predation rate, a better test is to search for a positive correlation between water level and predation rate.

Only the ING group had enough non-zero predation numbers for comparison with hydroperiod. In 1997, predation rate increased with water level (Figure 6: $R^2=0.84$, exponential increase). Measurable surface water was present when mean water depth was 10 cm below mean ground level (i.e. -10

DRAFT – results and conclusions subject to change with increased data or future analyses.

cm in Figure 5). The highest predation rates occurred when surface water was present, but not necessarily late in the breeding season.

Summary

Cape Sable Seaside Sparrows had variable success in breeding through space and time. Breeding success ranged from 26% to 56% across groups. Success decreased from 40% to 32% between 1996 and 1997 and from 43% to 18% between first and second clutches. All of the nest failures occurred in the eastern sub-population. Predation accounted for most nest failures. Higher predation rates coincided with the presence of surface water.

DRAFT – results and conclusions subject to change with increased data or future analyses.

Part II. Nest microhabitat preferences of the Cape Sable Seaside Sparrow. By:

Julie L. Lockwood and Katherine H. Fenn.

Methods

In 1997 we sampled plant composition and structure around 16 active nests. We divided these nests into three elevation/hydroperiod groups (see above). Seven nests were located within the three plots along Main Park Road (MPR), six within the three plots at the end of Old Ingraham Highway (ING), and three within the Shark Valley plot (SV). At each nest site, we sampled 1 m² quadrats around the nest and at distances 5 m North, South, East, and West of the nest. Within each quadrat we recorded percent bare ground, periphyton cover, dead cover and maximum height of vegetation. We identified and estimated percent cover of all live plants.

We also recorded effective cover and clumpiness in quadrats. The former we estimated by placing a notebook within the vegetation layer and measuring maximum height at which 5% of the notebook was visible. This crudely estimates the degree of camouflage and shelter a habitat provides. The latter we estimated by creating a scale based on the O'Meara and Marion (1985) definition of clumps (i.e. bunch-grass type growth form with a basal diameter of >5)

All vegetation data we evaluated for normality then compared using Wilcoxon Rank Sum, ANOVA, or Chi-Square statistics. When possible, we compared vegetation data between each group using a Student's t-test.

DRAFT – results and conclusions subject to change with increased data or future analyses.

Finally, we calculated a Jaccard's Coefficient of Similarity (Jaccard 19XX) for all group combinations.

We identified and weighed nesting materials from one nest at Dogleg and one at Shark Valley. This yielded a percent total volume for each species represented.

Using elevation data, we compared nest sites to random points within groups. Of the 51 nests found (we excluded the one nest found in Alligator Hammock), 22 came from the MPR group, 25 from the ING group and 4 from SV. At 225 random points across these groups we estimated elevation. The distribution of elevations were analyzed for normality and compared using the appropriate statistics. When possible each group was compared to all other groups using a Student's t-test.

Results

NEST SITE CHARACTERISTICS

Sparrows weave nests entirely of dead plants. Sawgrass (*Cladium jamaicenses*) comprised 46% of the total volume of the Dogleg nest. Muhly grass (*Muhlenbergia filipes*) and/or black-top sedge (*Shoenus nigra*), two species that are hard to distinguish once dried and dead, composed 14.5% of the total volume. Thirty-one percent was woven from unidentifiable plant fragments. Half of this volume composed the nest cup. **ADD SHARK VALLEY NEST INFO.**

Two of 5 grasses, sawgrass, muhly grass, black-top sedge, *Rhynchospora traceia* (or *microcarpa*), or *Schizachyrium rhizomatum*, dominated nest

DRAFT – results and conclusions subject to change with increased data or future analyses.

sites. There are 10 combinations of these five dominant grasses. Sparrows built nests in seven of those 10 mixes. Sparrows built seven nests within sawgrass+muhly (n=3 at MPR sites) or sawgrass+*Rhynchospora* spp. (n=3 at SV, n=1 at MPR). We found four nests within muhly+*S. rhizomatum* (n=2 at ING) or muhly+black-top sedge (n=1 at ING and n=1 at MPR). Sparrows built one nest within black-top sedge+*S. rhizomatum* (n=1 at ING) and black-top sedge+sawgrass (n=1 at MPR). We found no nests within Muhly+*Rhynchospora* spp., *S. rhizomatum* +*Rhynchospora* spp., or *Rhynchospora* spp. +Schoneus.

Species composition of nest sites varied moderately between elevation groups (see appendix B for all species found). Jaccard coefficients of similarity ranged from 39% to 68%. The MPR and SV nest sites had the highest coefficient of 68%. The ING sites followed with similarity coefficients of 48% and 39% to MPR and SV respectively. The most striking difference between groups was the absence of muhly grass, black-top sedge and swamp lilly (*Crinum americanum*) at SV. There, species which show up sporadically at other sites, *R. traceia* and spike rush (*Eleocharis cellulosa*), share dominance with sawgrass.

The ING sites differed most in species composition. Species present there were a small bay tree (*Persea* spp.), hemp weed (*Mikania scandens*), duck potato (*Sagittaria grandiflora*), and foxtail (*Setaria geniculata*). Absent from these nest sites were spike rush, water dropwort (*Oxypolis filiformis*), prairie sneezeweed (*Helenium pinnatifidum*) and white-top sedge

DRAFT – results and conclusions subject to change with increased data or future analyses.

(*Dichromena colorata*). The MPR site composition was a mix between SV and ING with no striking absense or presence of species. Despite the range of species around nests, certain species are common to all: sawgrass, *Rhynchospora* spp. and *S. rhizomatum* and *Panicum* spp..

Combining nest sites by elevation group and totaling the species found in all quadrats yields little difference in species richness (SV=20, MPR=22, ING=24). However, comparing species richness at nest sites alone yields differences between groups (ANOVA F-ratio=14.28, P=0.000, df=2). MPR and ING nest sites averaged 7.51 and 7.73 species per quadrat respectively whereas the SV nest sites averaged 10.67. Nest quadrats on average held eight species (n=80, sd = 2.15).

Degree of clumpiness and percent periphyton cover varied between groups. Deviations from expected values suggest that nest sites within SV are less clumpy than all other groups. The ING sites, however, are considerably more clumpy ($X^2=40.80$, P=0.0001, df=6). Percent periphyton cover is highly variable between groups ($X^2=43.63$, P=0.0001, df=10). SV samples have the most coverage (25-75%) and ING the least (5-10%). Nests sites cannot be identified based on these two characteristics.

Maximum vegetation height ranged from 170 cm to 75 cm (mean=106.61 cm, sd=8.43, n=70). Mean maximum vegetation height did not vary between groups (Wilcoxon Rank Sums approx. $X^2=2.25$, P=0.32, df=2). Mean maximum height of nest sites was 104.2 cm at MPR (sd=18.9), 108.8 cm

DRAFT – results and conclusions subject to change with increased data or future analyses.

at ING (sd=18.8), and 106.9 cm at SV (sd=12.6). Thus, we can identify this range of vegetation heights as characteristic of a nest site.

Similarly, effective cover height did not vary between groups (approx. $X^2 = 5.77$, $P=0.06$, $df=2$). SV had the lowest measurement of 11.7 cm (sd=11.7) followed by MPR at 19.7 cm (sd=12.7), and ING at 26.7 cm (10.5). Currently, we cannot show a statistical difference between means indicating that this is also a characteristic of nest sites. However, the range of effective cover heights is large and future data may overturn this result.

Percent dead cover and percent bare ground did not differ significantly between groups. Quadrats generally contained 10 to 50% dead cover with at least one quadrat per group reaching 75 to 100 % ($X^2=10.03$, $P=0.2632$, $df=8$). Percent bare ground varied even less ($X^2=15.03$, $P=0.1308$, $df=10$). Nearly two-thirds of all samples contained 10 to 25% bare ground. Of the remaining one-third most ranged from 5 to 10%. This provides two more characteristics by which to define nest sites.

MICROHABITAT SELECTION

We compared vegetation at nest sites with 10 random vegetation samples A. Mayer collected in a concurrent study. In two plots, Dogleg and North Mahogany, we compare clumpiness, maximum vegetation height, effective cover height, dead cover and periphyton cover. From this we identified preferred microhabitat characteristics.

DRAFT – results and conclusions subject to change with increased data or future analyses.

Sparrows prefer over 50% dead cover, around 20 cm effective vegetation height, and less than 50% periphyton cover. Dogleg nest sites had 27 cm mean effective vegetation height whereas random points had 4.3 cm (approx. $X^2=13.012$, $P=0.0003$, $df=1$). North Mahogany nest sites had 16 cm mean effective vegetation height compared to only 1.3 cm in the random points (approx. $X^2=9.115$, $P=0.0025$, $df=1$). Dogleg nest sites often had 50–100% dead cover whereas random sites had only 0–5% ($X^2=22.720$, $P=0.0009$, $df=6$). North Mahogany sites had 75–100% dead cover compared to the 0–5% of random sites ($X^2=10.723$, $P=0.0571$, $df=5$). Periphyton cover at Dogleg and North Mahogany nests was 25–50% but 75–100% at random points (Dogleg: $X^2=12.796$, $P=0.0051$, $df=3$; North Mahogany: $X^2=6.904$, $P=0.0317$, $df=2$).

Sparrows show some preference for sites that are less clumpy and have higher vegetation. Nest sites and random sites in Dogleg were equally clumpy ($X^2=4.857$, $P=0.0881$, $df=2$), but within North Mahogany nest sites were less clumpy ($X^2=16.22$, $P=0.0003$, $df=3$). Dogleg nest sites (mean=126.4 cm) had higher maximum vegetation heights than random sites (mean= 93.7 cm: approx. $X^2=12.393$, $P=0.0004$, $df=1$). North Mahogany nest sites and random sites had equal vegetation heights ($t=0.153$, $P=0.883$, $df=1$).

Of the elevation discerned under 51 nests, we found no difference between their mean elevations and the mean of 225 random points (Kruskal-Wallis $Z=0.518$, $P=0.604$, $df=1$). Since averaging across plots that differ in elevation may mask preferences, we compared nest sites to random sites within elevation groups. We again observed no preferences. Only when we

DRAFT – results and conclusions subject to change with increased data or future analyses.

compare nests to random sites within plots do we see preferences. Nests in Dogleg and Ingraham South show higher mean elevations than those of random sites (Dogleg $P=0.0014$: Ingraham South $P=0.0110$).

Sparrows also demonstrated a preference for the vertical space in which they build nests. Since flooding directly effects breeding success (Lockwood et al. in press, Fenn et al. Part I), we evaluated the influence of water on the height of the nest off the ground. At sites where the hydroperiod was long (e.g., the MPR or SV nest sites) we expected nests to be built higher off the ground. Conversely, in the drier plots (e.g., ING nest sites) we expected the reverse. However, the height of the nest above ground level did not vary between groups (Wilcoxon Rank Sum approx. $X^2=0.4572$, $P=0.7956$, $df=2$).

Similarly, when we plot nest site elevation against the height of nests off the ground there is no relationship (Figure 7). Elevation of nest sites reflected the elevational differences between the groups and did not show sparrow sensitivity to mean sea level (Wilcoxon Rank Sums approx. $X^2=38.07$, $P=0.0000$, $df=6$).

Summary

Cape Sable Seaside Sparrow nest sites are characterized by a 25 to 50% coverage of dead matter and by 10 to 25% bare ground. Nest sites show little variability in the amount of effective cover and maximum vegetation height provided. They pick nest sites that provide around 24 cm effective cover and 107 cm maximum vegetation height. Sawgrass, *Rhynchospora spp.* and *S. rhizomatum* and *Panicum spp.* define nest site composition. .

DRAFT – results and conclusions subject to change with increased data or future analyses.

The three groups show some differences in microhabitat. Shark Valley nest sites are more speciose and much less clumpy. Shark Valley and MPR are the most similar and have many species indicative of wetter areas (e.g. spike rush). The ING group holds species which are more indicative of drier areas (e.g. bay trees and foxtail) and appear much more clumpy.

Sparrows show some preferences for nest sites within plots. Sparrows do not prefer particular nesting materials nor do they prefer to build at a particular height off the ground. Sparrows show some preference for nest sites that are higher in elevation, have less periphyton cover and little vegetative clumpiness. They demonstrate strong preferences for nest sites with a large coverage of dead matter, high effective cover, greater vegetation heights, and moderate amounts of bare ground.

Conclusions

The eastern sub-population (B) demonstrates much variability in breeding success and nest site characteristics. Tenuous links exist between low breeding success and habitat structure and composition. The ING group, for example, was half as successful as the MPR group. Within the ING group, plant species were indicative of drier areas. This group also experienced four times as many dry days within the breeding season. Conversely, the MPR group had species indicative of wetter areas and experienced only 10 dry days within the breeding season. Thus, within the habitat range that sparrows occupy, drier habitat does not increase breeding success. However, data on the western sub-population (A) shows the limits wetter habitat imposes. Future

DRAFT – results and conclusions subject to change with increased data or future analyses.

surveys within the Shark Valley plot will provide these limits. Within this framework we have the means to examine the limits of sparrow breeding success in relation to hydroperiod.

Existing data does not readily explain the effects of fire frequency on breeding success. Fire frequency has been equal across the eastern plots (Curnutt et al. in review). Fire frequency in the western population is unknown. We suggest the establishment of a plot within sub-population E where fires occur more frequently but breeding individuals remain.

We have correlated the presence of surface water to higher predation rates within the drier ING group. We are not yet able to compare predation rate to surface water within wetter plots. We can only speculate that drier sites support more predators. Nests may become easier to find because water effectively decreases the vertical area predators survey.

Because the number of nests included in each plot is low (seven to 11 nests), one or two different outcomes could have altered success rates dramatically. A few more years of data on nesting and habitat characteristics will confirm or redirect these results.

DRAFT – results and conclusions subject to change with increased data or future analyses.

Literature Cited

Curnutt, J.L., A.M. Mayer, T.M. Brooks, L. Manne, O.L. Bass, Jr., D. M.

Fleming, and S.L. Pimm. In review. Population dynamics of the endangered Cape Sable Seaside Sparrow. *Biological Conservation*.

Jaccard 19xx.

Kushland and Bass.

Lockwood, J.L., K.H. Fenn, J.L. Curnutt, D. Rosenthal, K.L. Balent, and A.M.

Mayer. In press. Life history of the endangered Cape Sable Seaside Sparrow. *Wilson Bulletin*.

Mayfield, H. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456–466.

Nott, M.P., O.L. Bass, Jr., D. M. Fleming, S.E. Killefer, N. Fraley, L. Manne, J.L.

Curnutt, T. Brooks, R. Powell, and S.L. Pimm. In review. Water levels, rapid vegetational changes and the endangered Cape Sable Seaside Sparrow. *Biological Conservation*.

O'Meara, T.E. and W. R. Marion. 1985. Status survey and habitat evaluation of the Cape Sable Seaside Sparrow in East Everglades, Florida. Technical Report no. 19, Florida Cooperative Fish and Wildlife Reserach Unit, Gainesville, FL.

Pimm et al. 1996.

Schaub, R., R. Mumme, and G. Woolfenden. 1992. Predation on the eggs and nestlings of Florida Scrub Jays. *Auk* 109:585–593.

DRAFT – results and conclusions subject to change with increased data or future analyses.

Schroeder, R. and M. Armbruster. 1985. A habitat model for the Cape Sable Seaside Sparrow. Report to the U.S. Fish and Wildlife Service, Fort Collins, CO.

Werner, H. 1975. The biology of the Cape Sable Sparrow. Report to the U.S. Fish and Wildlife Service. Everglades National Park, Homestead, Florida.

Figure 2.
Hydroperiod for each elevational group (1997).

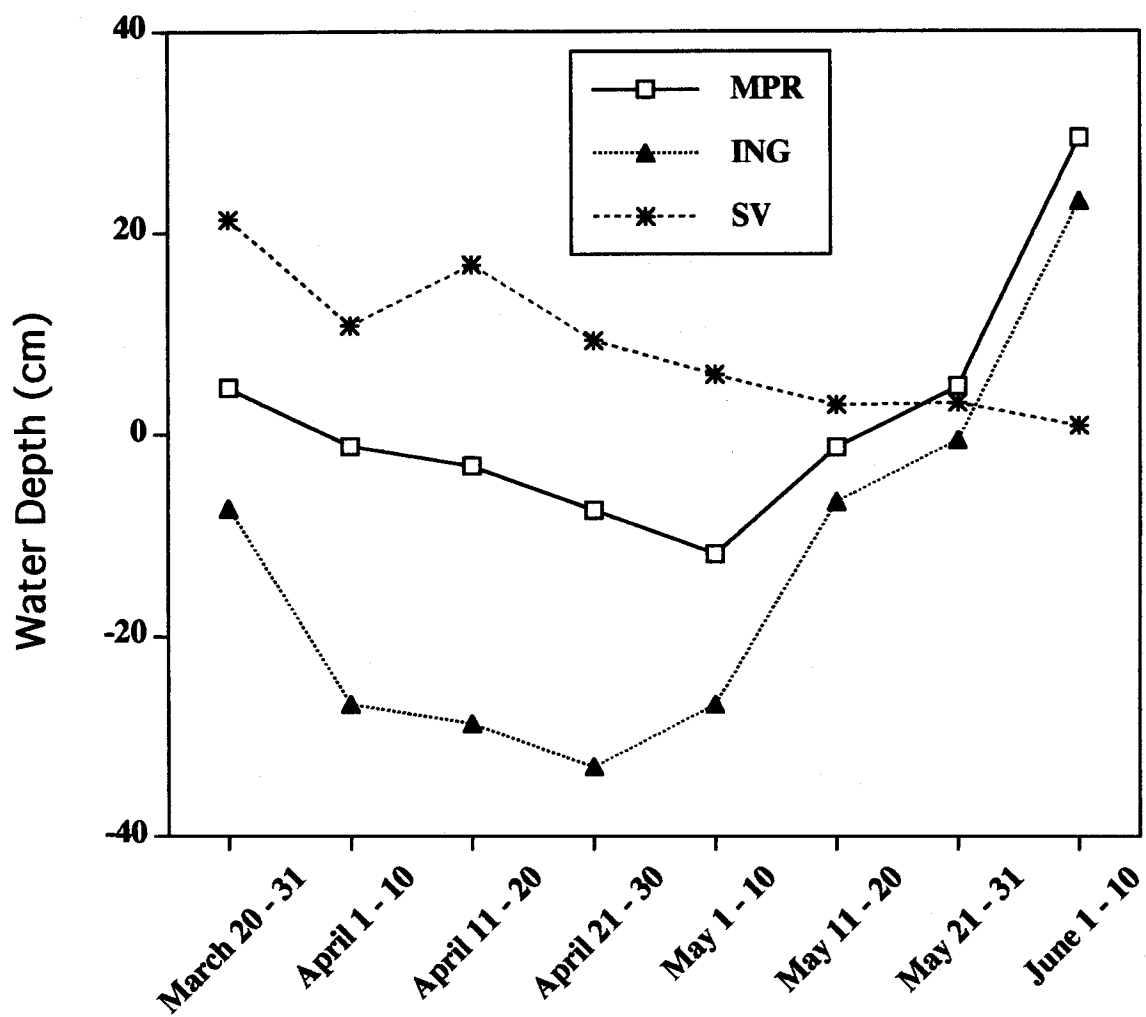


Figure 3. Breeding success through time.

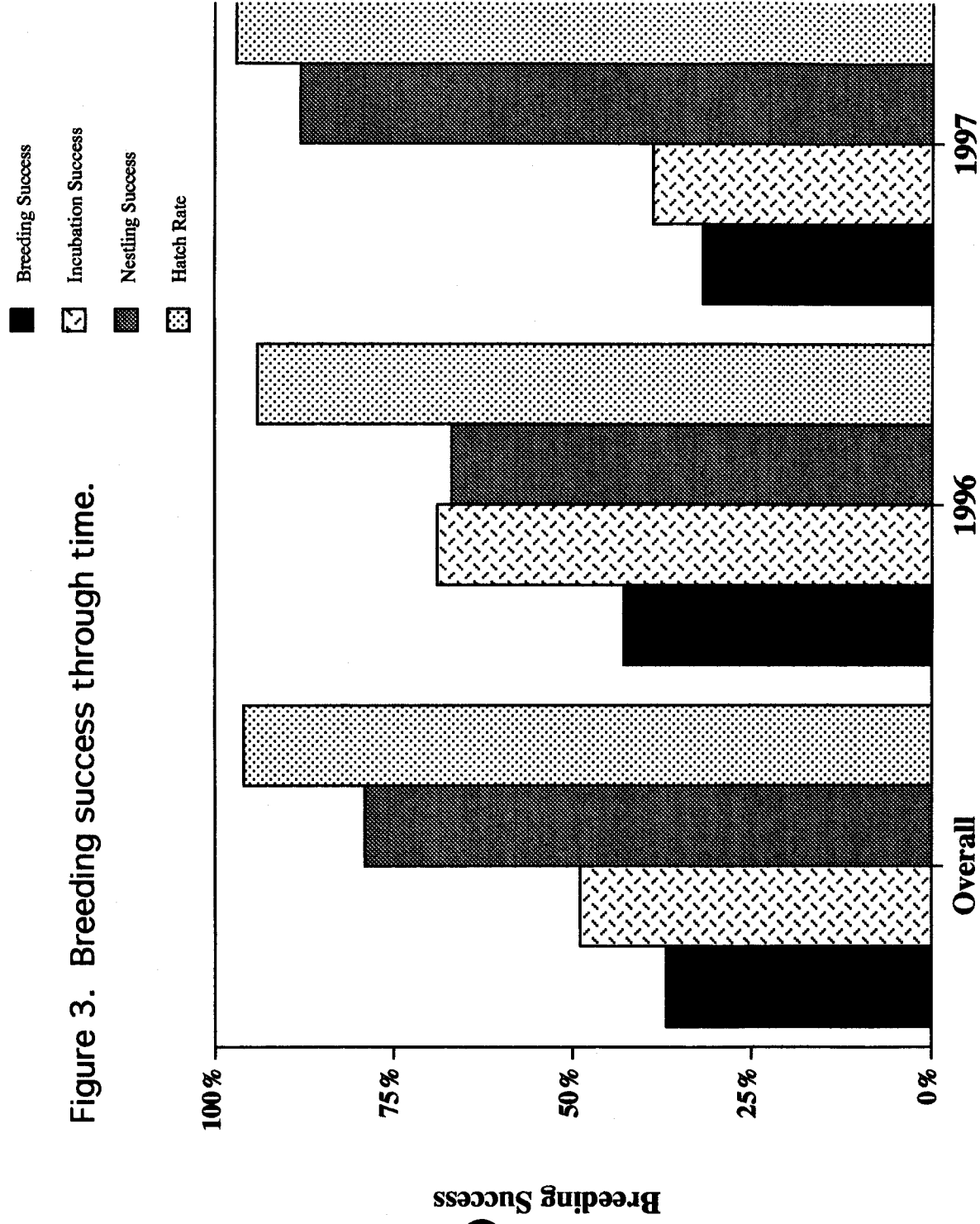


Figure 4.
Breeding success by elevation/hydroperiod
group. ING group had half the success rate
of MPR, mostly through losses of nests
during incubation.

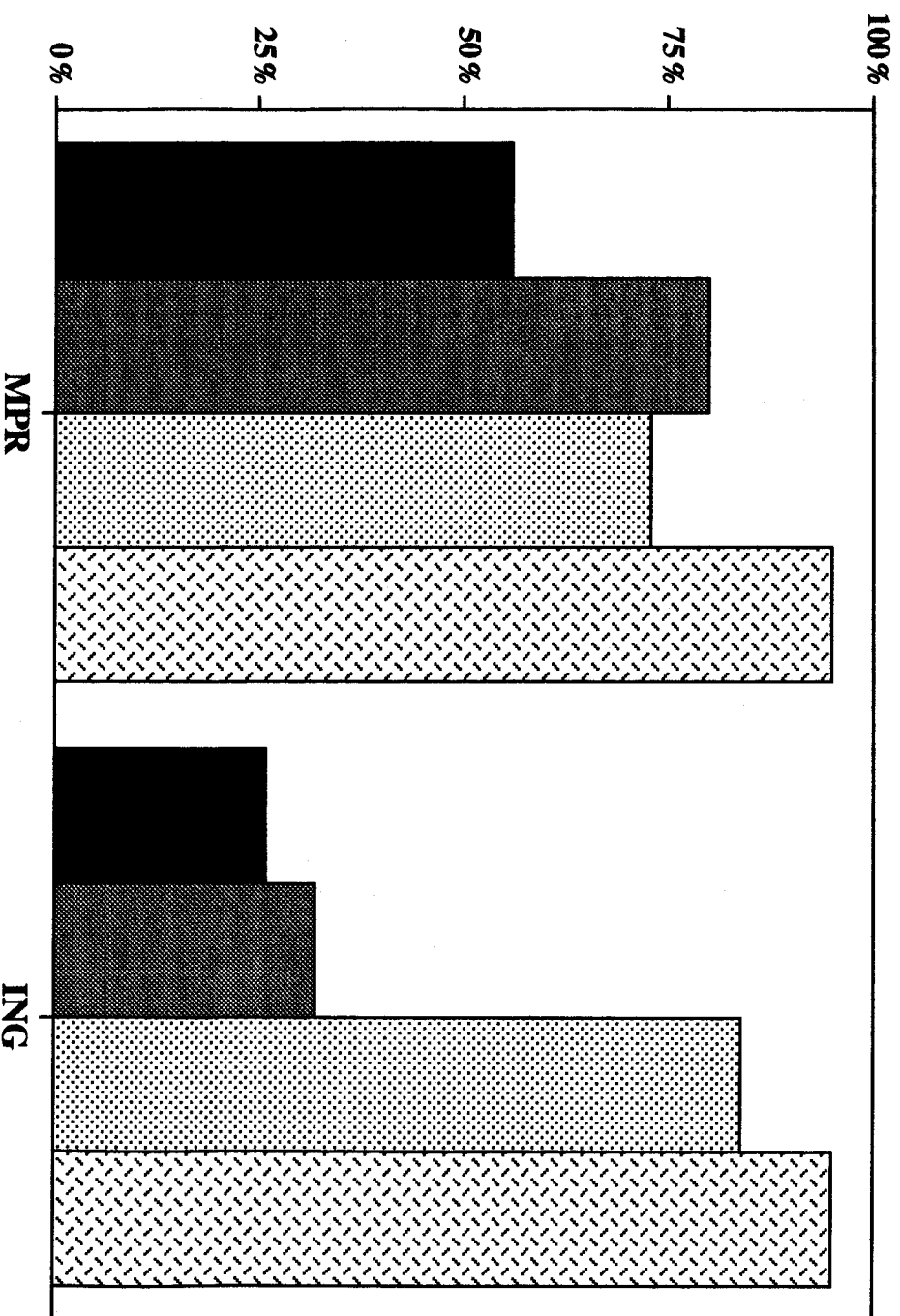


Figure 5.

Predation rate for 1996-97 nests through time.

Predation rate is highest at the beginning and end of the breeding season when surface water is more likely.

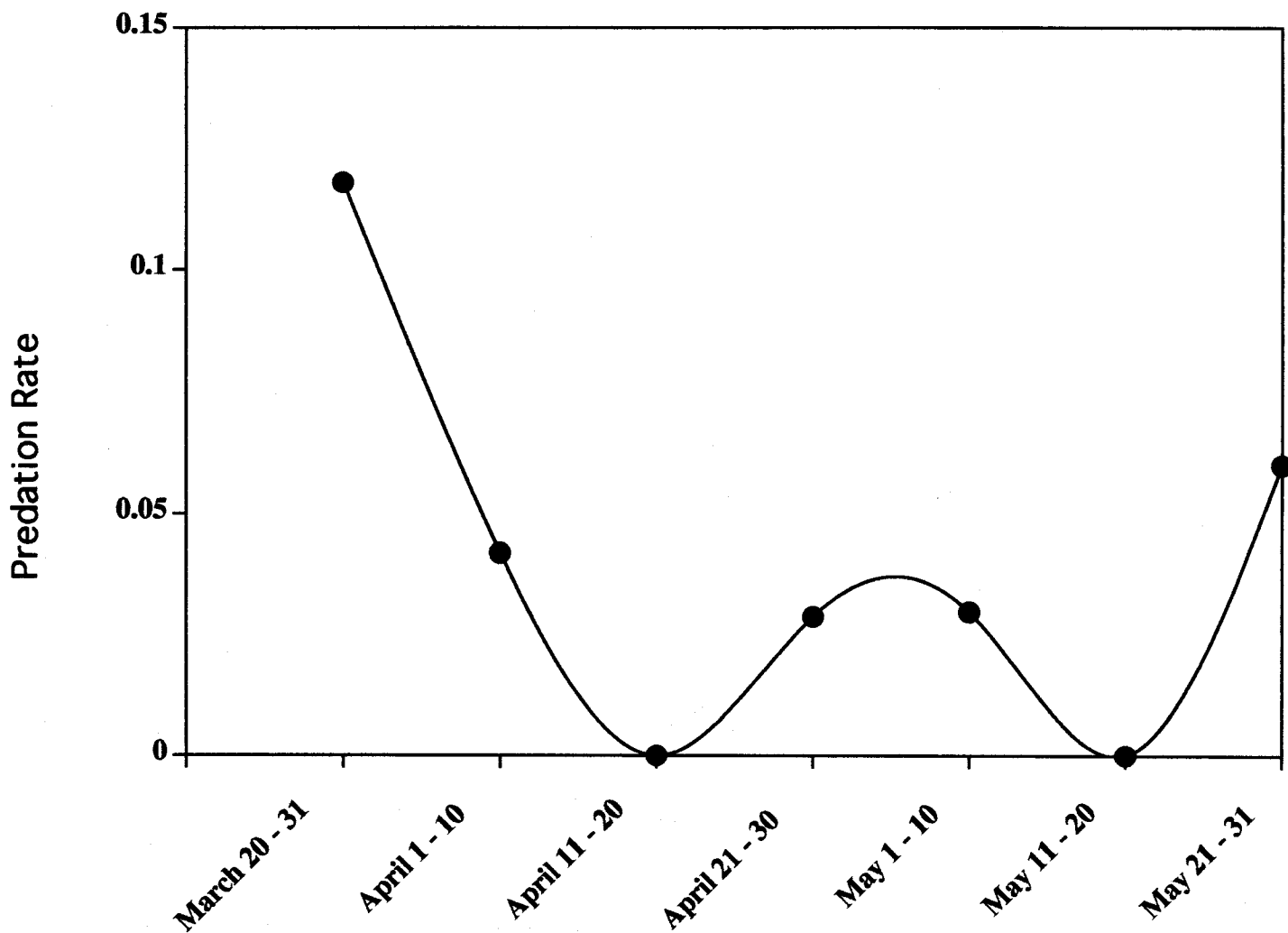


Figure 6.
Predation rate increases exponentially with increase
in surface water depth at the Ingraham Plots.

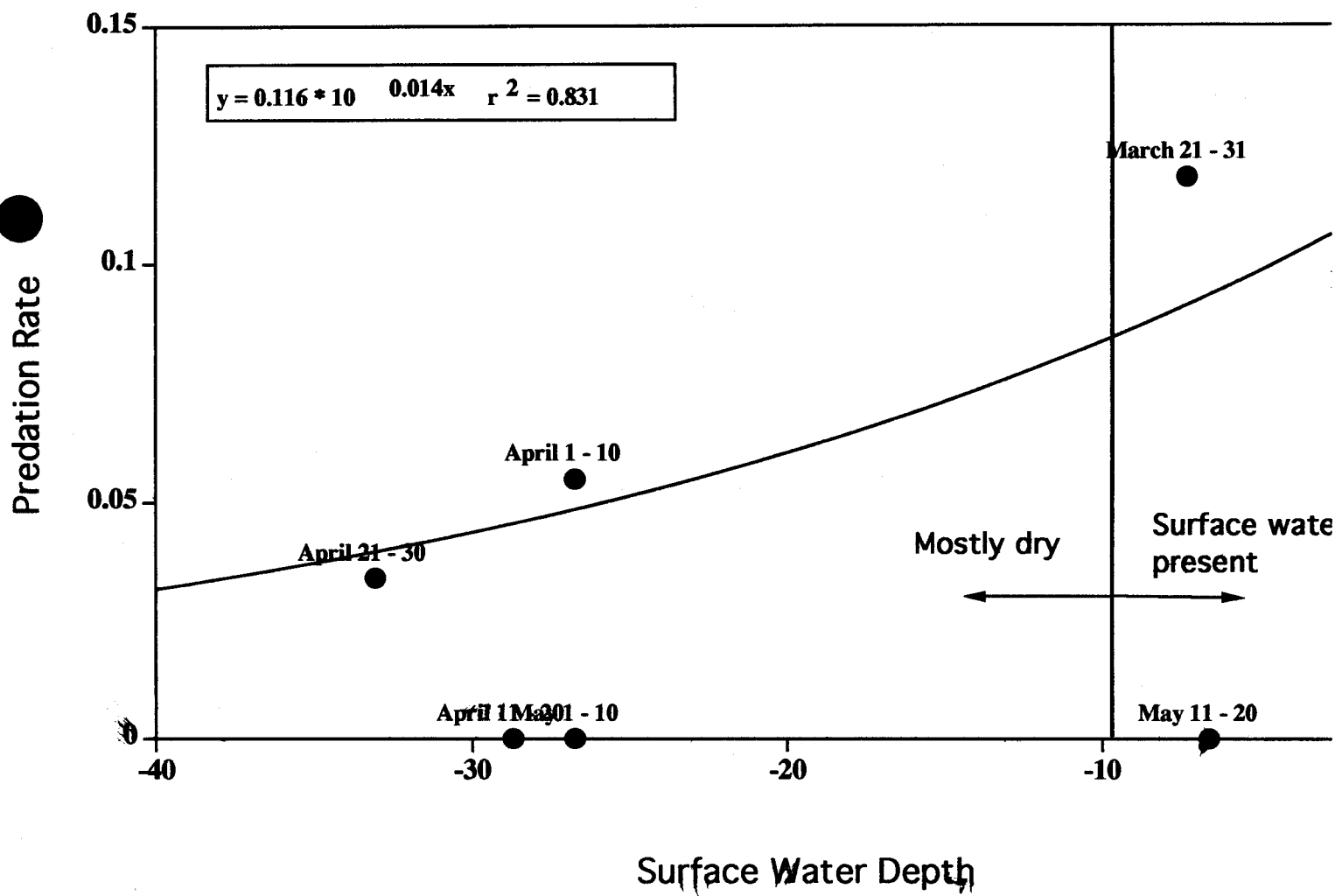
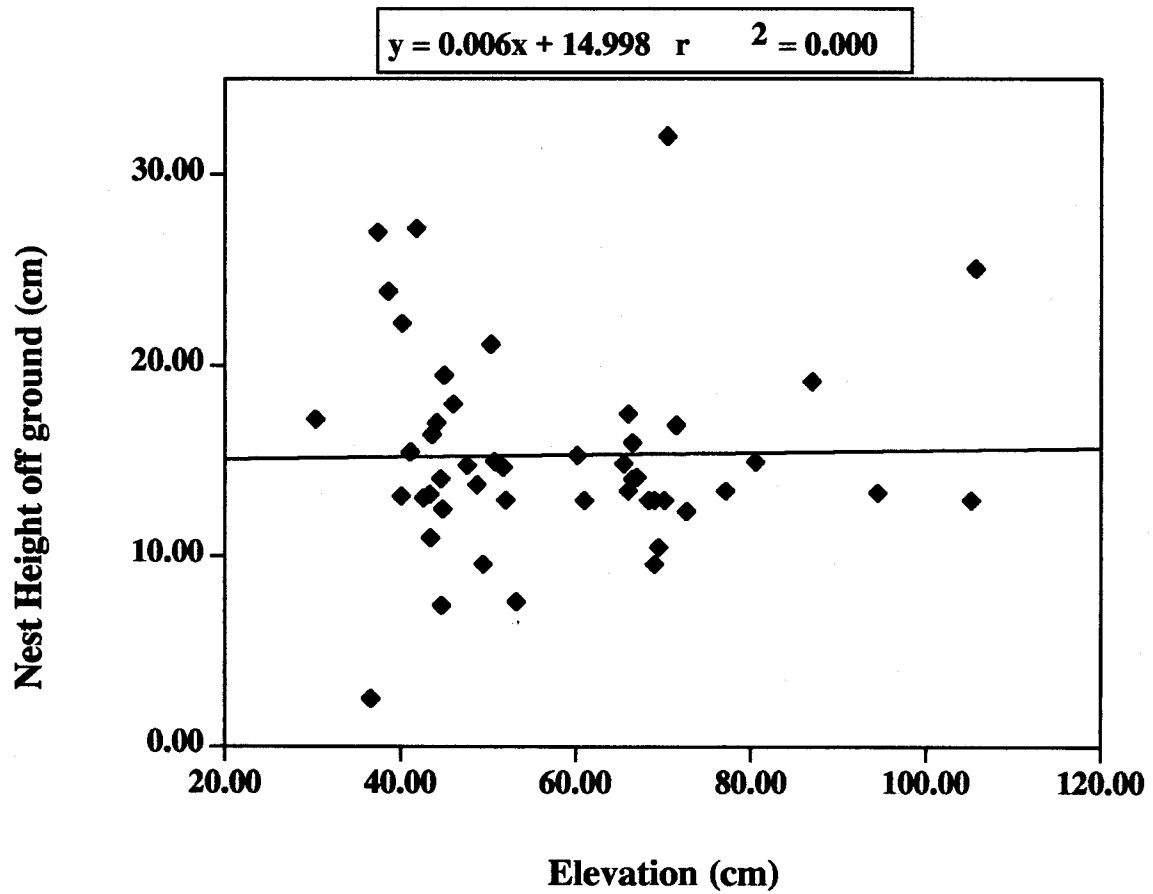


Figure 7.

Nest height off ground in relation to nest site elevation.
No relationship exists.



Appendix A. All nests found ordered by site. We also list the date found, color bands of male and female associated, number of eggs, number of nestlings, and date fledged. Nests believed to be depredated are denoted by 'P'.

Site	Date Found	Male (Right leg - Left leg)	Female (right leg-left leg)	No. of eggs	No. of nestlings	Date fledged or failed
Dogleg	4/13/95	red/alum. pink/yellow	unknown	3	3	4/18/95
Dogleg	4/18/95	red/alum. orange/black	unknown	4	4	4/24/95
Dogleg	5/4/95	red/alum. yellow/orange	unknown	4	4	5/8/95
Dogleg 1:A	3/22/96	red/alum. pink/yellow	unbanded	2	2	4/19/96
Dogleg 2:A	4/1/96	red/alum. red+missing	unbanded	4	4	P 4/9/96 sick
Dogleg 4	4/17/96	red/alum. pink/green	unbanded	2	2	4/18/96
Dogleg 5	4/20/96	red/alum. yellow/green	unbanded	3	3	4/23/96
Dogleg 6	5/18/96	red/alum. yellow/yellow	unbanded	3	3	5/20/96
Dogleg 2:B	5/13/96	red/alum. red+missing	unbanded	4	4	5/21/96
Dogleg 1:B	5/18/96	red/alum. pink/yellow	unbanded	3	3	P 5/23/96
Dogleg 7	6/5/96	unknown	unknown	4	3	P 6/11/96
Dogleg 8	4/14/97	aluminium only	unbanded	3	3	5/2/97
Dogleg 9	4/16/97	red/alum. yellow/white	unbanded	4	4	4/20/97 3 fledged
Dogleg 9:B	5/20/97	red/alum. yellow/white	unbanded	4	4	5/28/97
Sweetbay	4/27/95	blue/alum. pink/red	unknown	unknown	unknown	unknown
Sweetbay 1:A	4/10/96	blue/alum. pink/red	blue/alum. pink/green	3	3	4/24/96
Sweetbay 1:B	6/4/96	blue/alum. pink/red	blue/alum. pink/green	unknown	2	P 6/6/96
Sweetbay 1:C	6/20/96	unknown	blue/alum. pink/green	4	0	6/22/96 Flooded
Sweetbay 2:A	4/5/97	blue/alum. yellow/yellow	unbanded	3	3	4/18/97
Sweetbay 2:B	5/9/97	blue/alum. yellow/yellow	unbanded	4	4	5/14/97

Sweetbay 3	4/14/97	blue/alum. yellow/blue	blue/alum. pink/green	3	3	4/20/97
Sweetbay 4	4/16/97	blue/alum. yellow/black	unbanded	4	4	4/27/97
Mahogany (E) 1	4/3/96	unbanded	unbanded	4	3	4/22/96 2 fledged
Mahogany (W) 2	4/15/97	lt blue/alum. yellow/white	lt blue/alum. yellow/black	4	4	4/26/97
Mahogany (E) 3	4/17/97	lt blue/alum. yellow/white	unknown	4	0	P 4/30/97
Ingraham South 1	4/2/96	yellow/alum. red/black	alum. only	3	0	P 4/15/96
Ingraham South 2	4/2/96	yellow/alum. pink/red	unbanded	4	4	4/21/96
Ingraham South 3	3/20/97	unbanded	unbanded	2	0	P 3/27/97
Ingraham South 4	3/24/97	yellow/alum. black/black	unbanded	4	4	4/23/97
Ingraham South 5	3/24/97	unbanded	alum. only	3	0	P 3/27/97
Ingraham South 6	4/3/97	unbanded	unbanded	3	0	P 4/8/97
Ingraham South 7	4/10/97	yellow/alum. black/white	unbanded	3	3	4/25/97
Ingraham South 5:B	5/16/97	yellow/alum. black/red	unknown	3	3	5/22/97
Ingraham North 1	4/18/96	unbanded	unbanded	3	2	5/2/96
Ingraham North 2	4/18/96	green/alum. white/black	green/alum. white/red	3	2	5/3/96
Ingraham North 3	4/18/96	green/alum. yellow+missing	unbanded	unknown	3	4/27/96
Ingraham North 4:A	4/23/96	green/alum. black+missing	green/alum. yellow/yellow	unknown	3	4/26/96
Ingraham North 4:B	5/30/96	green/alum. black+missing	green/alum. yellow/yellow	3	0	P 6/6/96
Ingraham North 5	4/15/97	unbanded	green/alum. white/lt blue	4	4	4/19/97
Ingraham North 6	4/24/97	green/alum. red/white	unbanded	4	0	P 4/29/97
Ingraham North 7	5/3/97	green/alum. yellow/lt blue	unbanded	3	3	5/14/97
Ingraham North 5:B	5/25/97	green/alum. black/red	green/alum. white/lt blue	3	0	P 5/27/97
Far East 1	4/8/97	lt green/alum. black/white	unknown	3	3	4/18/97
Far East 2	4/14/97	lt green/alum. white/red	unbanded	3	3	P 4/28/97
Far East 3	4/17/97	lt green/alum. yellow/lt blue	lt green/alum. yellow/green	3	3	4/21/97
Far East	4/18/97	lt green/alum.	unbanded	3	3	4/22/97

4		red/red				
Far East 5	4/24/97	lt green/alum. red/yellow	unbanded	4	4	5/8/97
Far East 6:A	4/29/97	lt green/alum. yellow/black	unbanded	3	3	5/4/97
Far East 6:B	5/24/97	lt green/alum. yellow/black	unbanded	4	3	6/2/97 Flooded
Far East 7	4/29/97	lt green/alum. yellow/yellow	unbanded	3	2	5/5/97 1 died
Far East 8	5/17/97	lt green/alum. yellow/red	unbanded	4	0	P 5/26/97
Shark Valley 1	5/1/97	black/alum. yellow/yellow	black/alum. yellow/red	4	4	5/2/97
Shark Valley 2:A	5/1/97	black/alum. white/yellow	black/alum. white/red	2	0	abandoned
Shark Valley 2:B	5/3/97	black/alum. white/yellow	black/alum. white/red	4	4	5/24/97
Shark Valley 3	5/1/97	black/alum. blue/yellow	black/alum. blue/red	3	3	5/3/97
Alligator Hammock	5/16/95	unknown	unknown	4	0	P 5/18/95
Alligator Hammock 1	4/23/97	white/alum. red/yellow	unbanded	3	2	P 5/2/97

Appendix B. Species lists of the 16 nest sites categorized by elevation group

Species	Shark Valley (n=3)	Main Park Road (n=7)
Aster tenuifolium	1	1
Centella asiatica	1	1
Cladium jamacienses	1	1
Crinum americanum	0	1
Cuscuta campestris	1	1
Dichromena colorata	1	1
Hellinium pinnatifidum	1	1
Hymenocalus palmeri	1	1
Ipomoea sagittat	1	1
Mikania scandens	0	0
Muhlenbergia filipes	0	1
Oxyopolis filiformes	1	1
Panicum spp.	1	1
Pluchea rosea	1	1
Polygala grandiflora	0	0
Rhynchospora traceia	1	1
Rhyncospera microcarpa	1	1
Sagittaria lanciflora	0	0
Schizachyrium rhizomatum	1	1
Schoenus nigra	0	1
Setaria geniculata	0	0
Solidago	1	1
Eleocharis	1	1
Cloverish	1	0
Rosesharon like	1	0
Toothed foeb promnode	1	0
Giardia	1	1
Solidago like with stem	0	1
Cypress tree	0	1
Bay Tree	0	0
Tree#2	0	0
Marsh Pinks	0	0
Linum spp	0	0
Feunic 3	0	0
Total Species	20	22

p.	
Ingraham Highway (n=6)	
1	
1	
1	
1	
1	
0	
0	
1	
1	
1	
1	
0	
1	
1	
1	
1	
1	
1	
1	
1	
1	
0	
0	
0	
0	
0	
0	
0	
1	
1	
1	
1	
1	

WET SEASON DISTRIBUTION AND BEHAVIOR OF THE CAPE SABLE
SEASIDE SPARROW (*AMMODRAMUS MARITIMUS MIRABILIS*)

By:

KARLA L. BALENT^{1*}, JULIE L. LOCKWOOD², AND KATHERINE H. FENN³

¹ Dept. of Biological Sciences, SUNY College at Brockport, Brockport, NY 14420.

² Dept. of Ecology and Evolutionary Biology, Univ. of Tennessee, Knoxville, TN 37996.

³ South Florida Natural Resource Center, Everglades National Park, 40001 State Road 9336, Homestead, FL 33034.

*Corresponding author address: Dept. of Biological Sciences, SUNY College at Brockport, Brockport, NY 14420. Phone: (716)395-5748 Email: afn30425@afn.org

INTRODUCTION

Through its short history of discovery, alleged disappearance and rediscovery, the Cape Sable Seaside-Sparrow (*Ammodramus maritimus mirabilis*) is considered an elusive bird (Werner and Woolfenden 1983). Only recently have researchers begun to piece together the life history of the Cape Sable Seaside-Sparrow and to discover the requirements for its continued persistence (Pimm et al. 1994, 1995, 1996; Lockwood et al. 1997, Nott et al. 1997, Curnutt et al. 1997). One of the more enigmatic portions of its life history has been its winter, or wet season, habits. Although Lockwood et al. (1997) reported some post-breeding activities of the sparrow, we still lack important information on wet season dispersal and habitat requirements. When this information is available, results from population models will be applicable to management schemes. To provide this information we conducted systematic surveys during the winter of 1996–97 to determine the wet season distribution and habits of the sparrow.

Information on the wintering habits of most races of Seaside sparrows is sporadic (Quay et al. 1983, Greenlaw 1992, Post and Greenlaw 1994). Northern races are sometimes migratory (Post and Browne 1971, Quay et al. 1983) and southern races are not believed to migrate at all (Post and Greenlaw 1994). The climate of southern Florida is sub-tropical consisting of a wet and dry season with little variability in temperature. This climate is not only distinct from northern regions of the Seaside sparrow range, but also from regions in northern Florida. These climatic effects may or may not produce novel wet season (or over-wintering) adaptations. Sparrows may remain within freshwater marshes and become so secretive that observations are rare. They may move within their breeding range but outside the boundaries of our study areas. Since early sightings occurred during winter months within salt marshes (Howell 1919, 1932; Stimson 1956), the sparrow may still winter in these areas. For this reason, we

did not limit the scope of our surveys and included all areas accessible on foot and by car or boat within Everglades National Park.

STATUS OF *A. M. MIRABILIS*:

First discovered in the coastal prairies of Cape Sable on the west coast of south Florida, it was at that time considered "moderately numerous" (Howell 1919). The hurricane of 1935 apparently devastated the population on the Cape (Stimson 1956) but Werner (1971) found a small group of sparrows there in 1970. By 1979 they had disappeared from the Cape again and have not been found there since (Bass and Kushlan 1982; Pimm et. al. 1994, 1995 and 1996).

Other populations within Everglades National Park (hereafter referred to as ENP) and Big Cypress National Forest have similarly declined. Populations in Ochopee, near Big Cypress, had gone by 1980 (Bass and Kushlan 1982) and populations in Taylor Slough had gone by 1993 (Curnutt and Pimm 1993). The sparrow's low population numbers and numerous disappearances from historic sites helped lead to its listing as endangered on the Federal Register in 1967 (32 Federal Register 4001, 1967).

However, populations in east and west ENP remain, and while the sparrow's overall density remains stable, individual populations within its widespread range are declining sharply (Pimm et. al. 1995 and 1996). Studies have shown these declines to be tied to hydrology within the park (Nott et. al. 1997). The current range of the Cape Sable Seaside-Sparrow is entirely within the boundaries of ENP and Big Cypress National Preserve. This study concentrated on the *A. m. mirabilis* sub-population located in eastern ENP. This area currently holds the highest densities of Cape Sable Seaside-Sparrows. This sub-population has been the most stable of all the sub-populations not having declined over the past 20 years (Bass and Kushlan 1982, Pimm et al. 1996)

METHODS

Several study plots established in the eastern sub-population have been under observation during the breeding season for the past four years (Pimm et al. 1996). Within these plots more than 140 Cape Sable Seaside-Sparrows have

been color banded since 1994. All plots are *Mulenbergia* spp. dominated prairies, which are flooded during the wet season, usually June through December. Initially, we concentrated our efforts on these plots. Observations began immediately after the breeding season ended (mid-June 1996). We visited four of these established plots, each approximately 1000m², from June 1996 to March 1997. Two plots (Alligator Hammock and Dogleg) were visited an average of three times a week. The remaining two plots (Old Ingraham North and South) were each visited once a month.

As the wet season progressed we expanded the area of observation to include most of the southeastern portion of ENP, including Cape Sable. In order to determine if the sparrows migrate out of the marl prairies during the wet season, point count surveys were conducted in seven different habitat types found within ENP. Habitat types selected include: Marl Prairie (PR) is typical of the study sites, and is dominated by *Muhlenbergia* spp., *Cladium jamaicensis*, and *Rhynchospora* spp. It is usually inundated with water during the months of June through October, but is dry throughout the remainder of the year. Sparrows breed exclusively in this habitat type (Werner 1975, Bass and Kushlan 1982, Pimm et al. 1996, Lockwood et al. 1997). Mixed Prairie (MP) differs from Marl Prairie in its greater abundance of hardwood hammocks, small tree islands and sawgrass. This prairie is also flooded during the wet season. Dry Prairie or "finger glades" (DP) are so named because it is found between large stands of pine forests. This prairie does not flood in the wet season and is dominated by sawgrass and short grasses. Coastal Prairie (CP) is found at the southern end of the ENP along shorelines. This prairie is dominated by *Batis maritimus*, *Sesuvium portulacastrum* and *Salicornia* spp. Although other subspecies of Seaside Sparrows winter in coastal prairie habitats (Post and Greenlaw 1994) no Cape Sable Seaside-Sparrows have been recorded in this habitat as yet (Bass and Kushlan 1982). Pineland (PL) is comprised of slash pine (*Pinus elliottii* var. *densa*), with heavy undergrowth of saw palmettos (*Serenoa repens*). This area does not flood. Dwarf Cypress (DC) are forests comprised of tightly clumped to well dispersed Pond Cypress (*Taxodium ascendens*) interspersed with sawgrass. This area remains flooded throughout most of the year. Mangrove (MG) includes

stands of black and white mangroves (*Avicennia germinans* and *Laguncularia racemosa*) with little or no undergrowth. They flood in the wet season and are adjacent to brackish bodies of water.

These habitats are representative of ENP as a whole although most censuses were conducted in readily accessible areas (see Figure 1). Since there are no observations of Cape Sable Seaside-Sparrows during the wet season beyond that given by Stimson (1954) and Howell (1919), we chose not to narrow the search in any manner. However, we did budget our observation according to the habitat type in which we most often found sparrows (i.e., we spent the majority of observation time within the Marl Prairie habitat).

Following Gutzwiller (1991), we used an unlimited distance point count to survey each habitat type and identify all birds present. Count points were placed 200m apart. Each count duration was determined by using the gain rate of species (Hutto et al. 1986) for each habitat, and compensating for the difficulty in detecting *A. m. mirabilis*. For example, the gain rate for Coastal Prairie habitat was 5.5 min. Thus, after 5.5 min, 80% of all species eventually detected after 20 min had been counted. The average time to detect a sparrow was determined by recording the duration needed to identify one sparrow on two consecutive mornings during the non-breeding season (8 min.) within Marl Prairie habitat. This time was added to the gain rate resulting in a count duration of 12.5 min for CP habitat types. We conducted all surveys between 0700 hours and 1000 hours, the time during which the sparrows are the most active (Werner 1975). To account for differences in survey effort throughout the wet-season all results are expressed as the number of birds observed per observer per day. This number is typically calculated by totaling the number of birds observed in each category per month and dividing that total by the number of observers reporting observations.

Water measurements were taken at fixed points within two study plots (PR habitat) throughout the season.

Using colored flagging tape, we followed changes in sparrow distribution by marking all locations in which birds were found. Each resight of a banded bird was flagged with colors coordinated with its leg band combination.

Otherwise, each location in which we sighted a bird was marked with white tape. We used a Magellan Global Positioning System linked to a Magellan Differential Beacon Receiver (DBR), to record the locations of banded birds in UTM coordinates. The use of the DBR allowed a location to be specified to within 20m. We used UTM coordinates taken during the 1996 breeding season to calculate the distance banded individuals moved between breeding and non-breeding locations. We used the CA-CricketGraph III software program to map out each UTM coordinate on an X,Y graph. By scaling the graph into equal increments on the X,Y axis (i.e., 200m) we then calculated the relative distance each banded bird had moved from its breeding territory to each non-breeding resight location. This was only possible for banded birds, although all positions of unbanded birds were recorded as well.

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

Fifteen behavioral classifications were established during the 1996 breeding season (see Table 1) and we continued their use here. The number of birds observed exhibiting a particular class of behavior was recorded per day. The frequency in which each behavioral class occurred was plotted from March 1996 to February 1997. These plots allowed us to determine if particular behaviors were associated exclusively with the non-breeding season and to make better estimates of the beginning and end of the breeding season.

TABLE 1. Behavioral classifications established in the 1996 breeding season and continued here. The frequency with which these behaviors were observed helped define wet season behavioral norms and the beginning and end of the 1996–97 non-breeding season.

Behavior	Acronym	Examples–Description
Perch Song	PRSO	Perching over open prairie and giving full song
Ground Song	GRSO	Perching low in the grass within open prairie and giving full song
Flight Song	FLSO	Ascending into the sky at a height of 10 to 30 m and giving a series of chip notes and songs on descent (Werner 1975)
Dense Vegetation Song	DVSO	Perching within dense vegetation (e.g., sawgrass sways or small hammocks) and giving full song
Perching Over Open Prairie	PROP	Quietly perching over open prairie
Perching in Dense Vegetation	PRDV	Quietly perching within dense vegetation (see above)
Chasing Over Open Prairie	CSOP	Two or more individuals chasing each other over open prairie
Chasing in Dense Vegetation	CSDV	Two or more individuals chasing each other within dense vegetation (see above)
Flying Over Open Prairie	FLOP	A sustained flight over open prairie
Chipping in Defense	CHDF	Rapid and loud chip notes given in succession when alarmed

Non-Aggressive Vocalizations	NAGV	Any note given which is not an alarm call—usually considered a contact or communication note (examples included 'seep', 'tseet', and 'cedar call' of Werner (1975)
Epaulet Display	EPDS	Male cocks wings back slightly and displays yellow Epaulets during full song
Chew-Begging	CHBG	A series of notes made when a female or juvenile assumes the begging posture just before being fed
Flush	FLSH	Flushing an individual from the grass or ground while walking nearby
Gathering or Delivering Food	GDFD	Adult gathering or delivering food either to young or mate

RESULTS

Behavior and habitat use . Figure 2 shows the frequency in which we observed the various behavioral classes beginning March 1996 and ending in mid-February 1997. Using such graphs, we classified each behavior as breeding, non-breeding or undetermined. These graphs indicated that several behaviors could be attributed to only the breeding season. Some of these were as expected, such as delivering and gathering food. Others, not necessarily expected, included singing while perched in open prairie and chasing another individual over open prairie. Only two behaviors can be attributed solely to the non-breeding season. These are non-aggressive vocalizations, particularly 'seep' calls and quiet chipping, and perching in dense vegetation.

In addition, using only behavioral classes that can be clearly defined, we can illustrate when the breeding season ended and later began (Figure 3). It is clear from this graph that the 1996 breeding season ended in early June and the 1997 breeding season began in mid-February. This supports direct observations of early and late nests found by Lockwood et al. (1997) during the 1995 and 1996

breeding seasons. Based on these graphs, we considered observations as 'non-breeding season' if they occurred between 1 July 1996 and 15 February 1997. All results below reflect this decision.

Immediately following the end of the breeding season family groups of up to eight birds were found. Very often these 'flocks' consisted of one or two banded males and several unbanded individuals. We believe these are family groups as the unbanded individuals often gave a sub-song typical of juveniles and lacked the full length tail feathers of adults. These family group flocks broke down by September after which most observations were of two or fewer individuals.

The majority of detections throughout the wet season are of birds in sawgrass sways (81%). Occasionally, we found sparrows perched in small trees within hammocks (all within the plot in which they nested), saw palmettos, or road-side vegetation. This behavior is in contrast to typical activity seen during the breeding season when Cape Sable Seaside-Sparrows spend almost all of their time in the open prairie (Pimm et al. 1995 and 1996). Males did not sing during the wet season, though a number of juveniles sang sub-songs throughout the season.

Through July, August and September some birds showed signs of molt. Molting individuals remained within sawgrass sways presumably for cover. Smooth cordgrass, the non-breeding season habitat of other Seaside Sparrows, has higher concentrations of arthropods and seeds than dominant cover (Post and Greenlaw 1994), thus providing the birds with a rich source of food throughout the season. While feeding observations were rare during this study, a sparrow eating seeds from a sawgrass seed head was observed.

Wet-Season Distribution. Figure 4 shows the sum total of birds (total, banded, and unbanded) seen throughout the wet season per observer per day. The total number of *A. m. mirabilis* detected showed a steady decline beginning at the end of the breeding season in June. Detections reached a low of less than one bird seen per observer per day in November. Thereafter, the number of detections began to increase, until an average of two birds were seen per

observer per day by mid-February. At this point, male sparrows were regularly observed singing from high perches within open Marl Prairie.

However, when banded bird detections are separated from unbanded bird detections, a different pattern emerges. Detections of banded birds decline steadily with no subsequent increase as the non-breeding season progresses. Detections of unbanded birds, however, increase as the wet season ends (Figure 4) and the breeding season begins. Thus, the increase in total number of birds detected late in the non-breeding season can be attributed entirely to the increase in detection of unbanded individuals.

A total of 51 hours of point count surveys conducted throughout southeastern ENP during the non-breeding season found no Cape Sable Seaside-Sparrows in habitats other than Marl Prairie. These surveys included the fringe prairies of Cape Sable and Mixed Prairies or Dwarf Cypress stands lying adjacent to the Marl Prairies where *A. m. mirabilis* breeds. Simply, we did not detect sparrows outside of their breeding range despite the fact that sparrow detections within their breeding range declined steadily throughout the wet-season. Within the Marl Prairies, the sparrows moved from open prairie into small tree hammocks and large sawgrass sways, where they stayed throughout the wet-season.

Indeed, we observed little movement of *A. m. mirabilis*. Marking the locations of banded birds allowed us to follow individual movements throughout the non-breeding season. Twenty-one banded birds were resighted. Of these, 14 had all bands intact and could be positively identified. The remaining seven were either missing a color band (2 birds), or were not in visual contact long enough to be positively identified (5 birds).

The 14 banded birds positively identified were found an average of 277m (N=14, range=77m to 986m; Figures 5 through 8) from the spot where they were banded in the spring of 1995 or 1996. Interestingly, the majority of the all banded birds resighted (15 out of 21 birds) were only seen once. When locations of banded birds were revisited (sites were revisited at least once per month), the same individuals were not found again. The six individuals resighted more than

once were usually found within a 10 to 20m area, though two eventually moved to another study plot (Figures 6 through 8).

For example, the bird banded WH/ AL- YL/ WH was resighted on three occasions. This bird was first resighted 250m away from its breeding territory of spring 1996. This bird remained within 20m of its initial resight location during the month of September. In early October, this bird moved North to an area 326m away from its first resight spot (resighted October 1, see Figure 6) but only 115m from its 1996 breeding territory. It was not seen again during the wet season, and as yet has not been resighted within the 1997 breeding season (Lockwood pers. obs.).

Only two birds were resighted in a study plot other than the one in which they were originally banded. One bird from Alligator Hammock plot was found in Dogleg plot, and vice versa. These plots are separated by Main Park Road, a distance of no more than 20m. No birds from the Ingraham plots were found out of their original plot (i.e., where they were banded) despite the two Ingraham plots being separated by only 20 to 30m. These observations are consistent with the high degree of philopatry observed between breeding seasons (Pimm et al. 1996). No birds have yet been found breeding in one plot one year, and a different one the next (Pimm et al. 1995, 1996).

Influence of Water. Water depth increased dramatically within Marl Prairies with the onset of summer rains in early June (Figure 9). This increase coincided with the end of the 1996 breeding season and was directly attributed to the loss of two late season nests in 1996 (Lockwood et al. 1997). By mid-June however, water depth dropped substantially and remained constant until the Marl Prairies dried out in early November. For the next four months, these prairies contained no standing water, except in some deeper "alligator holes". The drier habitat types stayed dry throughout almost all of the wet season and those habitats that remain flooded throughout the wet season experienced lower than normal water depths.

Since we found *A. m. mirabilis* only in Marl Prairies we compared water levels within this habitat to sparrow detection frequency. When water levels were compared to the number of individuals detected (Figure 10), there appears

to be no correlation between water depth and the fall in number of birds detected nor with the onset of breeding.

DISCUSSION

Our results indicate that neither long-distance nor local migration occurs in the Cape Sable Seaside-Sparrow. At least a portion of the *A. m. mirabilis* population spends the winter in the same prairies in which they breed. This indicates that *A. m. mirabilis* may be completely dependent on the existence of Marl Prairies for their long term survival. They do, however, show a change in microhabitat use within those prairies. By the end of the 1996 breeding season, the birds begin to move out of the open prairies and into small tree hammocks and sawgrass sways (see also Lockwood et al. 1997). This movement to higher (stem-wise), and more dense vegetation coupled with the birds' already secretive nature, confounds the ability of an observer to readily find these birds. However, these sawgrass sways likely provide cover, refuge and perhaps an increased food supply for the sparrows during the wet season (Post and Greenlaw 1992).

We do report a decrease in observations of sparrows throughout the wet season (October, November, December) and a subsequent increase in their numbers and activity by mid-February. This pattern is suggestive of a migration or movement out of the Marl Prairies. However, we may also attribute this to the birds' change in behavior and its choice of non-breeding microhabitat. The increase in detection by mid-February is clearly a result of male birds competing for territories for the oncoming breeding season. While banded bird observations decreased through the wet season and remained low as unbanded bird observations increased, those banded birds that were seen had not moved more than 1km from their breeding territory.

In addition to protection during molt and food availability, sawgrass stands may provide an escape, in the form of higher perches, from rising surface waters due to spring rains. Marl Prairies usually stay inundated with water from June to March, and seeking higher "ground", the sparrows may move into sawgrass sways to avoid the rising water. The 1996-1997 wet season, however,

proved to be a particularly dry one. By mid-November, standing water had virtually disappeared from the Marl Prairies and did not return until late March. Had the prairies remained flooded for longer into the wet season, the sparrows may have abandoned the Marl Prairies and moved into a habitat which had remained dry, such as Coastal Prairie. This possibility seems unlikely because we never observed an individual move more than 1km during the wet season nor did we observe an individual in any habitat other than Marl Prairie. Continuing to monitor the habitat use and distribution of the Cape Sable Seaside-Sparrow through several years, some inevitably wetter, could account for this possibility.

ACKNOWLEDGMENTS

We thank S. Bass and S. Pimm for helpful advice and insight, T. Brooks and C. Norment for helpful comments on earlier drafts. We thank J. Hand and T. Obenauer for providing safe refuge. Funding was provided by a grant from the United States Fish and Wildlife Service to S.L. Pimm.

REFERENCES

- Bass, O. Jr. and J. Kushlan. 1982. Status of the Cape Sable Sparrow. South Florida Research Center Report T-672, Everglades National Park, Homestead, Florida.
- Curnutt, J.L. and S.L. Pimm. 1993. Cape Sable Seaside Annual Report. NBS/NPS, Everglades National Park, Homestead, Florida.
- Curnutt, J.L., O. Bass, Jr., M. Fleming, and S.L. Pimm. In prep. Response of the Cape Sable Seaside-Sparrow to fire.
- Gutzwiller, K.J. 1991. Estimating winter species richness with unlimited-distance point counts. *Auk* 108:853-862.
- Howell, A. 1919. Description of a new seaside sparrow from Florida. *Auk* 36:86-87.
- Hutto, R.L., S.M. Pletschet and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding season use. *Auk* 103:593-602.

Balent et al.

- Lockwood, J.L., K.H. Fenn, J.L. Curnutt, D. Rosenthal, K.L. Balent and A.L. Mayer. In press. Life history of the endangered Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*). Wilson Bulletin.
- Nott, M.P., O.L. Bass, Jr., D.M. Fleming and S.L. Pimm. In prep. Hydrologic regimes rapidly change the vegetational landscape and temporal breeding patterns for the endangered Cape Sable Seaside Sparrow.
- Pimm, S.L., J.L. Curnutt, M.P. Nott. 1994. Cape Sable Seaside Sparrow Annual Report. NBS/NPS, Everglades National Park, Homestead, Florida.
- Pimm, S.L., T.M. Brooks, J.L. Curnutt, J.L. Lockwood, L. Manne, A. Mayer, M.P. Nott, K.L. Balent and G. Russell. 1995. Population ecology of the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*). Annual report NBS/NPS, Everglades National Park Homestead, Florida.
- Pimm, S.L., J.L. Curnutt, J.L. Lockwood, L. Manne, A. Mayer, M.P. Nott, and K.L. Balent. 1996. Population ecology of the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*). Annual report, NBS/NPS, Everglades National Park, Homestead, Florida.
- Post, W. and J.S. Greenlaw. 1994. Seaside Sparrow (*Ammodramus maritimus*). Pp. 1-28. In The Birds of North America, No. 127. (A. Poole and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.
- Stimson, L.A. 1954. Cape Sable seaside sparrow: *Ammodramus mirabilis* (Howell). Pp. 479-481. In Florida Bird Life (A. Sprunt, Jr., ed.). Coward-McCann, New York, New York.
- Stimson, L.A. 1956. The Cape Sable seaside sparrow: Its former and present distribution. Auk 73:489-502.
- Werner, D.L. 1971. Cape Sable sparrows rediscovered on Cape Sable. Auk 88:432.
- Werner, D.L. 1975. The biology of the Cape Sable Sparrow. Report to Fish and Wildlife Service. Everglades National Park, Homestead, Florida.
- Werner, D.L. and G. Woolfenden. 1983. The Cape Sable Sparrow: It's habitat, habits, and history. Pp. 55-75. In The Seaside Sparrow, Its Biology and

Balent et al.

Management (T. Quay, J. Funderburg, Jr., D. Lee, E. Potter and C. Robbins, eds.). Occas. Papers of the North Carolina Biol. Survey 1983-5, Raleigh, North Carolina.

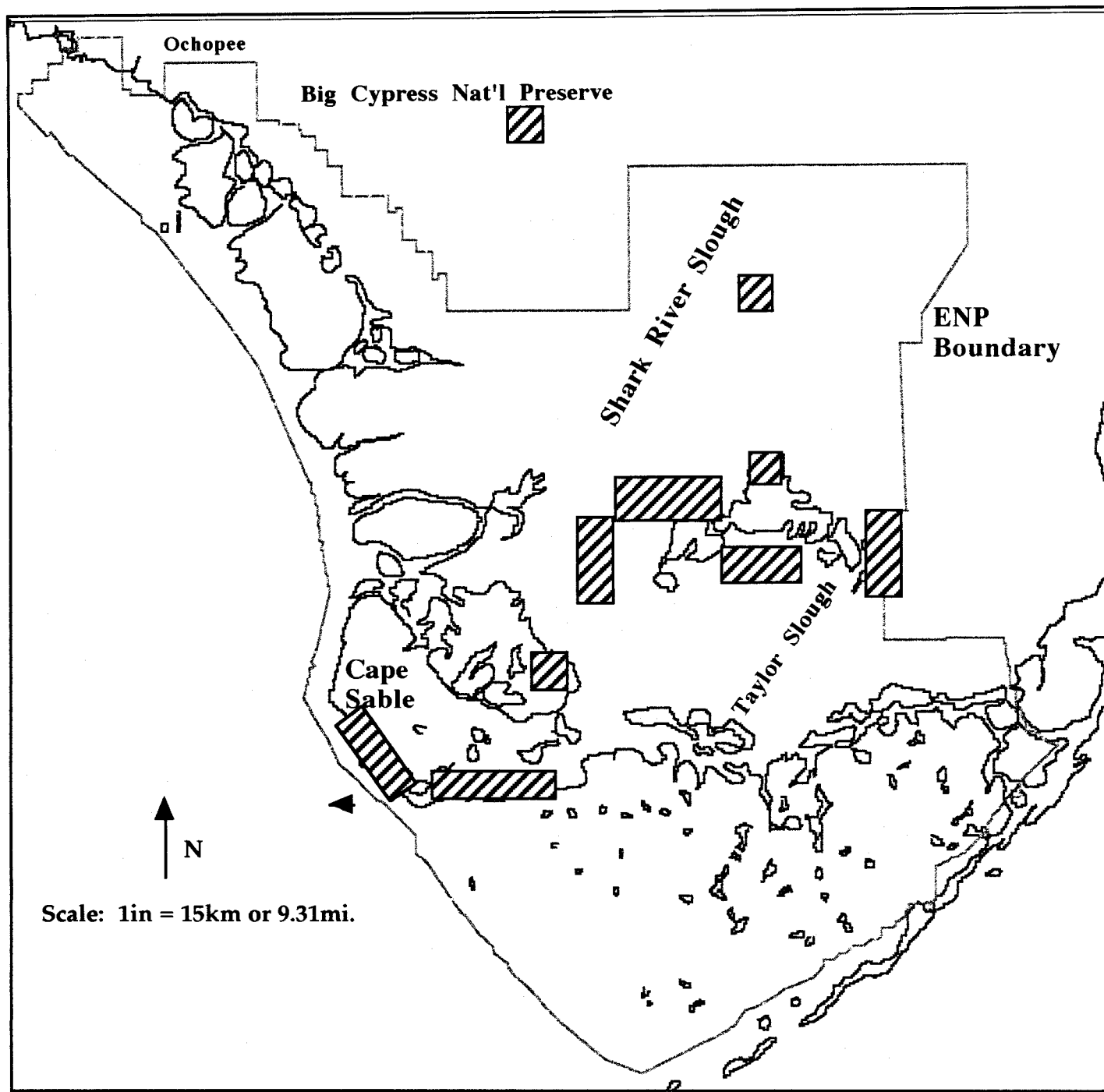


Figure 1. Areas surveyed for Cape Sable Seaside-Sparrows during the wet season of 1996-97.

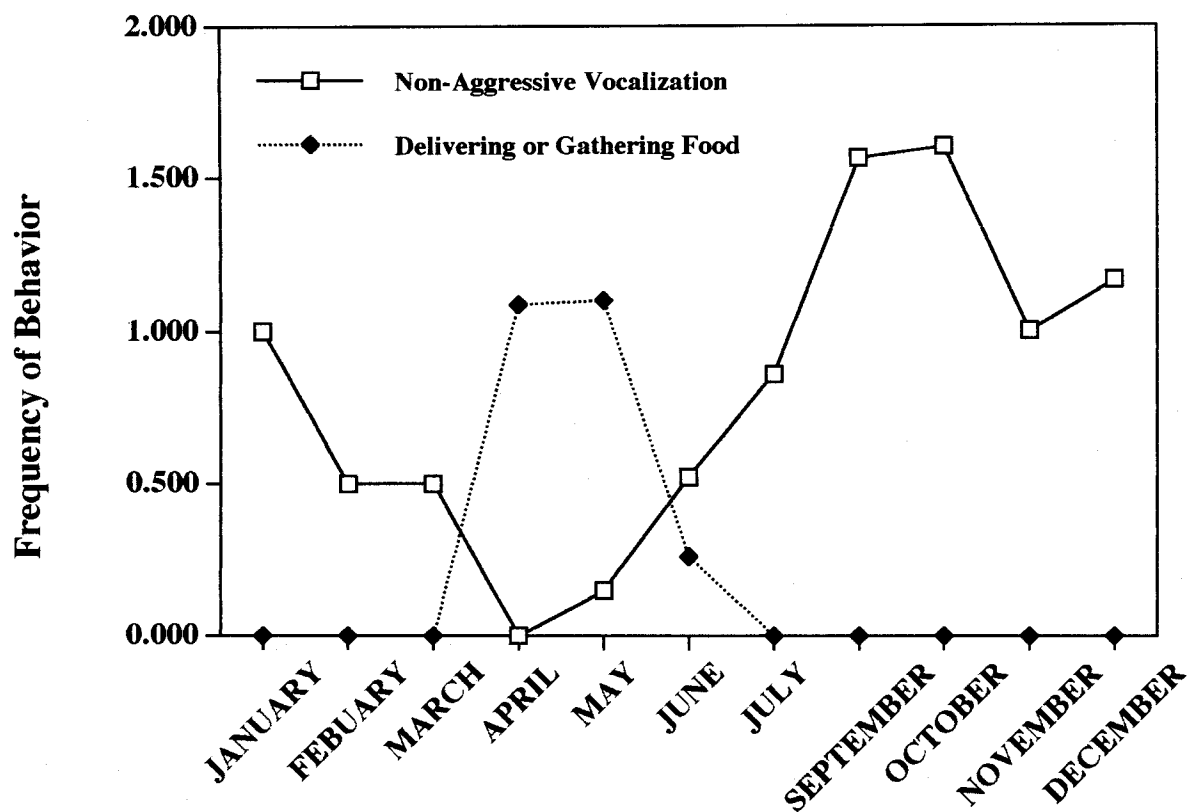


Figure 2. Examples of behavior that can be classified as either breeding season or non-breeding season.

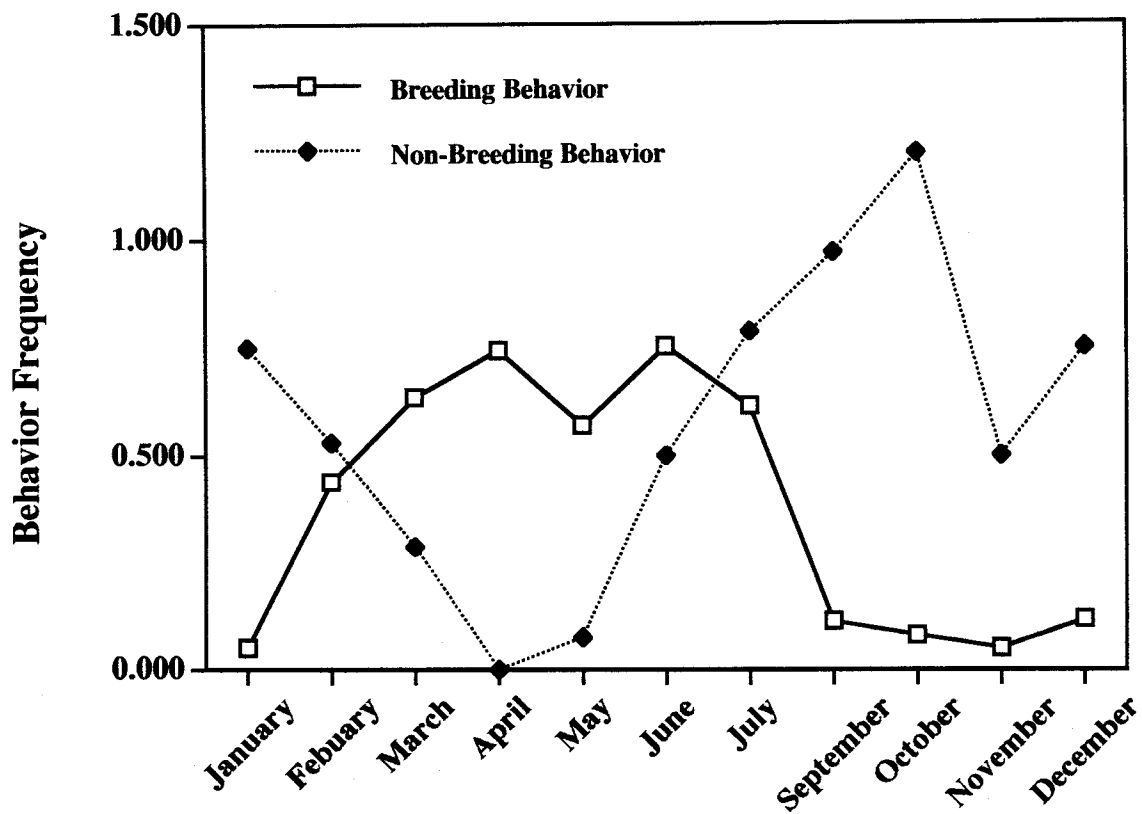


Figure 3. Approximate 1996 end (1 June) and 1997 start (15 February) of the breeding season.

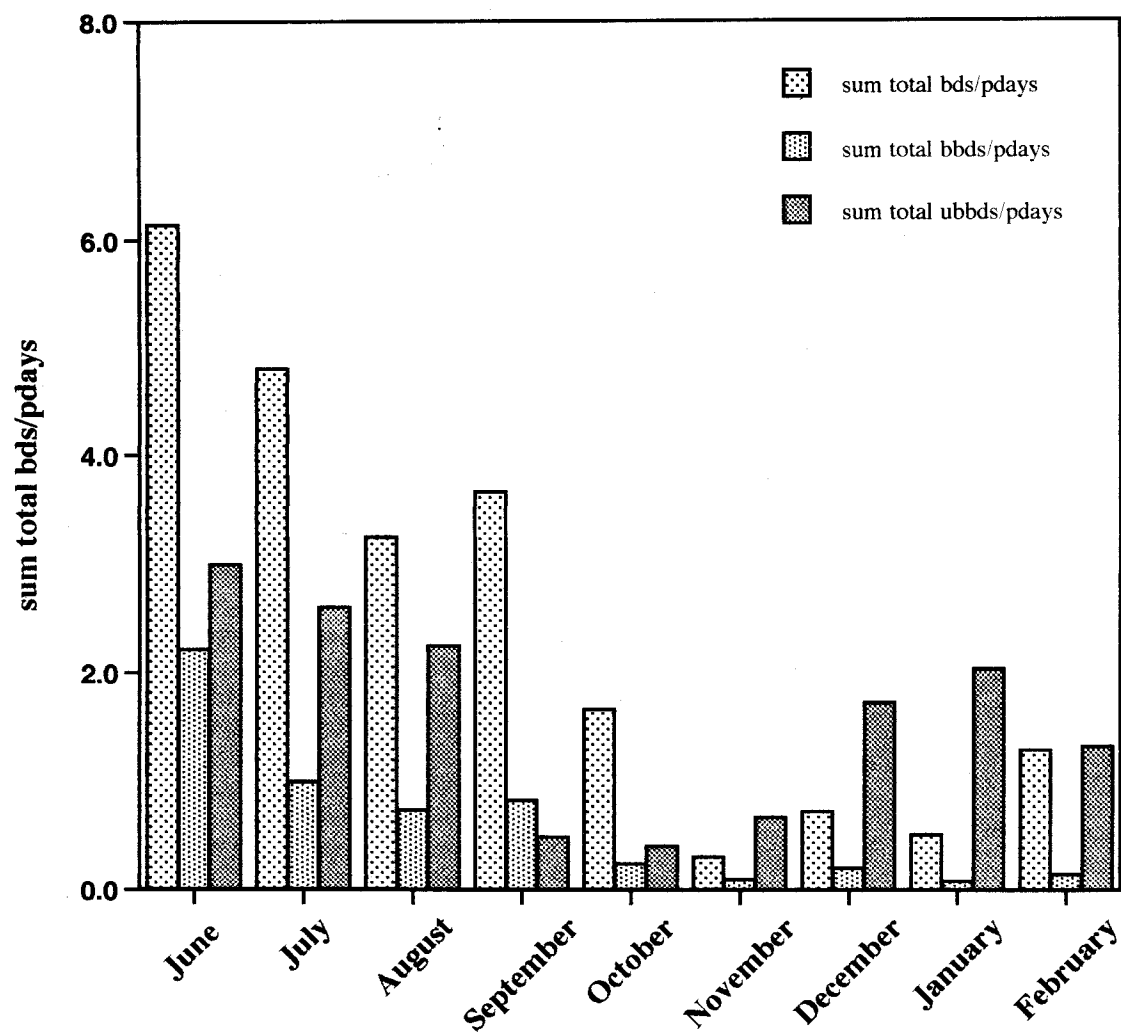


Figure 4. Sum total number of birds seen throughout wet season per person days. bds=birds; bbds=banded birds; ubbds=unbanded birds

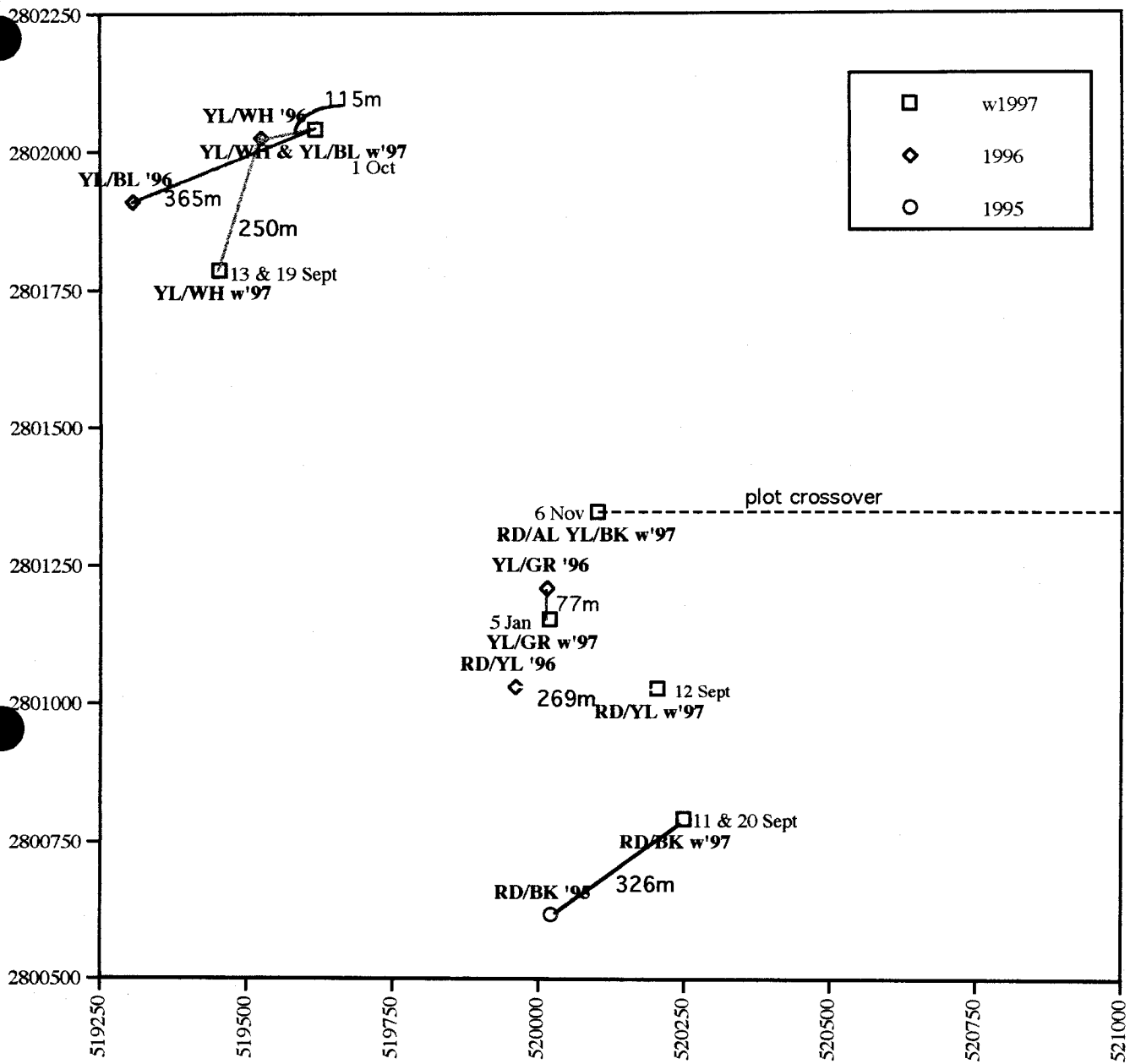


Figure 5. Alligator Hammock Plot. Distance individual birds moved from breeding territory of 1995 or 1996 to non-breeding, wet season resight spot in winter 1997. Color combinations indicate left leg band colors; all right legs banded WH/AL unless otherwise noted. Axes indicate Lat/Long position within plot.

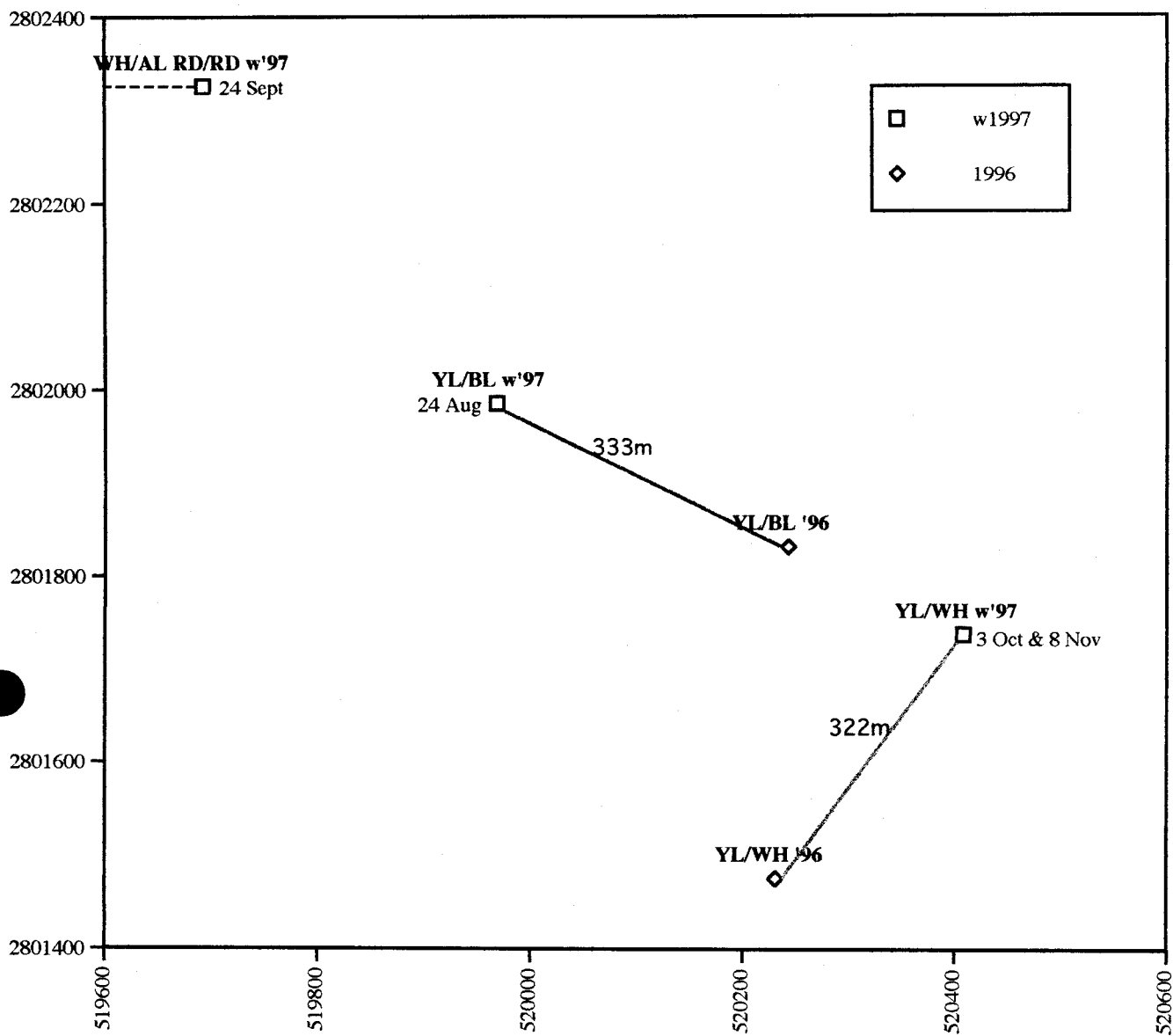


Figure 6. Dogleg Plot. Distance individual birds moved from breeding territory of 1996 to non-breeding, wet season resight spot in winter 1997. Color combinations indicate left leg band colors; all right legs banded RD/AL unless otherwise noted. Axes indicate Lat/Long position within plot.

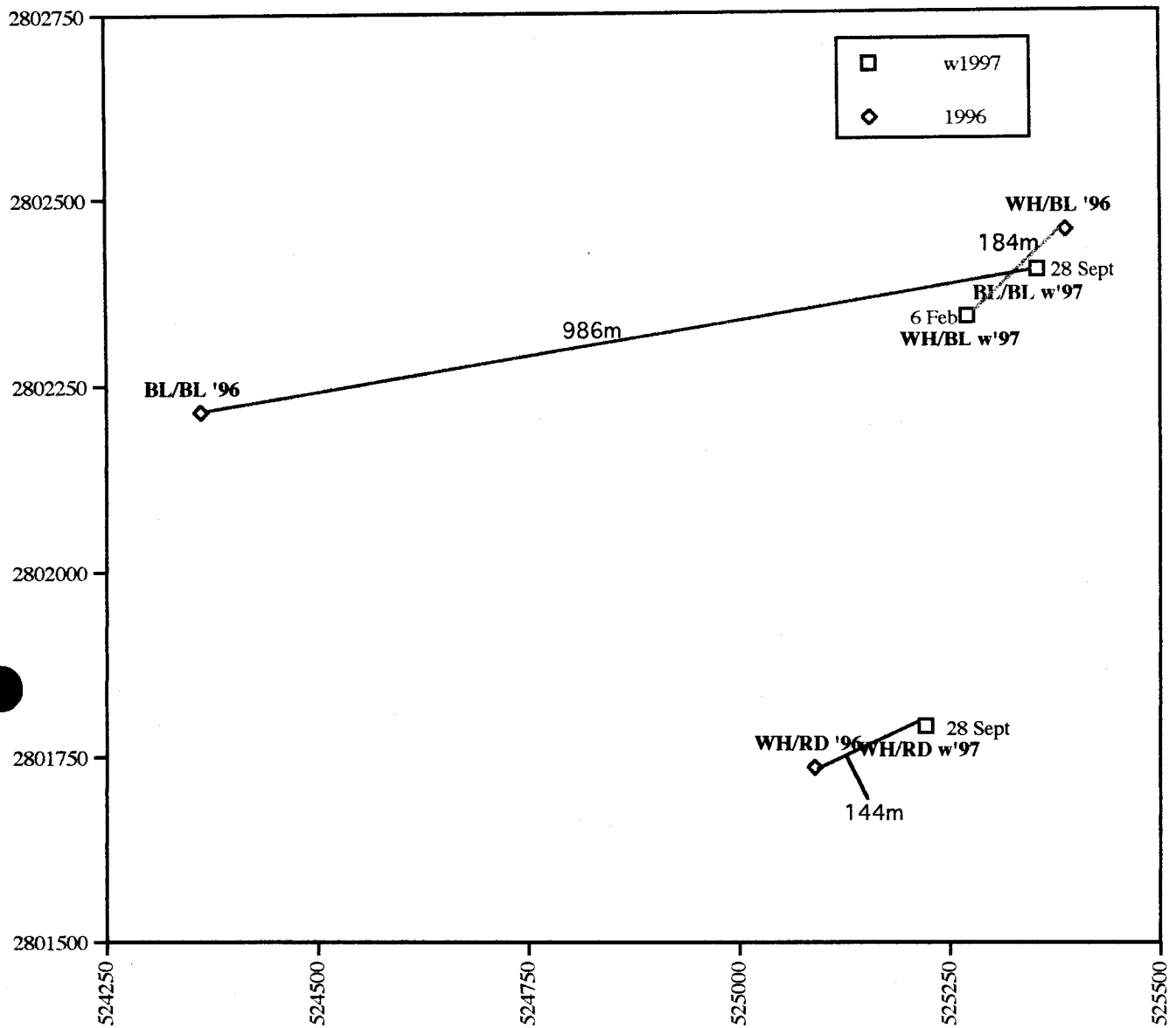


Figure 7. Old Ingraham North Plot. Distance individual birds moved from breeding territory of 1996 to non-breeding, wet season resight spot in winter 1997. Color combinations indicate left leg band colors; all right legs banded GR/AL. Axes indicate Lat/Long position within plot.

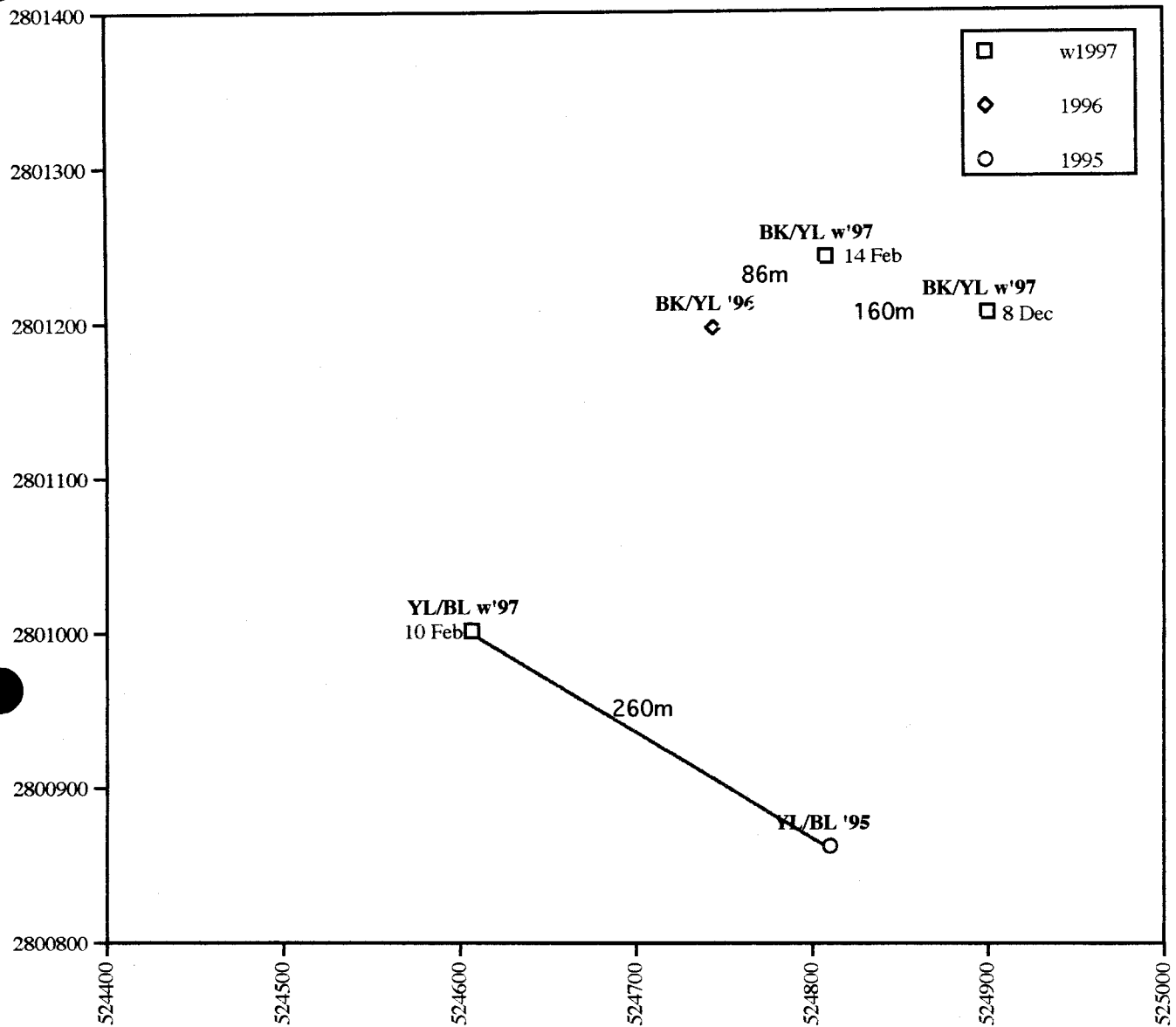


Figure 8. Old Ingraham South Plot. Distance individual birds moved from breeding territory of 1995 or 1996 to non-breeding, wet season resight spot in winter 1997. Color combinations indicate left leg band colors; all right legs banded YL/AL. Axes indicate Lat/Long position within plot.

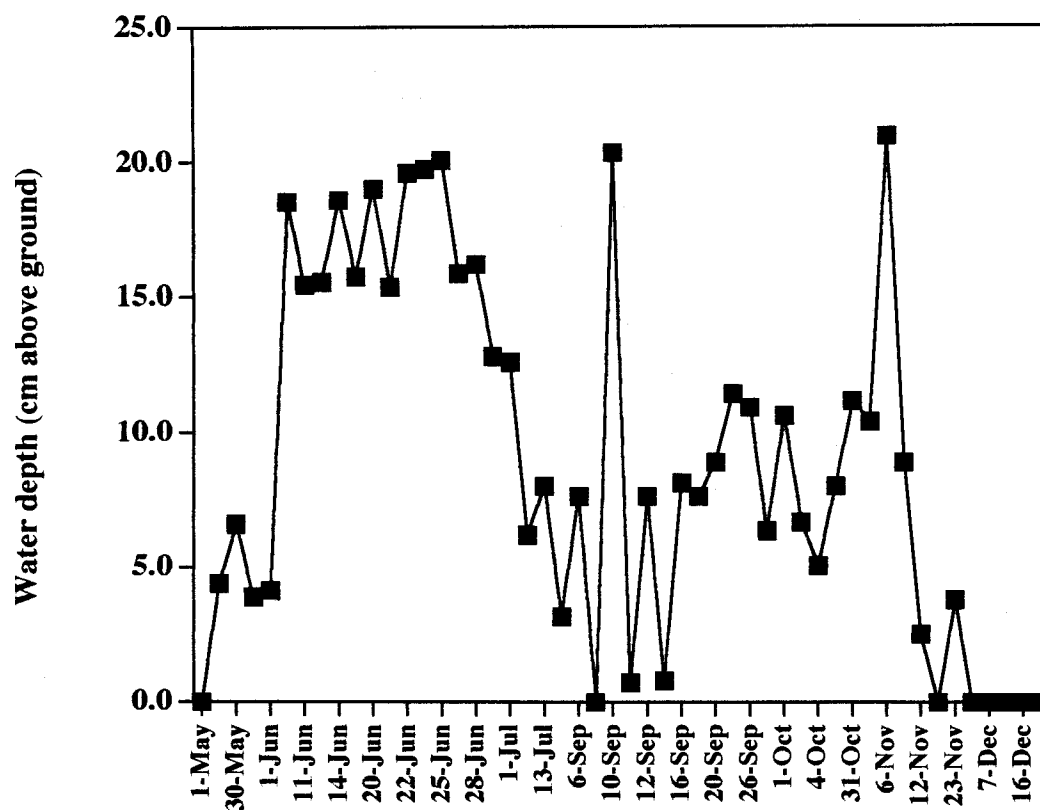


Figure 9. Water depths from May to December 1996 within the Marl Prairie study plots. The prairies have remained dry since the last water measurement plotted here (16 December to 15 March).

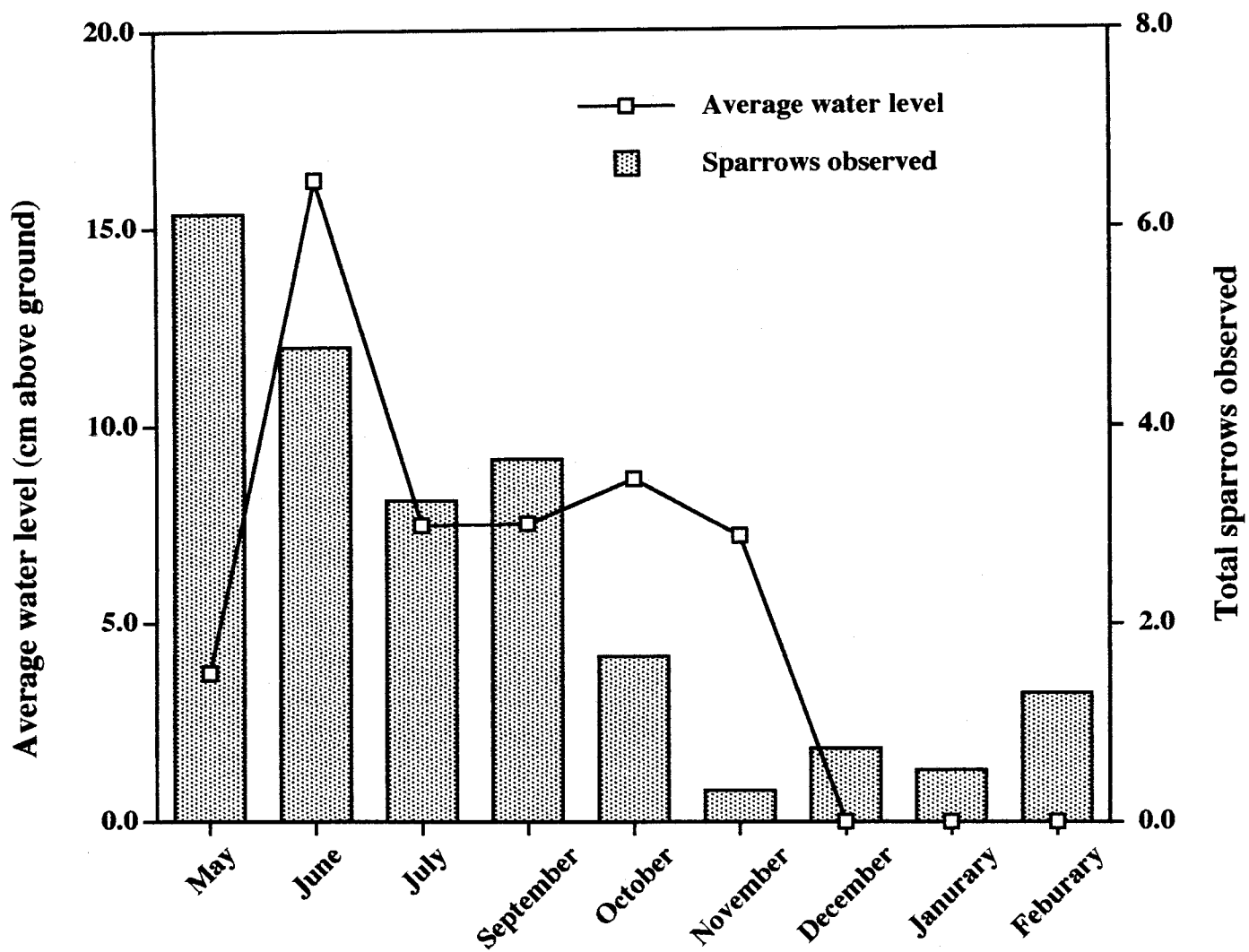


Figure 10. Water levels within Marl Prairies plotted against the total number of sparrows observed per month.

**Integrating endangered species protection and ecosystem management:
the Cape Sable Seaside-Sparrow as a case study**

Audrey L. Mayer and Stuart L. Pimm

National Parks and other biological preserves come in all shapes and sizes, but in sum protect about 5% of the land's surface. One goal for parks, large or small, is to maintain as large a set of species as possible. Large parks, which we define here to be roughly 10,000 km², or 1° latitude x 1° longitude block, may achieve this goal more successfully. Parks of this size are both rare and famous.

We discuss Everglades National Park and a species found only within its boundaries — the Cape Sable Seaside-Sparrow. Natural events of chance fluctuations and catastrophes, such as hurricanes, threaten the species' survival. So, too, do managed activities inside and outside park that control fires and floods. The sparrow has declined precipitously in the past decade, due partially to environmental disturbance, and partially to uninformed management. Due to the isolation produced by their highly modified surroundings, parks often resemble islands

instead of smaller versions of the original ecosystem. If endangered species are to persist, we must be constantly vigilant even in parks at this large spatial scale.

A-- Introduction

We should construct a global conservation system to encompass as many species as possible in protected areas. Such areas —“parks” for short — should require as little time, effort, and money to manage as is possible. How large must a park be to maintain its original species complement or for its ecosystem processes to be self-sustaining? This is an ecological question, but the answer comes as a statement of what is politically feasible. We will show that areas larger than $10,000 \text{ km}^2$ — roughly a square of one degree of latitude and longitude — are few. In our experience, such large parks are likely to be famous, flagships of their countries' efforts to protect the natural environment. It is on the lifestyles of one of these rich and famous parks that we concentrate.

Everglades National Park and its adjacent conservation areas cover $10,000 \text{ km}^2$ and encompass most of southern Florida. In the western hemisphere, few parks are larger or enjoy anywhere near the prestige and associated financial resources. Nonetheless, we show that these

areas will likely retain their species only through constant vigilance and active, informed ecosystem management.

A-- Parks in the Western Hemisphere

Currently, protected areas encompass ~5% of the earth's land surface, so perhaps the current rates of biological extinction should not surprise us (Ryan 1992). In industrial nations such as the United States, national parks are often islands surrounded by a sea of agriculture, pasture, and urban development. Even the largest of parks suffer invasions by exotic species and disturbance due to heavy tourism (Houston 1971). Roads and trails through parks increase the vulnerability of its interior to "edge effects", eliminating some of the advantages of large size. In less-industrialized countries, sometimes pristine habitats — but more often areas degraded by fires, clear-cutting, and agriculture — surround the park.

This "parks as islands" metaphor suggests an obvious calculation. In archipelagos of oceanic islands, the number of species scales as area raised to the $1/4$ power. This is the familiar species (S) to area (A)

relationship $S = cA^{1/4}$, where c is a constant (Rosenzweig 1995). Protect only 5% of the area and one might lose ~50% of the planet's species.

Two factors mitigate this bleak prospect. First, some species will survive in the human-dominated 95%. The number of survivors will depend on a complex of factors. These include the degree of protection of the park's surrounding matrix and the survival of the particular species within it. For many areas with burgeoning human populations — developing countries and regions like Florida — parks may represent the best hope for protecting biodiversity.

Second, we might be judicious in our choice of the 5%, protecting those areas rich in otherwise vulnerable species. Extinctions concentrate in "hot spots" — areas of many species with small geographical ranges (Myers 1990; Pimm et al. 1995). For example, the great majority of the world's ~1,100 bird species deemed likely to become extinct soon have geographical ranges less than 50,000 km² (Collar et al. 1994). Protecting such range-restricted species in their special places may save more than 50% of the planet's biodiversity.

A third factor exacerbates the potential loss of species from the 5% of protected land. Unlike oceanic islands, parks — particularly small ones — are surrounded by areas whose land use practices may severely impact their flora and fauna. Examining these impacts is this paper's major theme.

We start by asking how many parks are there? Table 1 catalogues the area protected by parks, the total number of parks and the number of large parks in each country in the Western hemisphere.

Table 1: Parks and other protected areas in the Western Hemisphere
(Source: World Resources Institute 1994). Countries are ordered by
increasing size.

North and Central America	Total area in country (km ²)	Area protected (km ²)	Number of parks	Number of parks over 10,000 km ²
Trinidad, Tobago	5,130	180	9	0
Jamaica	10,830	20	1	0
El Salvador	20,720	190	5	0
Belize	22,800	2,910	10	0
Haiti	27,560	100	3	0
Dominican Republic	48,380	10,480	18	0
Costa Rica	51,060	6,210	25	0
Panama	75,990	13,280	15	0
Guatemala	108,430	8,330	17	0
Cuba	109,820	8,940	57	0
Honduras	111,890	5,430	38	0
Nicaragua	118,750	9,520	21	0
Mexico	1,908,690	98,970	60	2
United States	9,166,600	984,560	937	21
Canada	9,220,970	494,480	411	12

South America	Total area in country (km ²)	Area protected (km ²)	Number of Parks	Number of parks over 10,000 km ²
Surinam	156,000	7,360	13	0
Uruguay	174,810	320	8	0
Guyana	196,850	590	1	0
Ecuador	276,840	111,360	15	1
Paraguay	397,300	14,830	19	0
Chile	748,800	137,150	65	5
Venezuela	882,050	275,340	104	5
Columbia	1,038,700	93,910	79	2
Bolivia	1,084,380	92,500	26	4
Peru	1,280,000	41,760	22	2
Argentina	2,736,690	93,360	100	2
Brazil	8,456,510	277,420	214	4

The amount of land set aside in parks does not increase significantly with the size of the country (World Resources Institute 1994). Wealth and aggressive conservation policies are likely key factors. Although Ecuador is only 2% of the size of North America, its proportion of land classified as "protected" (40%) is over twice that in the United States and Canada combined (16%). Large parks are few. Outside the United States and Canada, there are only 21 of them.

Large parks are surely better than small ones for species. By decreasing edge effects, large parks may also be better able to preserve its flora and fauna in the midst of encroaching environmental degradation and human activity. Our key question is: even given their size, are these flagships up to the task?

We now turn to Everglades National Park and Big Cypress National Preserve. It is a "flagship" park surrounded by ocean on one front, and the south Florida urban sprawl on the other. In particular, we examine the ability of this park to maintain the Cape Sable Seaside-Sparrow. This bird does not migrate, the park encompasses its entire range and

its individuals hold territories typical of such a small species. Can the park allow sparrows to survive within it while humanity monopolizes its surround?

A-- Everglades National Park and Big Cypress National Preserve

The comic referral of the two epochs in southern Florida, BC ("before canals") and AD ("after drainage"), betrays the seriousness of the hydrological transformation that has occurred there (Brown 1948). Before canals, the "River of Grass" was a 28,205 km² shallow river, extending from Lake Okeechobee in central Florida south to Florida Bay (figure 1; Light & Dineen 1994). At its peak flow in the wet season, it averaged 64 km wide and 0.5 m deep (U. S. Dept. of Interior 1994). The relatively flat terrain (0 to 6 m above sea level) allowed the water to flow in a vast sheet across the landscape, at up to 0.6 meters per minute (Rosendahl & Rose 1982).

The natural hydrology proved disastrous to fledgling agricultural endeavors (Douglas 1988). The wet season rains flooded many fields and villages. Their inhabitants had constructed them on seemingly

"high" ground in the dry season. To promote development in southern Florida, Congress passed the Swamplands Act of 1850. It paved the way for the construction of over 2,200 km of canals and levees, and over 40 water structures, gates, and pumps over the next 140 years (Light & Dineen 1994). In the 1930's, the construction of massive levees that impound Lake Okeechobee delivered the most profound change to the natural hydrology of southern Florida. These projects have concentrated the flow of water into narrow, flooded tracts while leaving other areas unnaturally dry (U. S. Dept. of Interior 1994).

The original expanse of Everglades is now divided into three land use areas. Three park areas, Everglades National Park (6,113 km²), Big Cypress National Preserve (2,306 km²), and Biscayne National Park (734 km²), preserve about 30% of the original extent of the Everglades for recreational and educational use (figure 2) (U. S. Dept. of Interior 1994). Three "Water Conservation Areas" north of the national parks encompass over 3,550 km². These protect another 37% of the original expanse of the Everglades and the national parks from run-off from the "Everglades Agricultural Area" (2,830 km²) downstream of Lake

Okeechobee. They bear little resemblance to the original habitat (U. S. Dept. of the Interior 1994). In sum, these protected areas, though large, are embedded in a greatly modified surround

B-- Endangered and Threatened species in south Florida

Everglades National Park, Big Cypress National Reserve and Biscayne National Park support over 1640 vertebrate species and 650 plant species (National Park Service 1996). Of these, 56 are listed as Federally Endangered or Threatened. Another 29 species are currently being considered for federal listing status (U. S. Dept. of the Interior 1994). These species depend on the mosaic of habitat types, including pinelands, mangrove forests, cypress swamps, and vast seasonally flooded prairies. Some of these habitats, such as the prairies, are highly dynamic, and can change rapidly in response to changes in hydrology (Nott et al. in prep.).

Over 400 species of migratory birds depend on habitats in the region (U. S. Fish and Wildlife Service 1996), and are greatly affected by changes in hydrology (Kushlan 1979). Several species, such as the wood

stork (*Mycteria americana*), snail kite (*Rostrhamus sociabilis plumbeus*) and Cape Sable Seaside-Sparrow (*Ammodramus maritimus mirabilis*) have experienced precipitous declines in the last decade. Critical to our discussion is whether our large parks offer enough protection from natural and human-caused disturbances. Alternatively, is active management essential to save these species from extinction?

As a case study, we describe our work on the ecology of the Cape Sable Seaside-Sparrow and the factors inimical to its continued survival. As we discovered, proper management can negate some effects. We can ameliorate others only by providing a large enough area for the sparrow to overcome adversity on its own.

A-- The Cape Sable Seaside-Sparrow

The Cape Sable Seaside-Sparrow's habitat preferences are unique among the seaside sparrows. They occupy seasonally-inundated freshwater marshes and not the saltwater marshes used by other Seaside-Sparrows. The closest relative of the Cape Sable race was the

Dusky Seaside-Sparrow. It went extinct in 1991 because of lost habitat (Post & Greenlaw 1994).

The range of the Cape Sable Seaside-Sparrow is fragmented and it occupies parts of that range episodically. Howell (1932) found the first populations on Cape Sable, a peninsula in the southwest corner of Everglades National Park. In 1935, a hurricane flooded the prairies on the Cape with a 4m saltwater storm surge. Eventually, this inundation caused major vegetational changes, destroying suitable sparrow habitat. (In short, the sparrow is a freshwater sparrow, not a seaside sparrow, and it no longer occurs on Cape Sable.)

Later populations, found in Everglades National Park and Big Cypress National Preserve to the north, have disappeared and reappeared with regularity. Werner (1975) and Bass & Kushlan (1982) conducted extensive helicopter surveys of Everglades National Park and Big Cypress National Preserve. Until then, the range of the Cape Sable Seaside-Sparrow was unknown.

B-- Current distribution (1981-1996)

Since 1992, we have continued an extensive helicopter survey first conducted by Bass & Kushlan (1982). Before 1993, the total sparrow population was divided into six subpopulations. Two core subpopulations (A, in the northwest section of Everglades National Park, and B in the southeast section) held the majority of the sparrows. Four other peripheral subpopulations, C-F, held small and variable numbers (figure 3). In 1992, Hurricane Andrew passed directly over subpopulation A, and the 1993 survey revealed the near-extinction of that subpopulation. As of 1996, that subpopulation remains at 16% of its 1992 abundance. Subpopulation B has remained approximately constant. Two of the four peripheral subpopulations (C to F) went extinct between 1992 and 1995, but were recolonized by small numbers in 1996. Peripheral subpopulation E has fluctuated in size since 1992.

B-- Hypotheses for the sparrow's decline

We have evaluated four factors that might explain these changes in population: chance population fluctuations, hurricanes, fire and

hydrology (Curnutt et al. in prep, Nott et al. in prep). Each one could cause the extinction of the sparrow. We cannot mitigate chance and hurricanes (apart from the costly process of transplanting individuals back into abandoned areas). We can manage fire and hydrology, but can we do so wisely?

Extinctions due to random fluctuations in populations have a higher probability of occurring in small populations (Pimm 1991). Of the six subpopulations, four are peripheral, smaller populations that have experienced several local extinctions and recolonizations. We first asked whether the duration of local extinction in some of the smaller subpopulations was longer than one should expect by chance alone.

We applied a population dynamics model developed by Curnutt, Pimm & Maurer (1996) for grassland sparrows in North America. This model used population variability data for ten grassland sparrow species, obtained over twenty years for the North American Breeding Bird Survey. It estimates empirically the chance that a population of a

given average size would be absent by chance alone for periods of 1, 2, 3... n years.

The model concluded that a three-year disappearance of birds from subpopulation C was unlikely to be due to chance alone. Three year extinctions in similarly sized populations of grassland birds happened in less than 5% of the cases. In contrast, due to their smaller populations, extinctions in subpopulations D and F were not significantly unusual. Finally, the large drop in subpopulation A from 1992 to 1993 had few precedents among the many small bird species for which we have long term population counts (figure 3).

We then explored whether hurricanes could better explain the unusual declines. Hurricane Andrew in 1992 swept over almost all of the subpopulations. It flooded none of the area, however. The storm was a relatively dry one, it passed east to west, and the storm surge affected only coastal areas. Our survey in 1993 found the greatest loss (83%) in subpopulation A (figure 3), while other subpopulations were less affected. This subpopulation has not recovered and has continued to

decline. From the details of the local declines between 1992 and 1993 and the lack of recovery afterward, we conclude that Hurricane Andrew was not the principal cause of the sparrow's decline. Given the intensity of the storm, however, it seems likely that some (and perhaps many) birds did perish in it.

Hydrology has the most profound effects on sparrow habitat. During the breeding season (March through June), above-ground water levels higher than 10 cm halt breeding activity. High water floods nests directly. It also leads to higher rates of nest predation (Lockwood et al. 1997). An increase in the length of the period of flooding — hydroperiod — also favors sawgrass (*Cladium jamaicense*) (Nott et al. in prep.). Sparrows do not inhabit areas dominated by sawgrass. Although natural rainfall alters water levels and their duration, water management practices control most of the hydrological dynamics in Everglades National Park.

The decline of the northwest core population (A) coincided with large water releases in 1993, 1994 and 1995 from several floodgates to the

north. Nott et al. (in prep.) obtained hydrological data on water levels, rainfall, and water releases from the floodgates at the north end of the Park. Statistical analyses demonstrated that water releases were crucial to determine the water levels in the sparrow's habitat (figure 4). Rainfall was not so important. Simply, managed water flows were most responsible for the bird's precipitous decline in subpopulation A.

Fire also affects the sparrows and their habitat. Sparrows abandon an area for several years after a fire, until suitable habitat has regrown (Werner 1975). Curnutt et al. (in prep.) mapped fire frequency for areas that support relatively stable populations, and compared these maps to population changes found on our helicopter survey. Sparrow density was highest in sites that burned once or twice in a ten year period, and approached zero in sites that burned seven or more times in that period.

The extinctions of subpopulations C and F are likely due to the high frequency of anthropogenically set fires along the Park's border. The generally drier nature of these areas is due, in turn, to water

management policies that move water to the west of Shark River Slough. In short, management floods the western areas of the sparrow's range and overdrains the eastern ones.

We can only manage for chance and hurricanes by protecting enough habitat to support a large sparrow population. Invariably, this would mean increasing the size of the park. For some parks, such as Everglades National Park, increasing the park into the degraded agricultural areas has proved expensive and politically difficult. In this way, Everglades National Park is much like an oceanic island.

We cannot manage fire and hydrology, however, by simply providing an island that is large enough. Allowing only lightning-ignited fires to burn would approximate the natural fire regime and this is the current policy. The ability to prevent unplanned human ignitions, including arson, is clearly limited. The hydrology of the Everglades cannot simply be left alone, as it will never return to its pre-drainage flows. Water management must actively pursue water release programs that

resemble this natural flow. This hydrological influence also affects the frequency and intensity of fire in the park.

A-- Ecosystem management and conserving endangered species

B —Parks as islands

The entire range of the Cape Sable Seaside-Sparrow exists within the boundaries of Everglades National Park and Big Cypress National Preserve — there is no habitat elsewhere. Because of this, it is tempting to visualize the park as an island surrounded by unsuitable habitat. Many other parks are similar and this metaphor is certainly not a new one (Shafer 1990).

All populations vary in numbers over time. This variation may bring a small population to the low level from which it cannot recover, whereas a larger one may survive the crisis. Obviously, islands of habitat hold populations of fewer individuals than did the habitat's original extent — thus island populations are at greater risk of extinction. Moreover, immigrants will rescue nearby populations more

often than isolated populations on the verge of extinction. These are the two familiar mechanisms to explain why islands have fewer species than mainlands — and why parks, when isolated, might be expected to lose species.

The Cape Sable Seaside-Sparrow offers an excellent illustration of these risks. Its population is fragmented into six isolated subpopulations of different sizes, whose numbers vary over time. The small, peripheral subpopulations have declined to zero for a few years, and were recolonized by sparrows dispersing from neighboring populations. As the total sparrow population declines within the Park, the chances of extinction for small subpopulations increase, and colonization from other subpopulations decreases.

Another threat to small, isolated populations is catastrophic disturbance. A hurricane may have a major impact on a sparrow population and so push it closer to extinction. If the disturbance has not drastically altered the vegetation or landscape, sparrows from less-affected populations can recolonize the area. Large numbers of

individuals spread over a large area is the natural defense against disturbance-caused extinction.

Such examples are not unique to Everglades National Park. For large mammal species in western North America, Newmark (1987, 1995) found even 10,000 km² parks were too small to support a full complement of the historic assemblage. Only the Kootenay-Baniff-Jasper-Yoho park assemblage, which covers almost 21,000 km², had no mammal extinctions since delineation of park boundaries. Unfortunately, the success of this park may not be completely dependent on its large size, but may also rely on the relatively pristine condition of the surrounding area. Newmark (1995) found that survival of large carnivores in the western parks relied upon habitat adjacent to the park.

B —The Park is not an island

Unlike true islands, where the oceanic surround poses little threat to the islands' species, isolated parks have to contend with threats that

penetrate the park's boundary. For Everglades National Park, these involve water and fire.

Water plays a key role for the sparrow. The South Florida Water Management District controls the area's hydrology through a vast system of canals, gates and levees. As ecological knowledge accumulates, the Water Management District alters water distribution and delivery rates to the Park. From the sparrow's point of view, Everglades National Park is not an island: it links too tightly to the sources of water and fires that surround the Park.

In general, the Water Management District must contend with several sources of adversity (U. S. Department of the Interior 1994). Drainage and flood control have dried and otherwise degraded historic wetlands, increasing fire frequency on the park's eastern boundaries. Freshwater diverted into estuaries on either side of the Park increases siltation, disrupting the saline balance of the waters and affecting fisheries and other marine systems in Biscayne National Park. Human pressures, such as increased urban sprawl (Miami and Homestead), agricultural

demands for water, polluted runoff, and mining for limestone prevent the Water Management District from effecting optimal water delivery programs. And changes in hydrology and hydroperiod have significantly changed vegetation and associated animal communities in the Park.

Kushlan (1979) found a similar dependence on adjacent land in two wading bird species in Everglades National Park. Although overall, the community of wading birds in the Park had dropped to 20% of its historic level, the decline was not equal among all species. In particular, the white ibis (*Eudocimus albus*), which has established breeding colonies outside park boundaries, did not experience as precipitous a decline as the wood stork (*Mycteria americana*). The wood stork remains dependent on breeding habitat in Everglades National Park. Water flow alteration and diversion by water management activity have severely altered its habitat. Even at 10,000 km², the "legal" boundary of the Everglades-Big Cypress-Biscayne park trio may not be large enough to encompass its "biological" boundary (Newmark 1985).

This was most certainly the entire watershed from Lake Okeechobee to Florida Bay.

Worldwide, flagship parks have a long, idiosyncratic list of external threats that jeopardize the survival of their unique species (Burton 1991). Oil spills constantly threaten the Northern Yukon National Park in Canada (10,169 km²). Flooding from hydropower projects and deforestation by wealthy ranchers and poverty-stricken squatters jeopardize the immeasurable biodiversity in Amazonia National Park (10,000 km²) in Brazil. In Russia, the Baikal Region National Park (15,640 km²) must contend with oil spills and pollution in the air, soil, and water. And in the Serengeti National Park and Ngorongoro Conservation Area in Tanzania (31,339 km²), cattle grazing and possible railroad construction compete with the impressive megafauna for water and other scarce resources.

A — Conclusions.

Flagship parks are few. Even the largest areas are not large enough to be indifferent to the ecosystem processes that surround them. Endangered

species — like the Cape Sable Seaside-Sparrow — provide clues to how we must manage those processes. Roughly, the west is sometimes too wet and the east is probably always too dry. Re-distribution of water from the west to the east would aid the sparrow's recovery. Such a redistribution would restore the water flows to something like their natural condition.

Outside influences make it impossible to treat this park as an island unaffected by its surround. The Cape Sable Seaside-Sparrow cannot survive natural disturbances in the face of profound hydrological alteration, even though the park boundaries protect the entire population. The sparrow's response to changes in water management practices can be a good indicator of our ability to approximate the original water flow and timing. Good ecosystem management is essential for the sparrow's survival. And the sparrow's survival is a measure of the quality of that management.

More generally, we cannot assume that, even if we design our parks to be technically large enough to support viable populations of the

megafauna, the parks will no longer require our services. We must continually track the species within, paying close attention to dramatic declines that may correlate to human activity inside or outside park boundaries.

A-- Acknowledgments

We would like to thank the National Biological Service, the National Park Service, the United States Army Corps of Engineers, and the United States Fish and Wildlife Service for funding for our research in Everglades National Park. Also, we extend our gratitude to those who provided invaluable service in the field: Karla Balent, Tom Brooks, John Curnutt, Tabby Fenn, Nancy Fraley, Stephen Killeffer, Julie Lockwood, Lisa Manne, M. Philip Nott, Gareth Russell, and Ester Stanton. Without the vision of Marty Fleming and Sonny Bass our work would never have been started. Their support, and that of Jon Moulding, made it possible.

A-- Literature Cited

- Bass, O. L., Jr., & J. A. Kushlan. (1982). Status of the Cape Sable Sparrow. Report T-672, South Florida Research Center, Everglades National Park. Homestead, Florida. 41 pp.
- Brown, A. H. (1948). Haunting heart of the Everglades. *National Geographic*, February, p. 145-173.
- Burton, R. (1991). *Nature's last strongholds*. Oxford University Press, N.Y. pp. 256.
- Collar, N. J., M. J. Crosby, and A. J. Stattersfield. (1994). *Birds to Watch 2: The world list of threatened birds*. Birdlife Conservation Series No. 4. BirdLife International, Cambridge, United Kingdom.
- Curnutt, J. L., S. L. Pimm, & B. Maurer. (1996). Population variability of sparrows in space and time. *Oikos* 76: 131-144.
- Curnutt, J. L., A. L. Mayer, T. M. Brooks, L. Manne, O. L. Bass, Jr., D. M. Fleming, and S. L. Pimm. (in prep). Population dynamics of the Endangered Cape Sable Seaside-Sparrow.
- Douglas, M. S. (1988). *The Everglades: river of grass*. Pineapple Press, Inc. Sarasota, FL. 448 pp.
- Houston, D. B. (1971). Ecosystems of national parks. *Science* 172: 648-51.
- Howell, A. H. (1932). *Florida bird life*. Coward-McCann, Inc. NY.
- Kushlan, J. A. (1979). Design and management of continental wildlife reserves: lessons from the Everglades. *Biological Conservation* 15: 281-90.

- Light, S. S. & J. W. Dineen. (1994). Water control in the Everglades: a historical perspective. In: Everglades: the ecosystem and its restoration, (Eds Davis, S. M. and Ogden, J. C.). St. Lucie Press.
- Lockwood, J. L., K. H. Fenn, J. L. Curnutt, D. Rosenthal, K. L. Balent, & A. L. Mayer. (1997). Life history of the Endangered Cape Sable Seaside -Sparrow. *Wilson Bulletin* **109**(4).
- Myers, N. (1990). The biodiversity challenge: expanded hot-spots analysis. *Environmentalist* **10**:243-256.
- National Park Service. (1996). NPFauna and NPFlora for the U. S. National Park Service. (WWW). Available: http://ice.ucdavis.edu/US_National_Park_Service/. (27 August 1996).
- Newmark, W. D. (1985). Legal and biotic boundaries of western North American national parks: a problem of congruence. *Biological Conservation* **33**: 197-208.
- Newmark, W. D. (1987). A land-bridge island perspective on mammalian extinctions in western North American parks. *Nature* **325**, 29 January 1987, 430-432.
- Newmark, W. D. (1995). Extinction of mammal populations in western North American national parks. *Conservation Biology* **9**(3): 512-526.
- 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 & S. L. Pimm. (in prep). Water levels, rapid vegetational changes, and the Endangered Cape Sable Seaside-Sparrow.
- Pimm, S. L. (1991). *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. The University of Chicago Press.

- Pimm, S. L., G. J. Russell, J. L. Gittleman and T. M. Brooks. (1995). The future of biodiversity. *Science* 269:347-350..
- Post, W. & J. S. Greenlaw. (1994). Seaside Sparrow (*Ammodramus maritimus*). In: The birds of North America, No. 127 (Eds Poole, A. & Gill, F.). Philadelphia: The Academy of Natural Sciences; Washington, D. C.: The American Ornithologists' Union.
- Rosendahl, P. C. & P. W. Rose. (1982). Freshwater flow rates and distribution within the Everglades marsh. Proceedings of the National Symposium on Freshwater Inflow to Estuaries, Coastal Ecosystems Project. (Eds Cross, R. D. & Williams, D. L.) U. S. Fish and Wildlife Service, Washington, D. C.
- Rosenzweig, M. L. (1995). Species diversity in space and time. Cambridge University Press. 436 pp.
- Ryan, J. C. (1992). Life Support: Conserving biological diversity. Worldwatch Paper No. 108. WorldWatch Institute, Washington, D. C.
- Shafer, C. L. (1990). Nature reserves: Island theory and conservation practice. Smithsonian Institution Press, Washington, D. C. pp. 189.
- United States Department of the Interior. (1994). The Impact of Federal Programs on Wetlands, Vol. II. A Report to Congress by the Secretary of the Interior, Washington, D. C.
- United States Fish and Wildlife Service. (1996). Endangered is not forever: A recovery plan for the Threatened and Endangered species of south Florida. South Florida Ecosystem Office.
- Werner, H. W. (1975). The biology of the Cape Sable Sparrow. Report to U. S. Fish and Wildlife Service. Everglades National Park, Homestead, Florida. 215 pp.

World Resources Institute. (1994). World Resources 1994-1995. World Resources Institute, Washington, D. C.

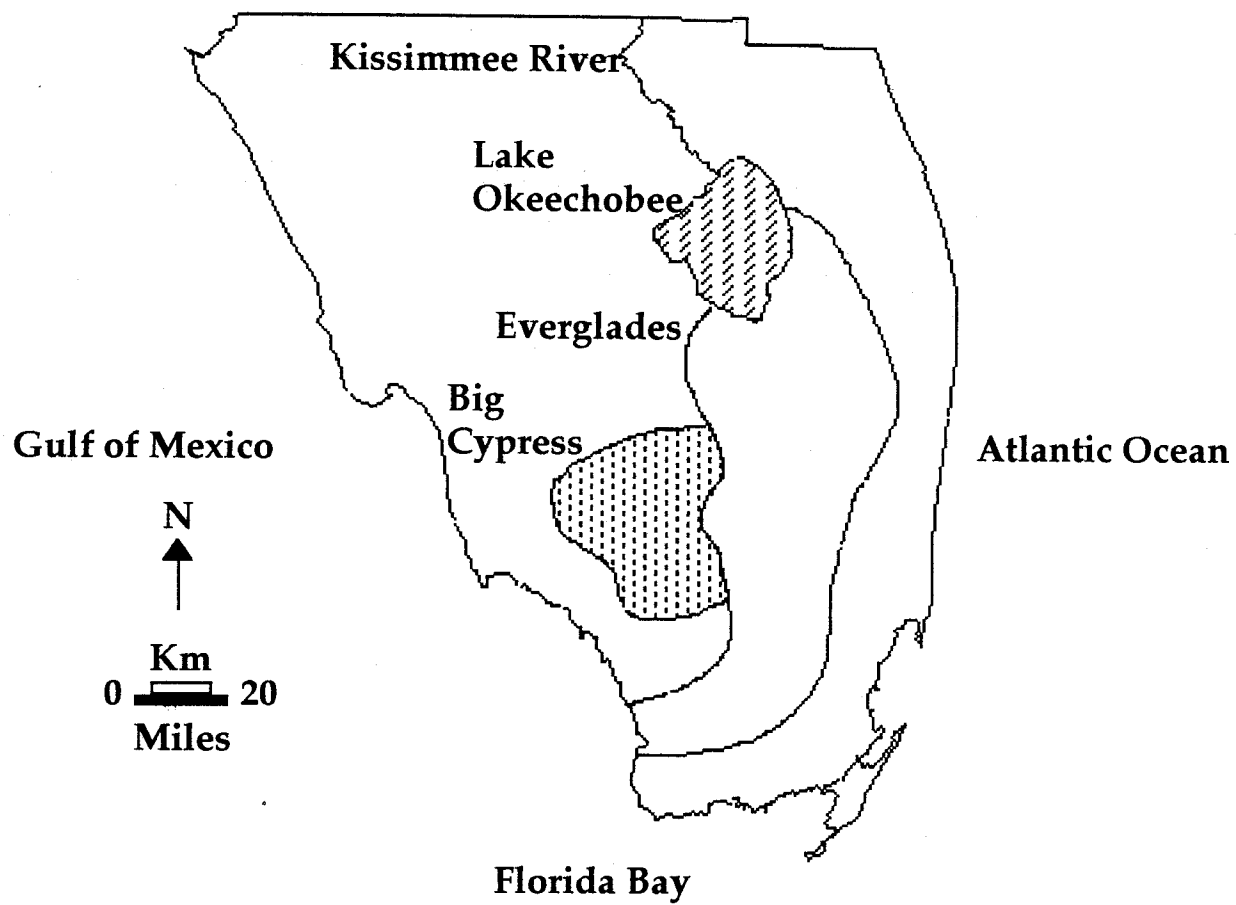
List of figure captions:

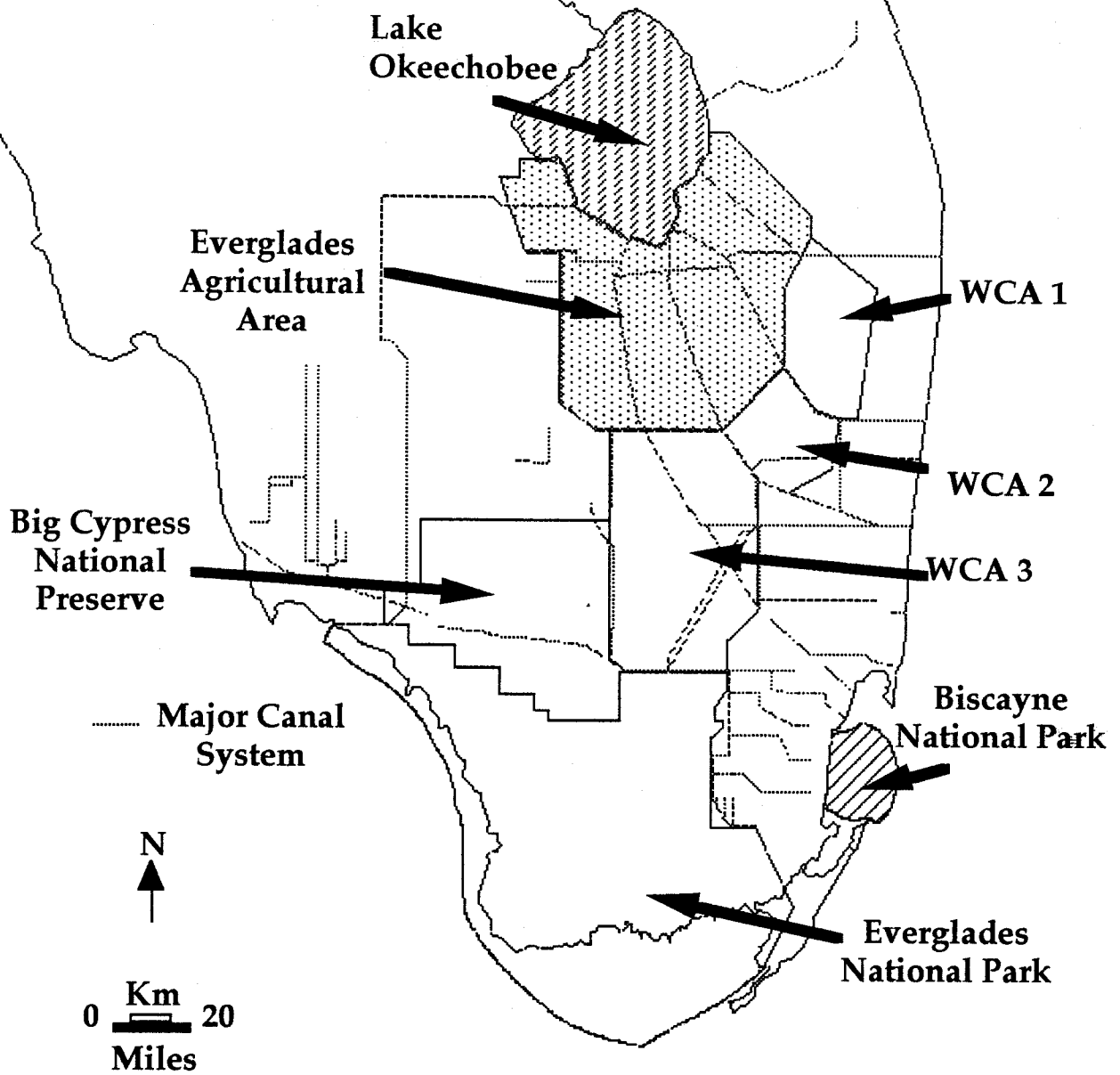
Figure 1. The historic drainage of the Everglades watershed, flowing uninterrupted from Lake Okeechobee to the Gulf of Mexico and Florida Bay.

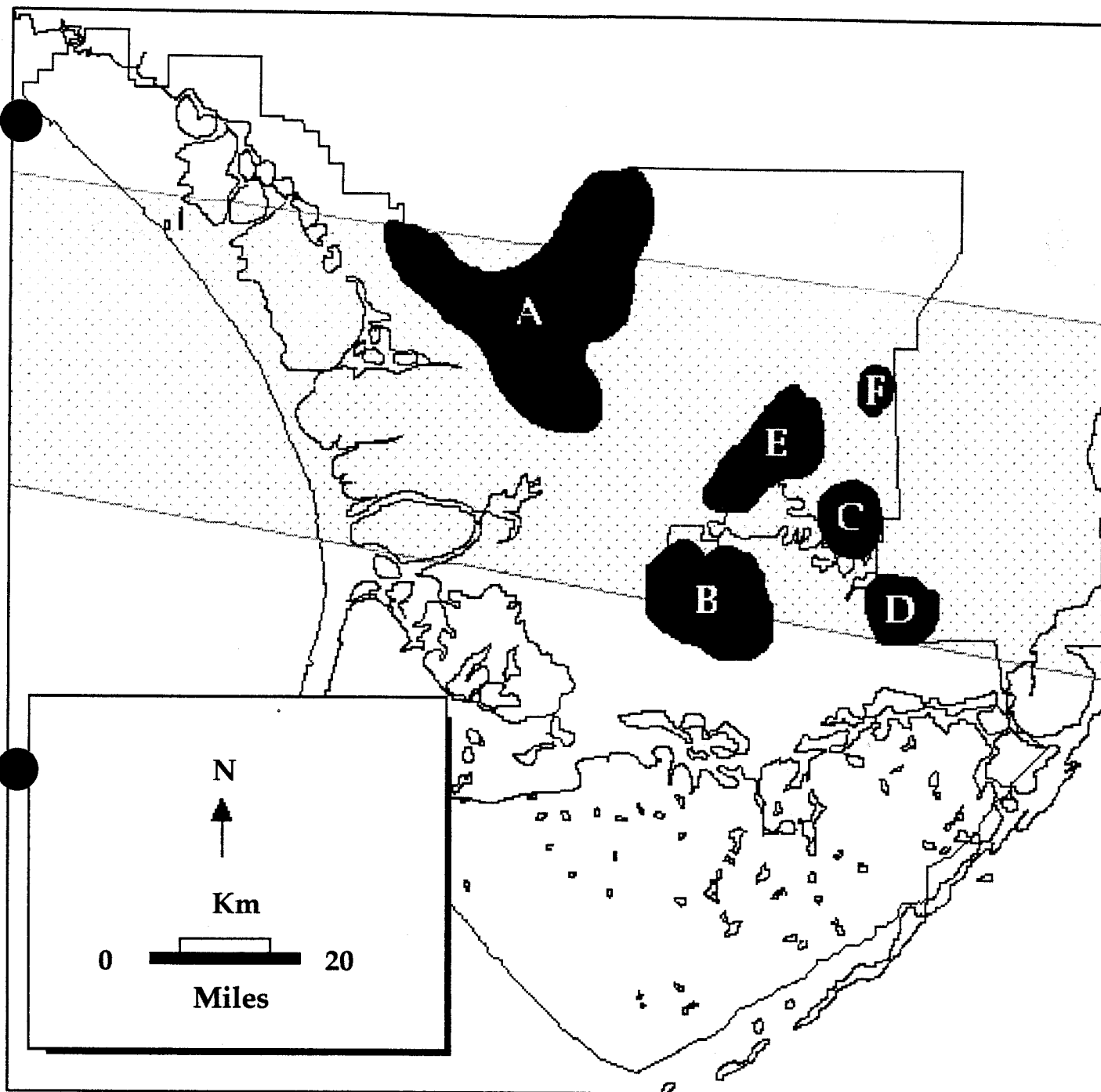
Figure 2. The three Water Conservation Areas filter polluted water from the Everglades Agricultural Area before it flows into Biscayne and Everglades National Parks, and Big Cypress National Preserve.

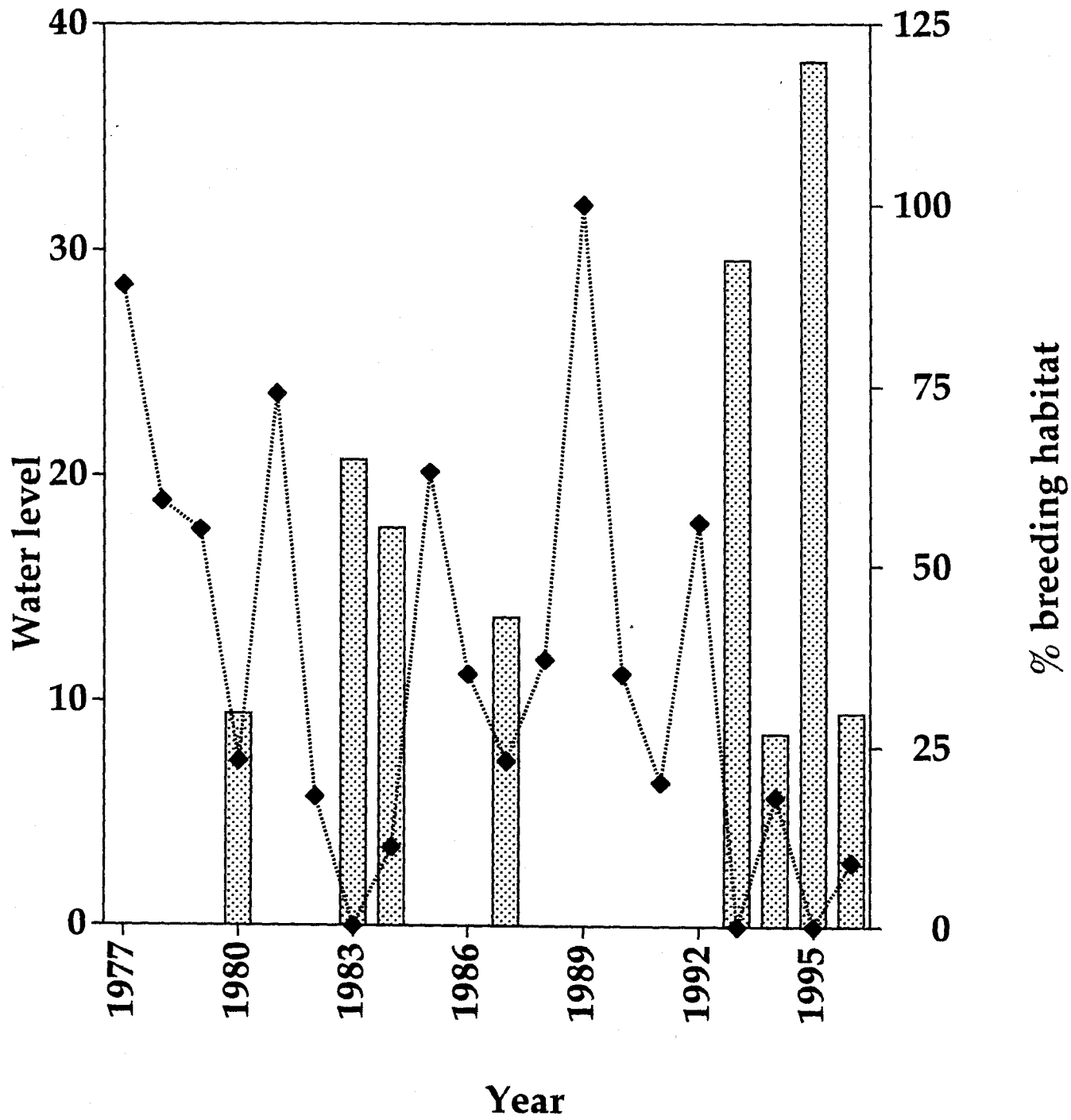
Figure 3. The path of Hurricane Andrew (shaded area) passed over almost all of the six subpopulations of Cape Sable Seaside-Sparrows (darkened areas).

Figure 4. Water depth during the breeding season (histogram, left scale, cm above Mean Sea Level) varies considerably from year to year. In wet years, there is almost no dry habitat in which the sparrows can breed (triangles, right scale, percentage of maximum habitat possible).

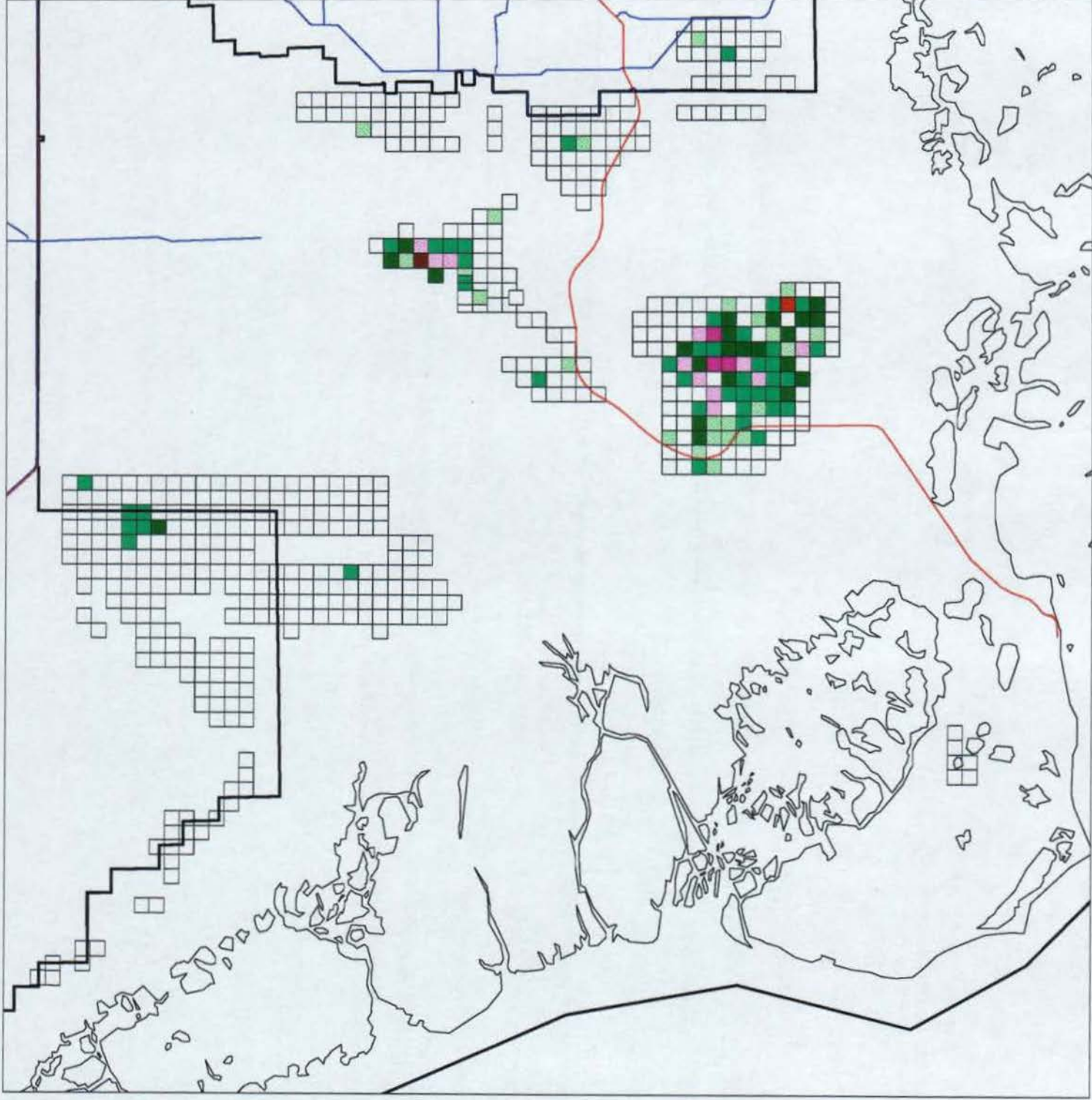
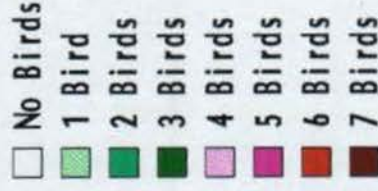








1997 Sparrow Sites Visited



Population Ecology of the Cape Sable Seaside-Sparrow

(*Ammodramus maritimus mirabilis*)

Plant Survey

Preliminary Report

1997

Audrey L. Mayer and Stuart L. Pimm

University of Tennessee, Knoxville

Department of Ecology and Evolutionary Biology

569 Dabney Hall

Knoxville, TN 37996-1610

(423) 974-6186 or -1981

amayer@utk.edu

StuartPimm@aol.com

Introduction

Cape Sable Seaside-Sparrows may use many vegetation cues to select their breeding habitat. We know that these sparrows occupy freshwater prairies. Past attempts to characterize the vegetation may have been too general to discern the vegetation characteristics that sparrows require. This may include both structural (such as biomass or maximum vegetation height) and floristic characteristics (plant species composition, associated dominant species).

Werner and Woolfenden (1983) conducted plant surveys at some of their helicopter survey sites. They recorded species occurrence and vegetative structure in 1 m² quadrats, and plotless sampling using a "closest individual method" (Cottam and Curtis 1956). Four habitat types are suitable for sparrows: clumped *Spartina* prairie, unclumped *Spartina* prairie, sparse *Cladium* prairie, and *Muhlenbergia* prairie. Different dominant plant species characterized each prairie type, as well as differences in average biomass, stem density, and stand height. Sparrows were most common in the *Muhlenbergia* prairies, with some occupied sites in the other three prairie types.

Kushlan and Bass (1983) conducted an extensive helicopter survey of all possibly Cape Sable Seaside-Sparrow habitat, and narrowed suitable habitat to three prairie types. Muhly prairie is dominated by muhly grass (*Muhlenbergia filipes*), but may also include considerable blacktop sedge (*Schoenus nigricans*) and sawgrass (*Cladium jamaicensis*); mixed prairie, where *Muhlenbergia* is absent and *Rhynchospora* sp. and *Panicum* sp. are more prevalent; and cordgrass prairie, a saltwater habitat dominated by cordgrass (*Spartina bakeri*). Sixty-seven percent of the occupied survey sites was muhly prairie. When we include the mixed prairie classification, roughly 96% of the habitat of occupied sites fell into these two categories. Kushlan and Bass (1983) concluded that sparrows were mainly restricted to these two prairie types.

Rotenberry (1985) and Wiens (1973) found that, on a territorial scale, other grassland sparrows (the savannah and grasshopper sparrows) may use floristic cues to establish and defend territories. However, on larger scales,

selectivity based on species composition may disappear, and may instead reflect structural characteristics of the vegetation. As the scale of the research may confound any patterns of habitat preferences, we designed our survey methods to allow us to make comparisons both between occupied and unoccupied sites. We may also be able to detect vegetation differences within study sites.

Study Sites

Table 1 Description of already established study plots

Taylor Slough (TS). This site is 1100 m by 600 m (66 ha) and lies within the site that Harold Werner established in 1974. Bisected by the Main Park Road, the site runs along the east side of Taylor Slough. The vegetation is a mix of sawgrass and *Muhlenbergia* and consists of large areas of "pinnacle rock" (exposed limestone) with infrequent patches of well-developed soil. Being at the edge of the slough, and downstream from a floodgate, this site can become inundated early in the wet season by rain or by the opening of the floodgate. During the spring and summers of 1996 and 1997, Park management burned portions of Taylor Slough, south of the road, in a patchwork pattern. These burned areas stimulated rapid new growth, and may have increased the overall species richness of the site.

Old Ingraham Highway South (OIHS) This site is 600 m by 800 m (48 ha) and is south of the west end of Old Ingraham Highway. In 1993, we marked its boundaries with PVC poles at four corners. The site is mixed prairie habitat dominated by *Muhlenbergia*, with no surface water throughout the field season, except in very wet years.

Dogleg (DL) This site, located between the Main Park Road and the remnants of the Old Ingraham Highway, is approximately 20 ha. The juxtaposition of roads and pinelands to the north account for this site's small area and unusual shape (dog-legged). The dominant *Muhlenbergia* cover is sparse in many areas due to thin soil and apparently recent fire activity.

Alligator Hammock (AH) This site is directly west of Dogleg (across the main road), and is also approximately 20-ha. Pinelands bound this site to the north and west, and a much wetter *Cladium*- area lies to the south. The vegetative cover is similar to that at Dogleg. We established permanent boundaries for this plot in late May 1996.

North Mahogany (NM) This site is north of Dogleg by approximately one-half mile along the main road. We have no set boundaries for this site yet, and have concentrated most of our efforts on the three to four territories found near the road. The vegetation of the *Muhlenbergia*-dominated site is short and very sparse in the burned area at the east end.

Methods

To determine habitat selection within the habitat type (marl prairie), we conducted plant surveys using a strip transect/1 m² quadrat method. Our occupied study sites supported a high to moderate density of sparrows, and one site (Taylor Slough) had no sparrows. In each study site, we used a stratified random sampling technique to place twenty 50m-strip transects (see figures 1-6). Each study area had boundaries, which were either permanent PVC poles at the site's corners, or natural boundaries such as a pineland ecotone. All transects have associated GPS coordinates. We determined the direction of the transect from the starting point by throwing a small plastic stake. With ten quadrats per transect, this scheme yields 200 1m²- quadrats of data per site. This satisfies Mueller-Dombois and Ellenberg's (1974) minimum sample area requirement for their "dry- grassland" and "hay meadow" habitat categories (the closest in structure to marl prairies) of 50-100 m².

In each 1 m² quadrat at every 5m interval along the transect, we collected the following data:

- Abundance – For every quadrat, we used the Braun- Blanquet method of estimating abundance (6 categories: 0 (sparsely or very sparsely present) to

5 (covering more than 3/4 of the area)) (Phillips 1959). To assure that our estimates were consistent, we counted actual stem densities for one quadrat of each transect (chosen at random), and compared these estimates to the actual density. This also allows us to make direct comparisons to our stem density data collected in previous years.

- Cover – We used the estimate scale used in previous years (and recommended by Mueller-Dombois and Ellenberg 1974): from 0 (0 to 1.0%) to 5 (75-100%).
- Species composition – We took presence/absence data, along with the above two estimates, for every species in each quadrat. We made every attempt to identify all plants to species, but when this was impossible, we resolved the taxa to genus. We cross-checked each species identification with samples in the Beard Center Museum and in the vegetation crew office.
- Stem density – For each plant species, we counted the number of stems per quadrat. Using data from our plant removal study in 1995 and 1996, we found a direct relationship between stem density and standing biomass. We used this relationship in this year's data to indirectly measure biomass in each quadrat.
- Maximum vegetation height – Especially critical to determine available perches, we measured the highest plant in the quadrat.
- Effective height (Wiens 1969) – Using a field notebook, we recorded the maximum height at which 90% of the side of the notebook is obscured by vegetation. While this is a crude measurement, it allows us to quantify an aspect of the habitat that may be important to the sparrow for predator evasion and thermal regulation.
- Association – For each quadrat, we determined the two species with the highest combined abundance and cover.
- Distance to nearest Cape Sable Seaside-Sparrow territory – for each transect, we calculated the distance between the transect and the nearest territory, using GPS coordinates and computer-generated maps. These distances have an error of 5 to 50 m associated with them, due to inaccuracies of the GPS unit.

Satellite Imagery

This year, we have access to satellite images of the Everglades ecosystem. Using successive years of satellite images along with the results from the extensive helicopter survey, we can determine how hydrology and fire regimes of the Everglades have caused changes in the vegetation. We will also see how these changes have affected sparrow occupancy rates. Satellite images offer a much larger scope than "traditional" field studies, and allow us to detect broad patterns of change that our plant surveys may not detect. Our daily field work is being used as ground-truthing for this aspect of the project. We are using some of the satellite results to determine the power of these analyses to predict and locate suitable Cape Sable sparrow habitat.

Results

All sites

Predictably, overall vegetation abundance and cover covaried, as well as dead matter abundance with dead matter cover, and periphyton abundance with periphyton cover (Table 1). Due to the high correlation of abundance and cover, we used only abundance measures in further analyses. High abundance and cover of periphyton were negatively associated with vegetation (both living and dead). We would expect these results, as increased abundance and cover of periphyton often occur in areas of less vegetation.

The effective height, an estimate of the thickness of the vegetation, was negatively correlated with the maximum vegetation height. Dogleg and Old Ingraham Highway South had the highest effective vegetation height, while Taylor Slough had the highest maximum vegetation height (table 1, figure 7). Average plant species richness for all sites was between 6.9 to 8.9 species, and total species richness ranged from 38 to 50 species.

Table 1. A comparison of the vegetation of Alligator Hammock (AH), Dogleg (DL), North Mahogany (NM), Old Ingraham Highway South (OIHS), Shark Valley (SV), Taylor Slough (TS). Numbers are an average of the twenty transects in each study site.

Study site	AH	DL	NM	OIHS	SV	TS
Square meters sampled (N)	200	200	200	200	200	200
Mean No. of species / square meter	7.3	8.7	8.0	8.9	8.0	6.9
Total No. of species present	44	46	38	50	42	42
Plant abundance	1.9	1.8	1.5	2.1	1.7	2.2
Plant cover	2.5	2.4	2.2	2.6	2.2	3.0
Muhly dominance by % cover	*	*	*	*	*	*
Sawgrass dominance by % cover	*	*	*	*	*	*
Mean Max. graminoid height (cm)	93.3	93.2	95.5	91.1	102.6	111.6
Effective height (cm)	2.6	4.0	1.0	4.2	.9	1.0
Clumpiness	2.5	2.1	2.2	2.1	2.0	2.2
Dead matter abundance	1.8	1.6	1.8	1.7	1.4	2.3
Dead matter cover	2.2	2.1	2.5	2.2	1.8	2.8
Periphyton abundance	4.8	4.6	4.7	4.6	4.9	4.2
Periphyton cover	6.8	6.7	6.7	6.5	6.9	6.0

Total plant biomass (gm)	*	*	*	*	*	*
Live plant biomass (gm)	*	*	*	*	*	*
Live plant biomass (%)	*	*	*	*	*	*

* indicates data analysis not completed

Alligator Hammock

We found three relationships to be significant. Abundance and clumpiness were positively correlated ($p < .0004$). Effective height varied negatively with periphyton abundance ($p < .0001$), along with species richness and periphyton abundance ($p < .0003$).

Dogleg

We found only one significant relationship. Effective height varied negatively with periphyton abundance ($p < .0001$).

North Mahogany

We found the effective height varied negatively with dead matter abundance ($p < .0001$).

Old Ingraham Highway South

Effective height varied positively with plant abundance ($p < .0001$) and negatively with periphyton abundance ($p < .0001$).

Shark Valley

As found in Old Ingraham Highway South, effective height varied positively with dead matter abundance ($p < .0003$) and negatively with periphyton abundance ($p < .0006$).

Taylor Slough

We found effective height varied negatively with periphyton abundance ($p < .0006$).

Table 5. A comparison of the vegetation of Taylor Slough between the years 1975 (from Werner 1975), 1995 and 1996. We determined species dominance for the 1995 and 1996 data by scaling percentage coverage measurements per square meter to percentage coverage of all live plants after Werner's method.

Parameter	1975	1995	1996	1997
Square meters sampled (N)	50	8	8	200
Mean No. of species / square meter	9.9	4.75	3.38	6.9
Total No. of species present	35	10	5	40
Muhly dominance by % cover	82%	17%	26%	*
Sawgrass dominance by % cover	14%	80%	74%	*
Mean Max. graminoid height (cm)	92.1	140.9	146.4	111.6
Total plant biomass (gm)	457	260	191	*
Live plant biomass (gm)	105	117	71	*
Live plant biomass (%)	0.23	0.45	.37	*

* indicates data analysis not completed

Yet to be completed:

1. Biomass analysis

We will calculate live biomass using stem density counts for all study sites. We will then add this variable to correlation analyses, and compared between sites, and within sites between transects. Taylor (1983) found that dead biomass and total biomass have an effect on sparrow presence. His results suggest that areas with 550gm/m² of dead biomass and 700gm/m² total biomass or higher are not occupied by sparrows. We will compare our 1996 (in which we did not find this result, see Table above) and 1997 results to Taylor's finding.

2. Vegetation differences/patterns within study sites

We will make comparisons between transects within 25m of a sparrow territory and further away, regardless of site.

3. Plant species associations

Analysis of plant species associations, and possible further delineation of "Muhly prairie" and "mixed prairie" into subclassifications, relevant to differences in sparrow occupancy.

4. Comparison of our results with past results

Werner and Woolfenden (1983) data:

Muhly prairie biomass: 100-1,100 gm/m²

Stem density: 1,300-2,400 ind./ m²

Stand height: 0.7 m

Sparse Cladium: biomass: 600-900 gm/ m²

Stem density: 800 ind./ m²

Stand height: 1 m

Unclumped Spartina: biomass: 500-3,100 gm/ m²

Stem density: 1,100 ind./ m²

Stand height: 1 m

Clumped Spartina: biomass: 3,100-3,400 gm/ m²

Literature Cited

- Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37:451-460.
- Kushlan, J. A. and O. L. Bass Jr. 1983. Habitat use and the distribution of the Cape Sable Sparrow. In *The Seaside Sparrow, its biology and management*, p. 139-146. N. C. Biol. Surv. and N. C. State Mus.
- Mueller-Dombois, D. and H. Ellenberg 1974. Aims and methods of vegetation ecology. John Wiley and Sons, Inc.
- Phillips. E. A. 1959. Methods of vegetation study. Henry Hold and Co., Inc.
- Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? *Oecologia* 67:213-217.
- Taylor, D. L. 1983. Fire management and the Cape Sable sparrow. Pages 147-152 in *The Seaside Sparrow, its biology and management*. N. C. Biol. Surv. and N. C. State Mus.
- Werner, H. W. 1975. The biology of the Cape Sable Sparrow. Report to U. S. Fish and Wildlife Service. Everglades National Park, Homestead, Florida. 215 pp.
- Werner, H. W. and G. E. Woolfenden. 1983. The Cape Sable Sparrow: its habitat, habits, and history. In *The Seaside Sparrow, its biology and management*, p. 55-75. N. C. Biol. Surv. and N. C. State Mus.
- Wiens, J. A. 1973. Interterritorial habitat variation in grasshopper and savannah sparrows. *Ecology* 54(4):877-884.

Appendix

Table 2: Plant species composition of study sites. Presence marked with an X.

Plant Species	AH	DL	NM	OIHS	TS	SV
<i>Agalinis fasciculata</i>	x	x	x	x	x	x
<i>Andropogon glomeratus</i>					x	
<i>Asclepias lanceolata</i>	x	x	x	x	x	x
<i>Asclepias longifolia</i>	x	x	x	x		x
<i>Aster dumosus</i>	x	x	x	x	x	x
<i>Aster tenuifolius</i>	x	x	x	x	x	x
<i>Bacopa caroliniana</i>	x	x	x	x	x	x
<i>Centella asiatica</i>	x	x	x	x	x	x
<i>Cladium jamaicense</i>	x	x	x	x	x	x
<i>Conocarpus erectus</i>	x	x	x		x	x
<i>Crinum americanum</i>	x	x	x	x	x	x
<i>Cuscuta campestris</i>	x				x	
<i>Cyperus haspan</i>		x		x		x
<i>Dichanthelium dichotomum</i>	x	x		x	x	x
<i>Dichromena colorata</i>	x	x	x	x		x
<i>Eleocharis cellulosa</i>	x	x	x	x	x	x

<i>Eragrostis elliotti</i>		x		x	x	x
<i>Erigeron quercifolius</i>	x	x		x	x	
<i>Erigeron strigosus</i>		x	x	x		x
<i>Eupatorium leptophyllum</i>	x				x	x
<i>Eupatorium mikanioides</i>		x	x	x	x	x
<i>Helenium pinnatifidum</i>	x	x	x	x	x	x
<i>Hymenocallis palmeri</i>	x	x	x	x	x	x
<i>Hyptis alata</i>	x	x	x	x	x	x
<i>Ipomoea sagittata</i>	x	x	x	x	x	x
<i>Justica crassifolia</i>	x	x				
<i>Lobelia glandulosa</i>		x	x			
<i>Ludwigia microcarpa</i>		x		x		x
<i>Mikania scandens</i>		x		x	x	x
<i>Muhlenbergia filipes</i>	x	x	x	x	x	
<i>Oxypolis filiformis</i>	x	x	x	x	x	x
<i>Panicum tenerum</i>	x	x	x	x	x	x
<i>Panicum virgatum</i>	x	x	x	x	x	x
<i>Phyla nodiflora</i>	x	x			x	

<i>Pityopsis graminifolia</i>					x	
<i>Pluchea rosea</i>	x	x	x	x	x	x
<i>Polygala grandiflora</i>	x	x		x		x
<i>Proserpina palustris</i>	x	x	x	x	x	
<i>Rhynchospora microcarpa</i>	x	x	x	x	x	x
<i>Rhynchospora tracyi</i>	x	x	x	x	x	
<i>Sabatia stellaris</i>				x		
<i>Sagittaria graminea</i>	x			x		
<i>Sagittaria lancifolia</i>			x	x	x	
<i>Schizachyrium rhizomatum</i>	x	x	x	x	x	x
<i>Schoenus nigricans</i>	x	x	x	x	x	x
<i>Setaria geniculata</i>	x	x		x		x
<i>Sisyrinchium atlanticum</i>	x					
<i>Solidago stricta</i>	x	x	x	x	x	x
<i>Teucrium canadense</i>		x	x		x	
<i>Vernonia blodgettii</i>	x					
Unknown A					x	
unknown forb		x	x	x	x	x
"gray hairs"	x	x	x	x		
"Schoenus"	x	x		x		x
Q1#8				x		

Q6#3 forb	x					
Q5#2 forb	x					
Q4#16 forb	x					
3/28 forb	x	x		x		
"prominent nodes"		x		x		x
"toothed forb"				x		
"like Bacopa"				x		x
unknown grass				x		x
unknown grass 1					x	
unknown grass 2					x	
"Juncus"			x	x		x
"cotton pod"						x
unknown sedge				x		
Q5#5 forb			x			
Q1#16 forb						x
Q3#14 forb			x			
Total species	44	46	38	50	42	42

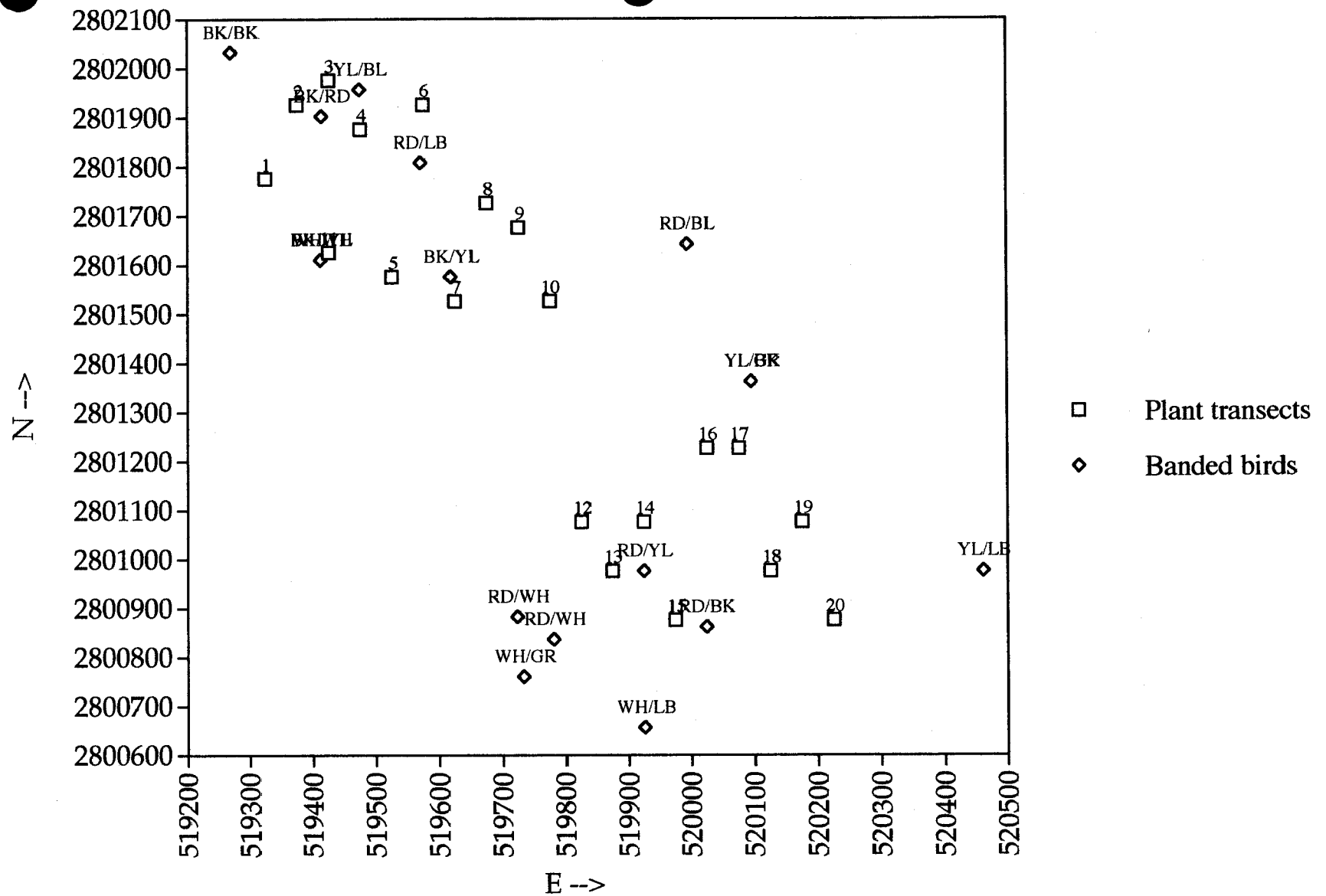


Figure 1. Alligator Hammock site map

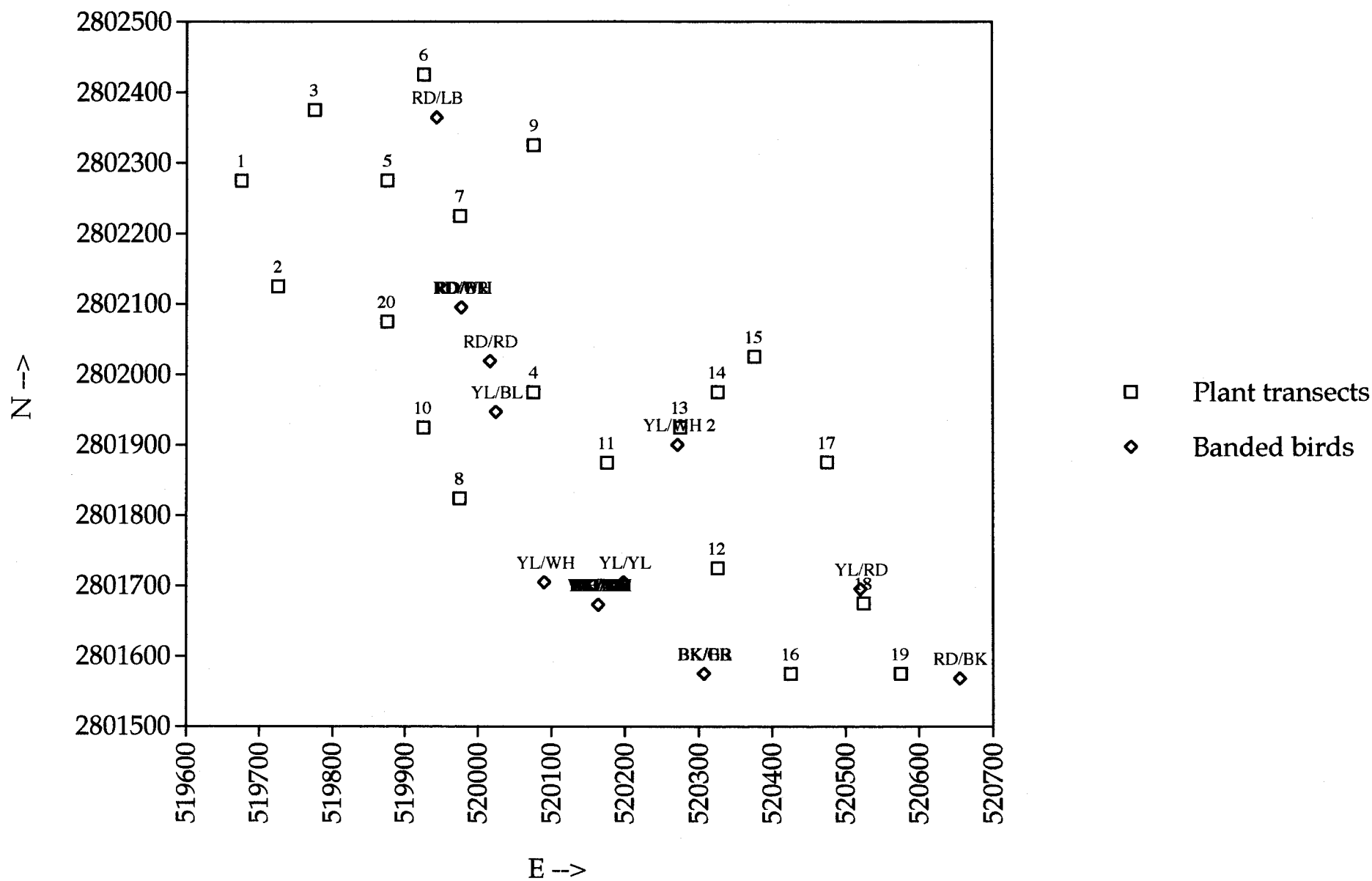


Figure 2. Dogleg site map

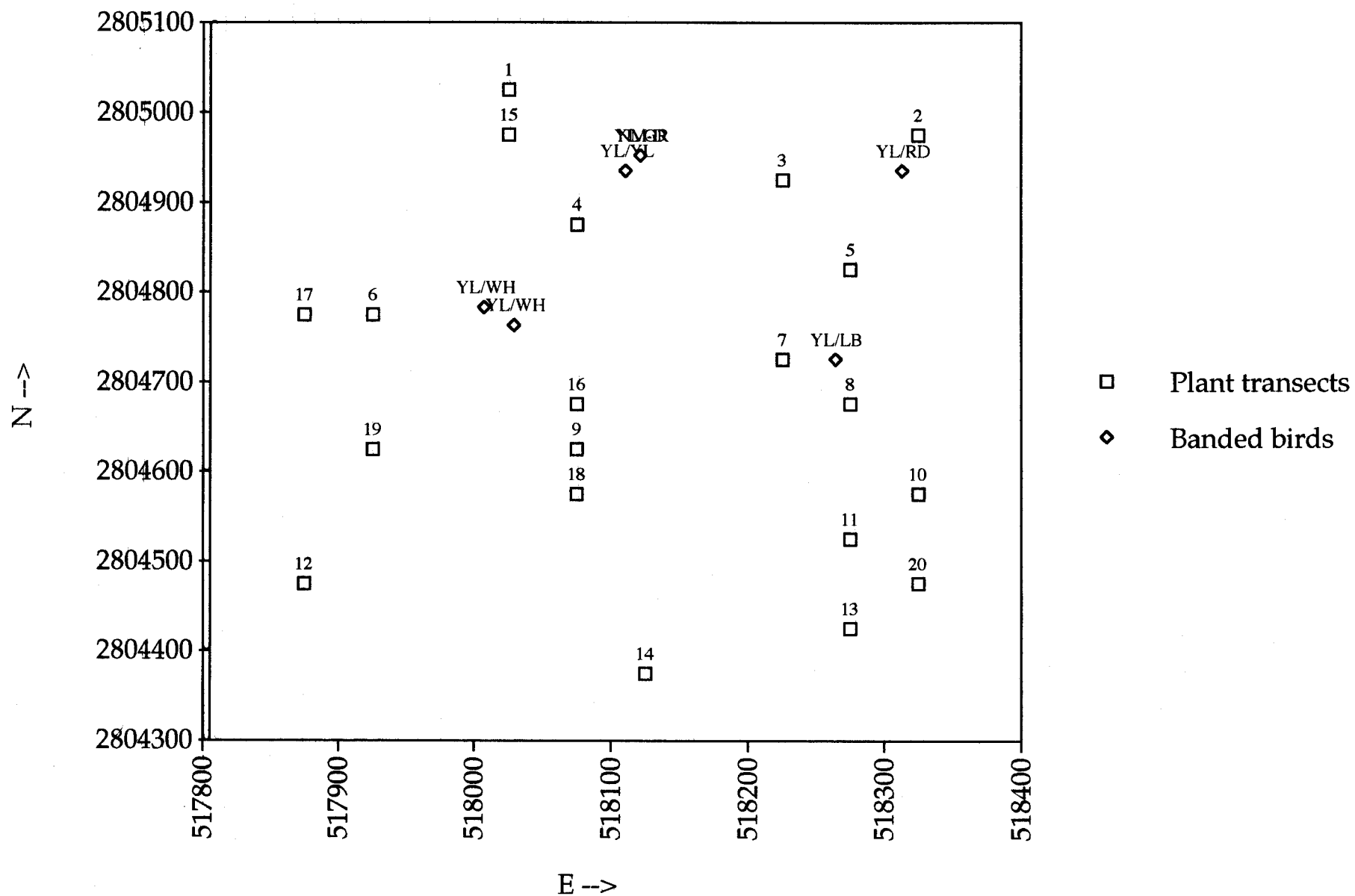


Figure 3. North Mahogany site map

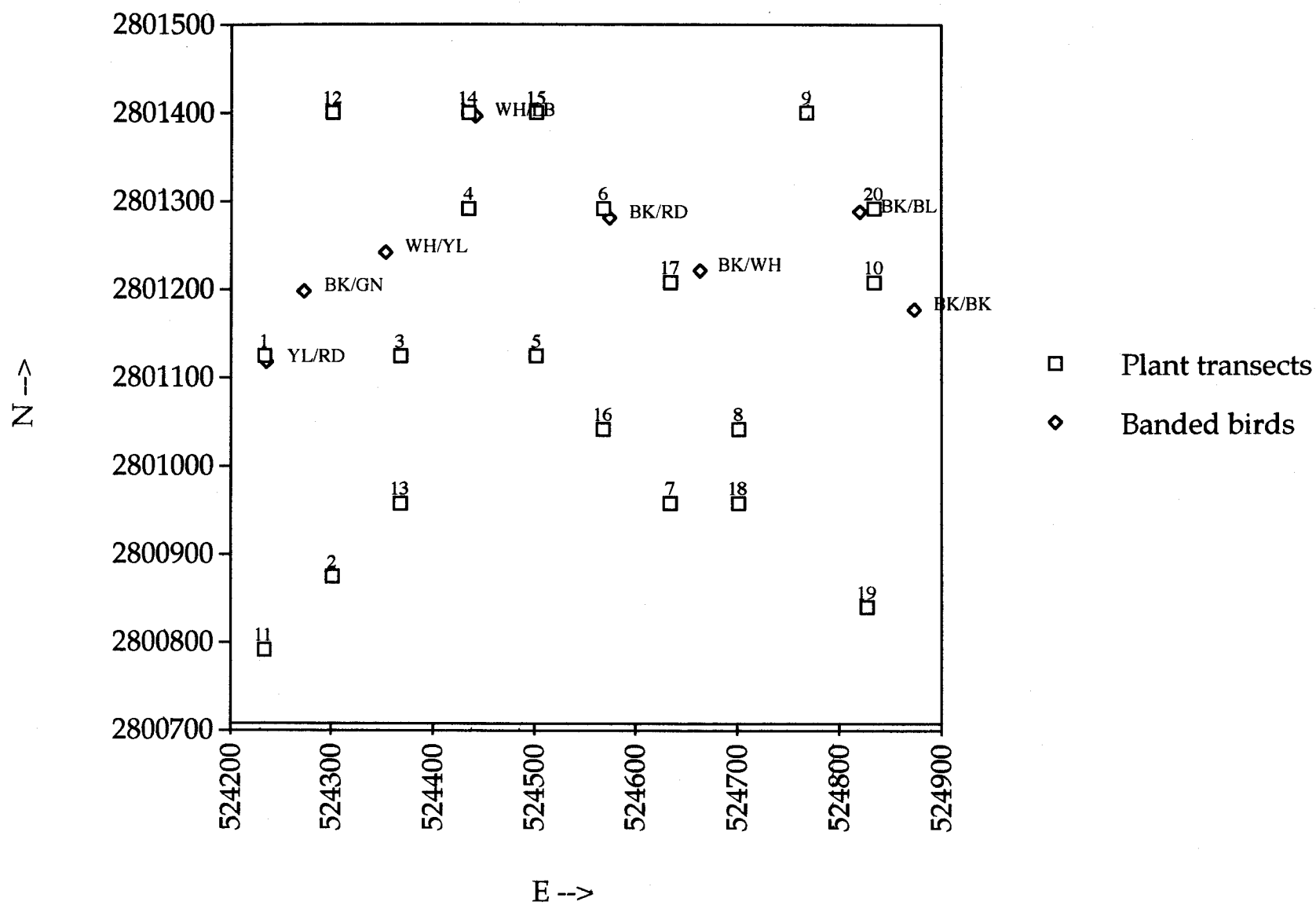


Figure 4. Old Ingraham Highway South site map

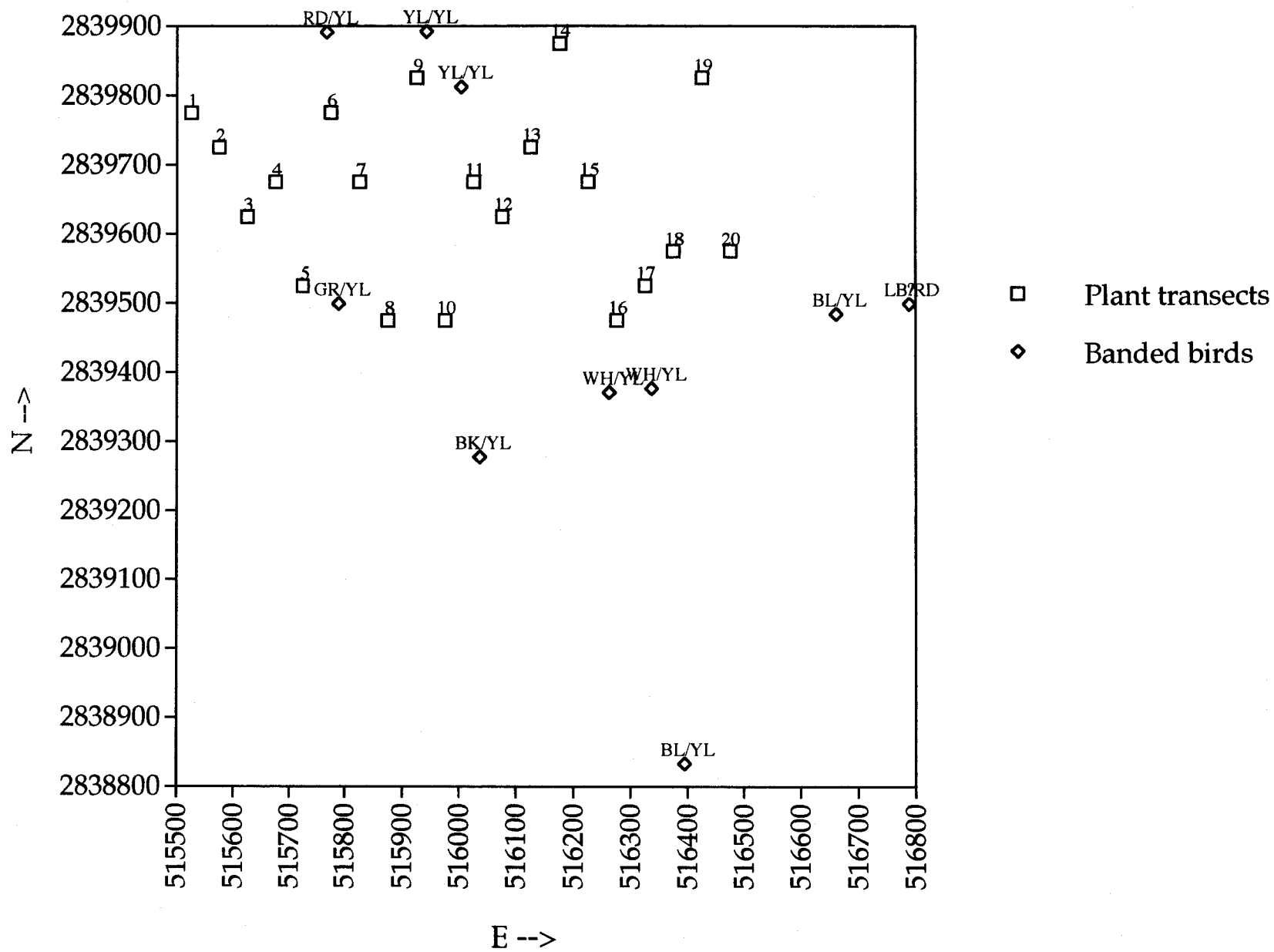


Figure 5. Shark Valley site map

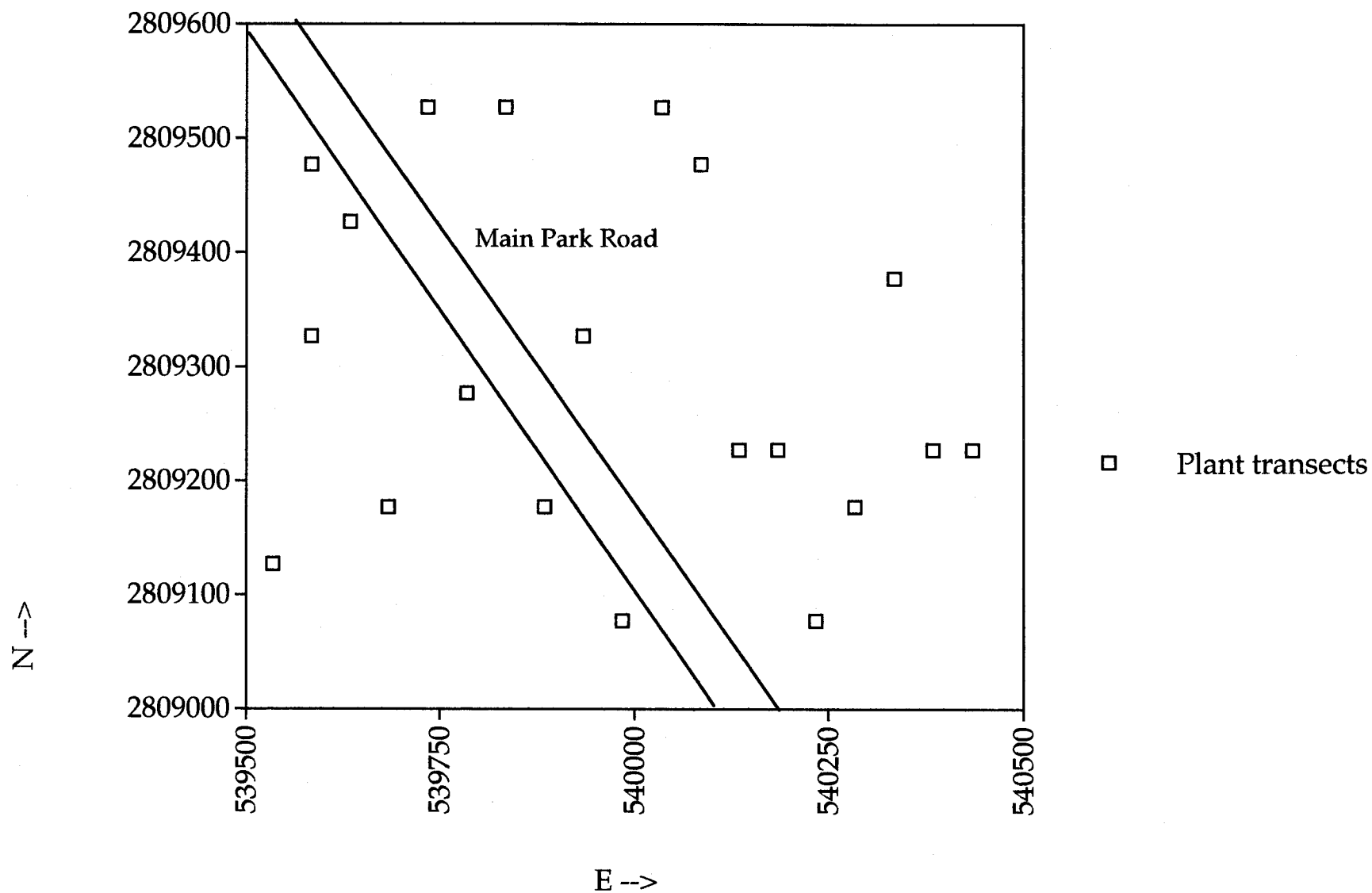


Figure 6. Taylor Slough Site map

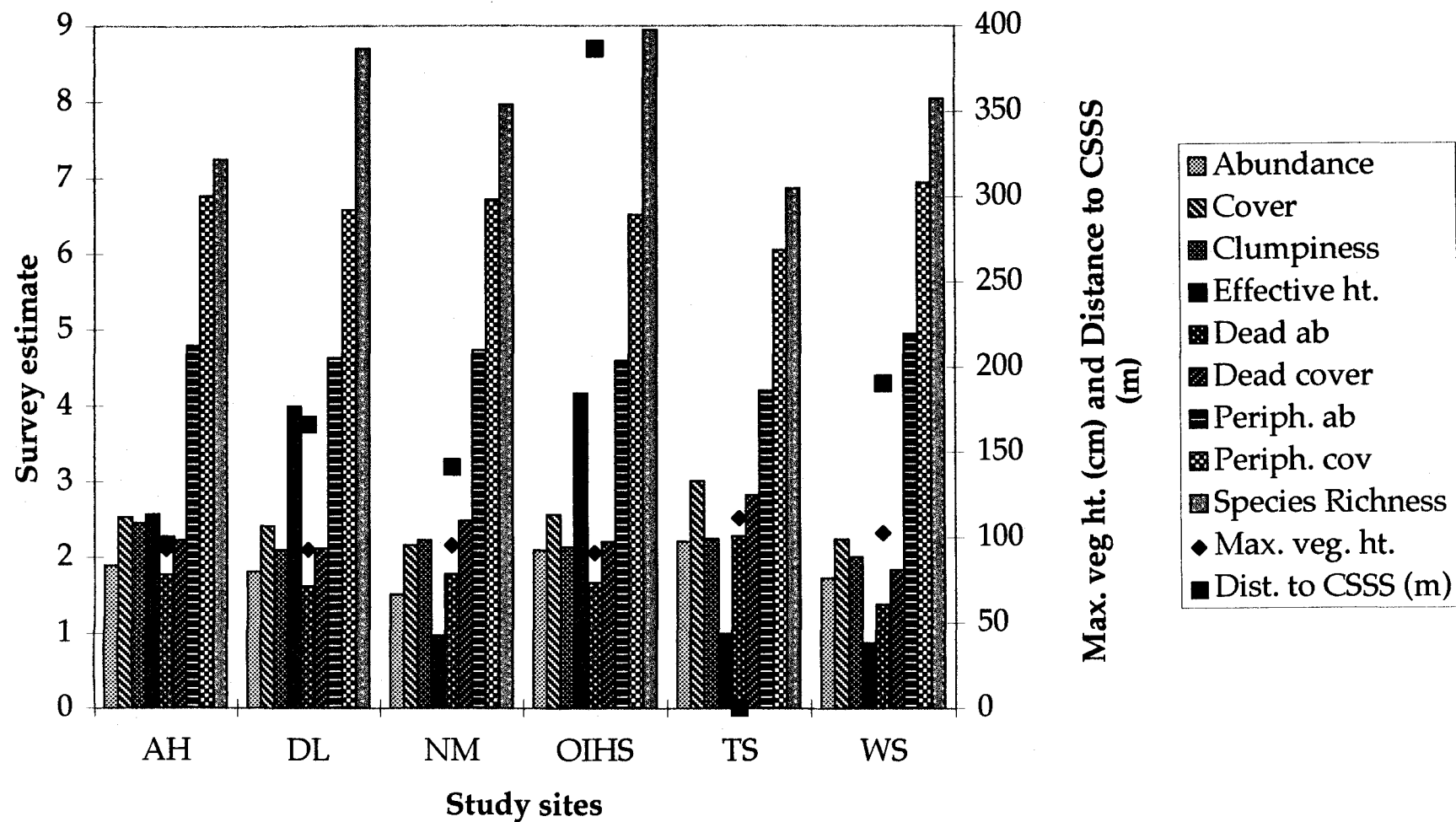


Figure 7. Average survey characteristics for all study sites

An assessment of the risk of extinction for the Cape Sable Seaside-Sparrow

Stuart L. Pimm

Introduction

The Cape Sable Seaside-Sparrow has declined dramatically since 1992 on the west side of Shark River Slough. It has declined similarly since 1981 in the north and east of its range. Only a population in the south and east has remained more or less constant. In previous papers and reports, these populations are labeled A, C, E and F, and B respectively. The key results of our research are these:

- o We attribute the decline in A to the inundation of the breeding habitat during the dry season by managed flows over the S12 structures.
- o We attribute the decline in C, E, and F combined to the very high fire frequencies these areas. 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 high fire frequencies are made possible by the unnaturally low levels of water during the breeding season. Water that would have naturally flowed through north-east Shark River Slough is diverted to the west and prevented from flowing to the east by a barrier: the L67-extension.

The key question is:

- o Can this endangered sparrow survive if restricted to population B?

I performed separate risk analyses for each of the three areas.

1. The population west of Shark River Slough (A) will decline further and eventually to extinction if the pattern of managed flows over the S12s for the last 20 years repeats itself. **If breeding season flows over the S12s are stopped, this population will flourish (figure 1).**
2. The declines of the populations in the north-east have declined to near extinction (figure 2). **These declines will continue unless the fire regimes are changed.**
3. **On its own, the population in the south-east (B) will slowly decline to extinction because of episodic large-scale fires (figure 3).**

These model predictions arise from our knowledge of the bird's breeding biology and of the water and fire-regimes in the park. They are not "curve fitting exercise" to the census data that we have collected. Importantly, results

1 and 2 predict the timing and magnitude of the changes in the existing data. This confirms that the models are both sensible and complete.

Result 3 — the decline to extinction of population B is a prediction of future events and thus one not confirmed by our short term data. Yet the consequence of this prediction is extremely important:

- o Without changes in current fire and water management practices, the Cape Sable Seaside-Sparrow will become extinct.

Notice a more subtle problem: if the currently least affected population (B) 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 1989 Ingraham fire — that are likely to be outside its previous experience. The second is that the sparrow has become locally extinct on occasion and then be recolonized from other populations.

Although, lack of data prevent my modelling it, this second possibility makes good sense. Years of naturally high water west of Shark River Slough would harm the population there, but in flooding the north eastern populations may suppress natural fires there and so their spread to the south eastern 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. A complete exploration of these possibilities will require a combined water and fire model. Nonetheless, I offer the following tentative conclusion:

- o The Cape Sable Seaside-Sparrow will only survive if it has at least three healthy populations. In a period of a few years, natural disasters may bring each one of these to low levels, their recovery made possible by immigration from less affected populations.

To implement this requirement:

1. The breeding areas west of Shark River Slough must not be flooded in the breeding season.
2. Water levels should be raised in the north-east of Shark River Slough to reduce the incidence of fires there.

Technical details

From the work of Lockwood et al. (1997) we know that Cape Sable Seaside Sparrows lay an average of 3.2 eggs per clutch. Only about 90% of these hatch. However, to be conservative, I assume that all do. (Some of the failures to hatch involve nest losses to predators and when this happens I assume that the birds will quickly re-lay a clutch.) Some 62% of the first clutch hatchlings survive to fledge, and 49% of second clutch hatchlings survive. To be conservative, I round these numbers up to 65% and 50%. Our (as-yet unpublished) survivorship data suggest that 50% of the birds survive from year to year. Using this figure is also very conservative, for it is based mostly on territory holding males — the easiest birds for us to catch and band. It is likely that first year birds do not survive as well as these adult males.

Under the best of circumstances, these parameters allow the population to increase by a factor of 1.8 from one year to the next. Unfortunately, a variety of factors prevent all the birds in a population from producing two or even one brood each year. It is the magnitude of these risk factors that determine each population's fate. They differ among populations.

For simplicity, I assume that each population starts at 2000 birds and has a population ceiling, set by available habitat, of 3500 birds.

The population west of Shark River Slough.

From Nott et al. (in press), we know that 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, Curnutt et al., in press). Nott et al. calculate the extent of available breeding habitat for each of 20 years, classifying the areas into those that remain dry enough for just one brood to be raised, and those that could produce two. It is a simple matter to calculate how many sparrows would be produced each year from the breeding and survival parameters scaled by the available habitat.

The results (figure 1) show that the population would decline to extinction if the last 20 years of water levels were repeated. Extensive water releases over the S12s occurred in 1983, 1984, 1986, 1987, 1993, and 1995. What if water were not released? For simplicity, I assume that 100% of the breeding habitat would be available for one brood in each of these years without the S12 flows. I then recalculate the sparrow's numbers. The population dips below its population ceiling periodically, but persists indefinitely (figure 1).

The model's predictions fit extraordinarily well with the known census data for 1981, and 1992 to the present. The years 1981 and 1992 were peak years, and the model predicts this. The population declined rapidly from 1993 to the

present because of high water levels. Following the good year of 1992, there should have been many sparrows in 1993. With high water levels, the birds do not sing and we do not count them. By 1996, water levels had dropped, and we should have accurately counted the surviving birds. The model's prediction closely match the actual counts. This provides an important check on the survival parameter of 0.5. Were this parameter much higher (say 0.6 or higher) then the population in 1996 would have been much higher than actually counted. Were the parameter much lower, the population would already be extinct.

The populations in north-east Shark River Slough

Here, frequent fires burn the prairies, in some areas, annually. We do not find birds in areas that are burned as often as once every two years (Curnutt et al. in press). To be conservative, I assume that a burned area prevents breeding in only the next breeding season and that no adults are killed by fires.

I have not undertaken a formal statistically analysis of the size distribution of fires. However, from inspection, it appears that at about 10% of the area will burn each year and that one year in ten as much as 90% will be burned. I assume a random proportion of burned areas each year, chosen with equal probability. The conservative assumption is that the proportion of area burned in one year is statistically independent of the proportion in the previous years. I would suspect that there is some serial correlation — as there is in most climatic time series — leading to a series of "bad" fire years.

Figure 2 shows the results of five simulations. In all cases, the population declines to extinction. Interestingly, it does so in a few decades and at a rate consistent with our census data of this population over the last 16 years.

The population in the south-east

This area does not burn regularly; yet in 1989 most of it burned. I model this episodic burning with a statistical distribution (see figure 4) that allows severe burns in a few years — but never ones that burn more the 95% of the habitat. In most years, only a small fraction of the habitat is unavailable. To be conservative, I allow two broods in areas not burned. We have excellent breeding data for this area and many birds do not complete a second brood before rising water levels terminate breeding.

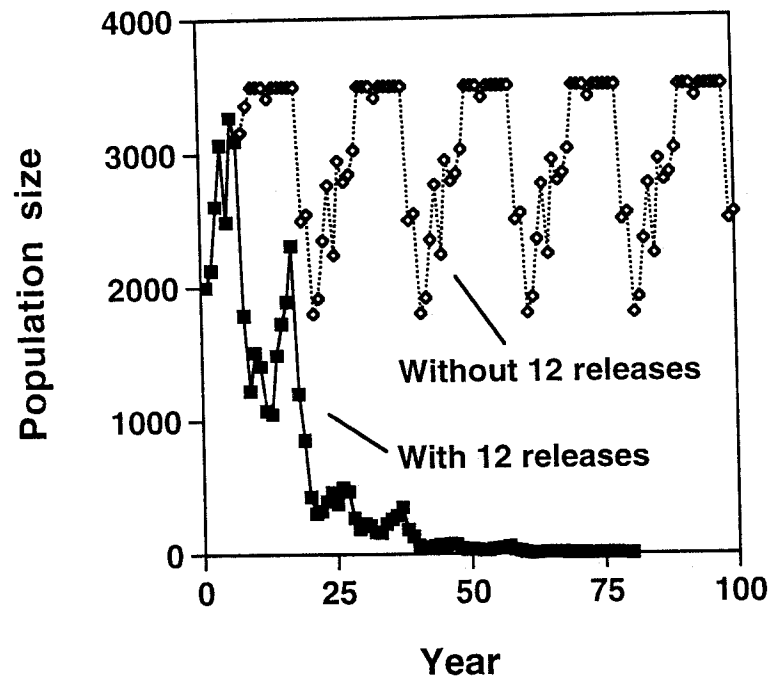
The sample of five simulations (figure 3) shows a slow, but consistent decline to extinction.

I have explored a variety of other statistical distributions of fire sizes. (The distribution I employ has a single parameter to describe the how frequent

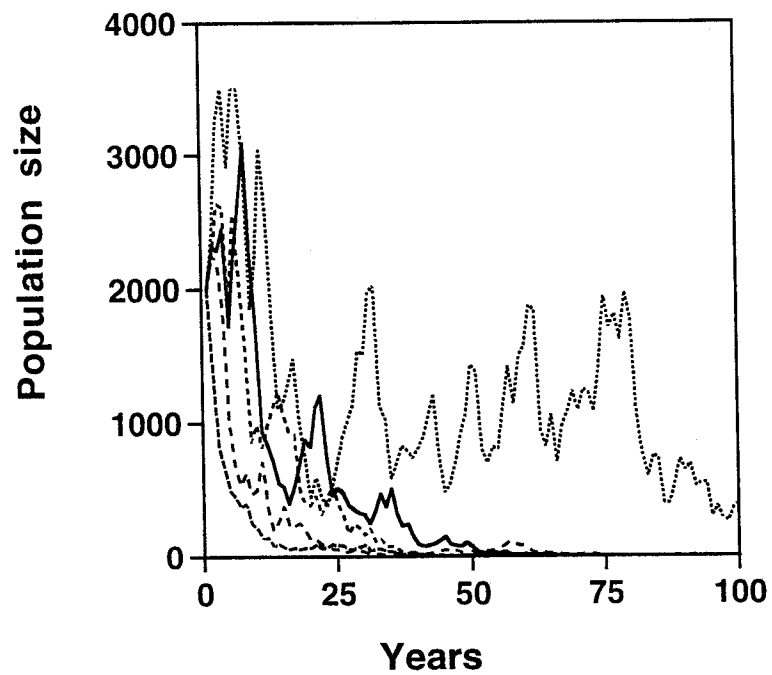
large fires will be.) The one I show in figures 3 and 4 seems plausible in terms of the Park's fire history. Moreover, it generates a year to year relatively variability in sparrow numbers (coefficient of variation) that averages 0.7. This is in excellent agreement with what one observes for other well-known grassland sparrow populations (Curnutt et al. 1996). Less frequent serious fires generate population fluctuations that are too small to be realistic.

There is a second check on this result. Worldwide, populations that total only about 2000 individuals are all in serious danger of extinction — considerable experience tells us this. Moreover, given what we know about the size of population fluctuations in healthy populations (Pimm 1991) we should expect this. Even in an absence of obvious malevolent factors, a population of this size would be expected to encounter levels of 200 birds or less within a couple of decades. This fact alone tells us that sparrow will not likely survive if it is restricted to only one small population.

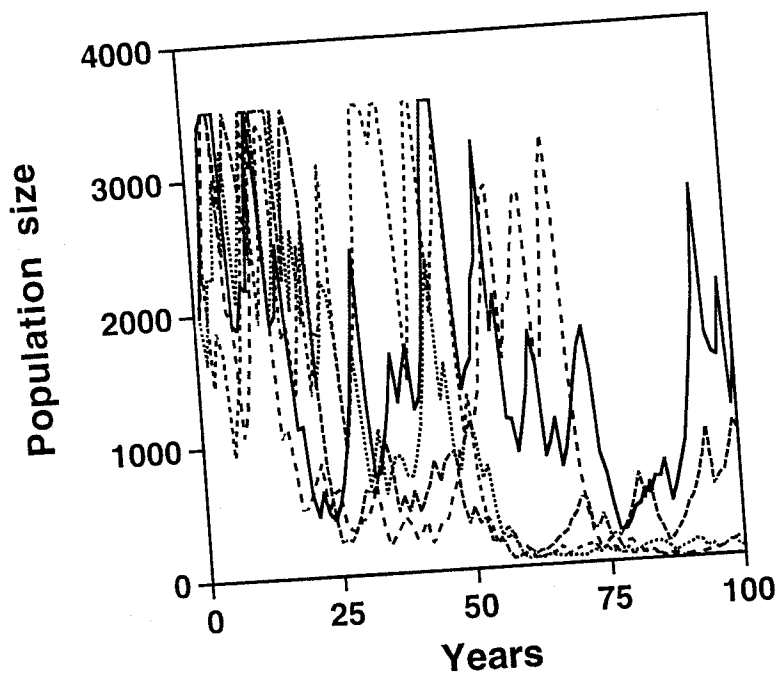
West side of Shark River Slough



North and eastern



South-eastern (main core)



Distribution of available habitat

