

Demography and breeding behavior of the Cape Sable seaside sparrow.



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Overview

The Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) is an endangered subspecies endemic to the marl prairies of the southern Everglades ecosystem. Its current range lies entirely within the federally protected lands of Everglades National Park (ENP) and Big Cypress National Preserve. Despite this level of protection, this subspecies faces threats from alterations in regional fire and flood regimes that have rendered reaches of habitat unsuitable for sparrow breeding. Understanding basic aspects of the sparrow's breeding biology, and how demographic characters vary according to fire and hydrology, are necessary for effective long-term management. This report summarizes efforts to obtain this information during the 2000 breeding season.

The contents of this report are best viewed as a continuation of field research begun in 1994. Each season we have added to our knowledge of the sparrow while responding to specific management needs as they arise. This report was written for readers familiar with these developments. For readers not familiar with continuing issues in the management of the sparrow, past work and concurrent investigations, see the following web page <web.utk.edu/~grussell/csshtml/csss.html>. Several references within the ensuing pages can be found at this web address. Specifically, I have given only cursory background information concerning routine field methodologies (e.g., finding and monitoring nests) as they have not changed since this web site was first published in 1998. Any new investigations include a complete accounting of methods and statistics used.

I extend my thanks the 2000 fieldcrew for their extraordinary efforts and tolerance (listed above). I thank the following individuals and groups for their continued support: Sonny Bass and lab, Stuart Pimm and lab, Gary Carnall and ENP fire cache, Bob Lockwood, Danny Lockwood, Eric Knight, Biscayne Helicopter, Ruth Franklin, Gordon Anderson, Stephanie Beeler, Dan Obenauer, Toby Obenauer, Troy Mullins and ENP computer support, ENP dispatch, John Deck and UCSC GIS lab, and Rochelle Lambert.

Summary

CHAPTER 1. THE ROLE OF FIRE IN SUSTAINING POPULATIONS OF CAPE SABLE SEASIDE SPARROWS WITHIN THE SOUTHERN EVERGLADES.

1. In order to test several predictions put forth by Werner (1975) and Taylor (1983) about fire, sparrow density, vegetation, and soil depth, we overlaid 17 years of ENP fire records with six years of sparrow density data from the extensive survey. In the 2000 extensive survey, observers collected soil depth information from each survey site. We use this information to divide all survey locations east of Shark River Slough into two soil depth groups. Those sites with soil depths greater than the overall median depth of 12.17cm are considered 'deep' and those sites with soil depths less than 12.17cm are considered 'shallow'.
2. When we plot sparrow numbers against time since fire, a humped distribution results. Maximum sparrow density is attained eight years post-fire and begins to drop off after 10 years post-fire. When we divide the data by soil depth it is clear that the tails of this humped distribution are produced by the spatial differences in soil depths across survey sites. Deep soil sites produce the right-hand tail and shallow soil sites produce the left-hand tail. This complicates the interpretation of such a graph for fire management purposes and indicates the spatial pattern of fire management is of equal importance to the temporal pattern.
3. Deep soil sites are more likely to support plant associations dominated by sawgrass, whereas shallow soil sites are more likely to support associations dominated by muhly grass. Vegetation cover (grouped into four ordinal categories) over deep soil sites increased faster and obtained higher mean coverages after fire than shallow soil sites. Sparrow numbers increase as vegetation cover increases, reaching maximum density at sites with 50 to 75% vegetation cover. Given this relationship, we expected that sparrow numbers would show similar responses to fire when comparing deep and shallow soil sites. Instead, we find that shallow soil sites increase in sparrow numbers after fire, but deep soil sites show no relationship between sparrow numbers and time since fire. The time lag between when a site burns and when sparrows re-occupy that site is negatively correlated to soil depth. Maximum sparrow density is reached four years sooner over deep soils (4 years post-fire) than shallow soils (8 years post-fire).

4. All of these results are consistent with what Werner and Taylor predicted. However, they do not address the reasons why sparrows will (or will not) abandon a site after many years post-fire. Thus, although we produce similar management recommendations for fire interval as Taylor (1983), spatial differences in habitat response to fire still leaves doubts surrounding its implementation. Differences in the response of muhly and sawgrass associations to fire and flood are possible avenues for further investigation.

CHAPTER 2. ESTIMATING DETECTION PROBABILITY FOR THE CAPE

SABLE SEASIDE SPARROW.

1. Based on recommendations made by the AOU review panel, we conducted point counts within our study plots following the extensive survey protocol. By comparing these counts to territory maps of the same areas, we calculated detection probabilities. Average detection probability was 0.58 and ranged from zero to 1.67. Over-estimating the number of sparrows within a 200m radius was rare, occurring in only 5% of all point counts (over 200 total counts). False negatives (i.e. counted no birds when some were resident) occurred in 4% of all counts. Detection probability did not vary according to depth of surface water (maximum recorded water depth was 17cm from soil surface). Detection probability did vary according to observer, wind speed, month, time of day and density. At high sparrow densities (more than five males per count area), observers had lower detection rates. Highest detection rates occurred among counts conducted before 9:00am and on days with very low winds (probability of detection >0.60).

CHAPTER 3. DEMOGRAPHY AND BREEDING BEHAVIOR.

1. We found 76 Cape Sable seaside sparrow nests in the 2000 breeding season. Forty-six nests were early-season nests (i.e. had hatch dates before 1 June) and 20 were late-season (i.e. had hatch dates after 1 June). Among the Main Park Road plots, 49 nests were first, 11 were second, and five were third clutches. All successive clutches were confirmed by observing the banded attending adults.

2. Breeding success, as indexed by Mayfield daily survival probability, was 0.21 for the 2000 season. This is similar to the 1999 Mayfield score of 0.15. These two scores are calculated for all nests active between April and July. In previous years, Mayfield scores were calculated using nests active from April through May, which corresponds to 1999 and 2000 early-season nests. The early-season Mayfield score for 2000 were 0.28; a value equivalent to the 1999 early-season score of 0.30 but slightly lower than previous year's scores of 0.40. Late-season nests were less successful than early-season nests (Mayfield score of 0.14). Nests found in the subpopulation E once again had the highest Mayfield score of 0.38 (early-season nests only).

3. All 2000 results confirmed information in Lockwood et al. 1999b. We were also able to collect several new pieces of demographic information. Females lay an average of 8.3 eggs per breeding season. This is surely an under-estimate as we did not find all the nest attempts made by these females. A pair of banded sparrows that successfully fledged three broods did so in 115 days, or about 38 days per clutch. We observed the first instance of natural polygyny in Cape Sable seaside sparrows, and seaside sparrows in general. Two of four banded pairs 'divorced' mid-way through the breeding season and one banded pair from 1999 re-paired for the beginning of the 2000 season. This indicates that sparrows are moderately fidelic to mates within and between breeding seasons. We found the nests of 11 individuals that were banded as nestlings in previous years. This indicates that Cape Sable seaside sparrows are capable of breeding in their first season out of the nest and that they are philopatric to their natal sites.

4. Based on observations of banded fledglings, we conclude that juveniles remain dependent on their parents up to eight days post-fledging. Fledglings become independent and join loose flocks at around 30 days post-fledging. These flocks roam areas of up to one kilometer using dense sawgrass and the edges of tree islands for perching substrate and feeding sites. Flock composition fluctuates through time, although there may be a tendency for nest-mates to associate. One or two adults are regularly observed in these flocks, however they are not the parents of any of the juveniles in the flock nor do they travel with the flock. Among the nestlings banded in Main Park Road nests, 23% were re-sighted by July.

CHAPTER 4. FATE OF SHARK VALLEY STUDY POPULATION.

1. The Shark Valley study population was absent during the 2000 breeding season. After extensive search efforts, we could not locate any of the 22 adult or eight juveniles banded in this plot since 1997. We did find two pairs well outside our study plot. We found an active nest belonging to one of these pairs on 6 July and observed nesting behavior in the other pair.
2. From analyses of nest microhabitat information, we conclude that vegetation within the Shark Valley study plot has become more sparse (i.e. less clumped and showing more non-vegetated space) through time. This contrasts vegetation changes in other study plots over the same time interval. It is possible that these vegetation changes rendered this area unsuitable for sparrow nesting. We did not observe large periphyton mats that crushed vegetation after dry-down as was seen in 1996.

THE ROLE OF FIRE IN SUSTAINING POPULATIONS OF CAPE SABLE SEASIDE
SPARROWS WITHIN THE SOUTHERN EVERGLADES.

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Introduction

Between 1948 and 1992 the wetland areas of Everglades National Park experienced 752 fires for an average of 17 fires per year (Gunderson and Snyder 1994). The plants and animals of this region are adapted to these frequent burns (Robertson 1953, Egler 1952). Fire is a necessary component of the Everglades. It maintains a habitat mosaic and prevents hardwood shrubs from invading the characteristically open Everglades marshes (Taylor 1983). The Cape Sable seaside sparrow (*Ammodramus miratimus mirabilis*), an endangered subspecies endemic to the southern Everglades, relies on a specific type of Everglades marsh (Werner 1975). The sparrow places its nest near the ground, woven into graminoid plants such as muhly grass (*Muhlenbergia fillipes*), black-top sedge (*Schoenus nigra*), and sawgrass (*Cladium jamicense*) (Lockwood et al. 1997, Werner 1975). This vegetation association is restricted to seasonally dry marshes in marl, inorganic soils (Gunderson 1994). As it has proved difficult to delineate the extent of these marl prairies, the role of fire in their maintenance is largely unknown. However, sparrow biologists believe that fire maintains suitable breeding habitat (Werner 1975, Taylor 1983, Kushlan and Bass 1983, Curnutt et al. 1998). We first review this work, making explicit the proposed mechanistic links between fire, sparrow occupancy, vegetation, and soil depth. We then test aspects of this mechanism by combining two long-term data sets, one on sparrow density and the other on the spatial extent of fire within the southern Everglades.

The History of Sparrows and Fire

The first accounts of fire effects on sparrows portrayed burning as a threat. Stimson (1956, 1968) recorded the loss isolated populations of sparrows due to the effects of recent fires. Fires move through the Everglades marshes fueled primarily by grass (Gunderson and Snyder 1994). Given that sparrows place their nests near the ground and well within the grass layer, a fire that burns during the breeding season (the driest time of the year) will almost certainly cause the destruction of most active nests. It is not as clear whether fire causes the death of adults since they are highly vagile and there are no obvious impediments to their escaping fire via flight.

H. Werner in the 1970s (Werner 1975, Werner and Woolfenden 1983) identified fire as an important component to sparrow management. Werner deduced, based mostly on incidental observations within and around his study site near the Taylor Slough bridge, that sparrows were capable of recolonizing a burned site after one year post-fire. He also observed a decline in sparrow density within sites that had burned for three and four years. This led Werner and others to conclude that fire, by preventing shrub invasion and decreasing the accumulation of dead vegetation, was a necessary component to the maintenance of sparrow populations (Werner and Woolfenden 1983, Kushlan and Bass 1983, Taylor 1983).

D. Taylor conducted a follow-up study in 1981 using Werner's study population.

Taylor recognized that the rate at which vegetation regenerates post-fire is the principle determinant of how quickly sparrows will return to a site (Taylor 1983). Taylor showed that vegetation grows quickly over deep soils and thus will return to pre-burn biomass levels two or three years faster than vegetation over shallow soils. Based on this, Taylor suggested that sparrows would respond to previously burned sites differently based on soil depth. While accepting Werner and Woolfendens (1982) conclusion that sparrow populations increase up to four years post-fire and then decline, Taylor did not attempt to test or quantify this supposition.

Together these two biologists outlined a mechanistic relationship between fire, vegetation growth, soil depth, and sparrow density. Figure 1 illustrates how this mechanism operates under normal conditions. Sites are ill-suited for sparrow occupancy immediately following a burn because they lack any vegetation cover. Some cover is required for the placement of nests and the concealment of adults and recently fledged young from predators (Werner 1975, Dean and Morrison 1998).

Sites that have deep soils will begin to re-sprout vegetation almost immediately. Sawgrass, the principle graminoid of Everglades marshes, can reach heights of 20cm to 40cm within two weeks post-fire as it's growing bud lies underneath the soil and does not burn (Kushlan 1990). The rapid re-growth of sawgrass, and supposedly other marl prairie vegetation, often produces enough cover for sparrow use by the next breeding

season (Taylor 1983, Werner 1975). The same can not be said of vegetation overlying shallow soils. Re-growth there is much slower. Thus, it takes far longer for the burned area to accumulate enough cover to attract sparrows.

The second component of the Werner–Taylor mechanism, is the rate at which habitat becomes unsuitable after fire (Figure 1). Burned sites will continue to accumulate biomass, some live and some dead. The ratio of live to dead biomass is initially weighted heavily toward live growth, but as time passes, the ratio tends in the other direction. It is the accumulation of dead vegetation that is proposed to render a site unsuitable for sparrow occupation. Dead vegetation tends to lie horizontal to the soil surface creating impenetrable mats (Werner 1975). The presence of these mats may prohibit sparrow movement on the ground, a characteristic behavior of this subspecies that allows it to enter the nest undetected, forage, and hide from predators (Werner 1975, Lockwood et al. 1997).

Although not often made explicit, the Werner–Taylor mechanism predicts that over deep soils this transition will occur much sooner than over shallow soils. Thus, sparrows may occupy a burned site sooner if the soil is deeper. However, they will soon find themselves in sub-optimal habitat. Burned sites that have shallow soils will not support sparrows for several years, however sparrows that occupy these sites will enjoy prime conditions for longer periods of time.

This mechanism allows us to make several predictions about the relationship between fire, soil depth, vegetation and sparrow density. First, the rate that vegetation increases after a fire should be faster over deep soils than over shallow soils. Second, sparrow density should increase as vegetation cover increases. If these two predictions are correct, we can make further predictions that include sparrow density. First, increases in sparrow density post-fire (i.e. the slopes of lines in Figure 1) should be distinctly different among sites with deep soils versus those with shallow soils. Second, the lag time between a fire and sparrow re-occupation should be longer among sites with shallow soils than among those with deep soils. Finally, maximum sparrow density should be attained earlier in deep soil sites than in shallow soil sites. We test each of these predictions below.

Data sets

Beginning in 1981, and then continuing from 1992 to present, ENP personnel have conducted a range-wide survey of the Cape Sable seaside sparrow. Points are laid out along a one kilometer grid that encompasses all known locations of the sparrow. These count locations are visited once every breeding season (April and May) via helicopter. Each point is referenced with a latitude/longitude coordinate generated from a Global Positioning System (GPS). At these points, once the helicopter has flown off, the observer records the number of birds seen, or heard singing. Other information is also

recorded such as water depth, plant association, and percent cover of vegetation. For a more detailed account of the methods and assumptions of these counts see Curnutt et al. (1998) and Kushlan and Bass (1983).

Through aerial surveys, ENP fire managers have mapped the spatial extent of all fires occurring within park boundaries since 1982. This coverage includes the entire range of the Cape Sable seaside sparrow. We overlay these fire maps onto the results of the point count surveys in order to test each of the above predictions. Thus, unlike most studies of the effects of fire on vertebrate populations (Whelan 1995), we have the luxury of using two long-term data sets that encompass all of the sparrow's range.

As part of an overall review of sparrow biology, Curnutt et al. (1998) combined these same two datasets to understand the effects of fire. After instituting a series of rules that excluded point count locations that were likely influenced by factors other than fire (e.g., excessive water, and shrub invasion), Curnutt et al. (1998) found two significant relationships. First, the mean number of sparrows recorded was positively related to time since fire and no evidence of a drop in density occurred up to the limit of their records (10 years post-fire). Second, sparrow numbers were highest in areas that burned once or twice within a 10 year period. Very frequent fires (one fire every one or two years) appeared to preclude sparrow occupancy.

As we use the same datasets, updated with information to 1999, we consider our results an extension of Curnutt et al. (1998) and do not re-evaluate their conclusions.

However, we do institute a slightly different set of rules that are designed to more efficiently filter non-fire effects. Some of these are related to sampling and some to the physical condition of the point count sites.

Data Processing

The first modification to the methods of Curnutt et al. (1998) is to recognize the imprecision of the point count locations. Although not accurately known, we estimate a 200m error associated with the yearly location of the actual spot in which point counts are made. This is due partially to technological changes in navigation over the last two decades, but also because of the difficulty in landing the helicopter in an exact location under various weather conditions. Furthermore, the GPS units used to locate survey points have an inherent error of between 20 and 200m. Given that the detectability radius around each observer is assumed to be another 200m (Kushlan and Bass 1983), we delineated a 400m circle around the lat/long coordinate of each point count location. It is within this circle that we are certain the birds counted actually reside.

Second, we assumed there is a similar error in recording the edges of fires. In the 1980s fire maps were created using photointerpretation. Beginning in the early 1990s, fires were mapped using GPS either by walking or flying around the perimeter of the burn (K. Thatcher pers. com.). The error surrounding the generation of these maps is also unknown. However, through limited comparisons of aerial to GPS interpretation of fire

perimeter we determined that the delineation of fire edges has a maximum error of 200m. Thus, we consider any point count location 'burned' if 50% or more of the area encompassed within 400m around that point are mapped as 'burned'.

The remaining modifications relate to the physical conditions of the survey sites. As in Curnutt et al. (1998), we exclude all point count locations in which sparrows have not been recorded during the period of record. These sites may not hold sparrows for reasons other than fire but for which we have no measure (e.g., shrub invasion). We also exclude sparrow populations west of Shark River Slough as they are known to have been influenced by extensive flooding since 1992 (Nott et al. 1998).

Curnutt et al. (1998) further exclude all point counts in which water depths of over one centimeter were recorded at survey time. We do not incorporate the same filter here. Our data shows a negative correlation between water depth and number of sparrows counted (linear regression, $P = 0.0044$, $df = 1$), however the explanatory value of water depth is very low ($R^2 = 0.006$). The maximum water depth recorded during any survey was 16cm. The majority of sites (98%) held less than 5cm of water at the time of survey. Based on detailed demographic studies we believe these water levels will not influence the presence, or detection rate, of sparrows (JLL pers. obs. and chapter two). Thus, we did not exclude any point count locations based on water depth. These filters left 139 point count locations and 1606 density estimates.

All mapped fires and survey results were converted into ArcView format.

Associated information, such as date of fire ignition, was also included. We delineated a grid of 400m radius circles that represent the point counts. Using ArcInfo, we attached the date of last fire to each count of sparrows for every year counts were made. Thus, for every sparrow count and for every year of the survey, we have an associated time since last fire. For some analyses, records are separated into year classes (e.g., one year since fire) with every 'year' starting after the completion of the range-wide survey (no later than 1 June).

In the 2000 range-wide sparrow survey, the observers recorded the soil depth at each point count location by sinking a meter stick into the soil until it hit bedrock. This was done six times at every location to account for extreme microtopographic differences in soil depth. We used the median of these six measurements as a guide to the soil depth within each 400m point count zone. Although very hot fires can burn organic peat soils, and thus lower soil depths in other Everglades marshes, the inorganic marl soils associated with sparrow habitat do not burn (Kushlan 1990). Soil accretion rates are largely unknown in the southern Everglades, but soil deposition is believed to operate at the of scale centuries (Gunderson 1994). Thus, the soil depths recorded in the 2000 sparrow point count very likely reflect predominate conditions over the entirety of our records.

Soil depth ranged from zero to 65cm, with the median at 12cm. We excluded sights with no measurable soil depths recorded (e.g., observer was standing on pinnacle rock outcropping) and two sites with extreme soil depths (i.e. over 50cm). We divided the point count locations into two groups, shallow or deep soils, based on the median soil depth calculated with these extreme points excluded (12.17cm). As the distribution of soil depths is approximately normal, it is possible to divide the soil depths into more categories thus better reflecting this distribution. However, when points were divided into four groups rather than two, those groups above and below the median plotted as parallel lines in all subsequent analyses. Thus, we continued to use only two soil depth groups.

Statistical analyses

We began by looking for relationships between soil depth and vegetation. Cape Sable seaside sparrows can exist within a range of vegetation compositions as long as these compositions provide the necessary structure needed for nest placement and feeding (Werner 1975, Lockwood et al. 1997). Individuals whom conducted point counts identified the dominate plants, and percent cover of vegetation, within approximately 10m of their location. Percentage cover is divided into four ordinal groups starting with zero to 25% cover. Percentage cover can not exceed 100%. Observers typically identified two or three of the dominate plants to the taxonomic level of species. We have

grouped these dominate plants into three associations; muhly mix, muhly+sawgrass, and sawgrass mix. The first association includes all sites where muhly grass was considered dominate, or was co-dominate with other sedges besides sawgrass. The muhly+sawgrass association includes sites where muhly and sawgrass co-dominate. The sawgrass association includes sites where sawgrass dominates, or co-dominates with sedges and grasses besides muhly. Only sites where the dominate vegetation was identified to the species level and only grasses and sedge identifications were included in these associations. We looked for a non-random occurrence of these plant associations within the two soil groups using a contingency test.

We then tested the first set predictions stated above. First, we expected that vegetation biomass (here measured as percentage cover) will increase more rapidly after fire at deep soil sites than at shallow soil sites. For each soil depth group, we performed an ordinal logistic regression of vegetation cover against days since last fire. We compared the slopes and elevation of these two lines using log-likelihood estimators with soil depth and time since fire as crossed factors (Zar 1984).

The second assumption made by Taylor and Werner is that sparrows respond positively to vegetation cover. Thus, in our next analysis we looked for differences in mean sparrows counted according to percent vegetation cover using ANOVA.

Next, we tested our second set of predictions concerning the effects time since fire on sparrow density. We expected that sparrows will respond to time since fire in the

same way as vegetation cover. Thus, for each soil depth group, we performed a simple linear regression of sparrow density against days since last fire. We compared the slopes and elevation of these two lines using ANCOVA (Zar 1984). Second, for sites that burned during the period of record (1992-1999), we computed the time to sparrow re-occupation after the last fire. We then regressed these recovery times against the soil depth at these sites. Finally, we calculated the number of years before, and after, maximum sparrow density was obtained post-fire. We compared these counts for deep and shallow soil sites using a Fisher's Exact Test. If the Werner-Taylor mechanism is correct, we expected the number of years before maximum densities are obtained to be significantly fewer in deep soil sites than in shallow sites.

Results

Figure 2 is a graph of sparrow density according to number of years since last fire. Two things are apparent from this figure. First, sparrows regularly colonize sites one year post fire. Second, the relationship between time since fire and sparrow density is humped such that sites that have not burned in 10 years or more have fewer sparrows. Maximum sparrow density is reached at eight years post fire (mean = 1.262, standard deviation = 1.610, $n = 107$). The lowest density is reached after 15 years post-fire (mean = 0.378, standard deviation = 0.143).

This relationship becomes much more complex when we add soil depth to Figure

2. Shaded circles represent shallow soil sites. Black squares represent deep soil sites.

Using this shading scheme, it is apparent that the tails of this distribution are a by-product of site specific soil profiles.

When we look for differences in dominant vegetation between soil groups, there is a significant tendency for shallow soil sites to support muhly mix plant associations and deep soil sites to support sawgrass mix associations ($\chi^2 = 51.71$, $df = 2$, $P < 0.0001$).

These two associations, however, are not exclusive to each soil group (i.e. it is still possible to observe muhly mix association within the deep soil sites). Muhly-sawgrass associations are equally divided between the two groups.

According to the work of Taylor (1983), shallow soil sites will recover to pre-burn biomass levels at a slower rate than deep soil sites and vegetation cover will positively influence sparrow density. We found vegetation cover to be positively correlated to time since fire (Wald $\chi^2 = 45.09$, $df = 1$, $P < 0.0001$). Cover increases at a faster pace in deep soils than in shallow soils (Wald $\chi^2 = 4.74$, $df = 1$, $P = 0.029$). Vegetation cover reaches higher mean values in deeper soils than in shallow soils (Wald $\chi^2 = 8.54$, $df = 1$, $P = 0.004$).

Further, mean sparrow densities between the vegetation cover categories were significantly different ($F = 5.45$, $df = 3$, $P = 0.001$). Mean sparrow density reached

maximum levels at 50 to 75% cover (1.28) and minimum levels at zero to 25% cover (0.64) and over 75% cover (0.98). Thus, the first part of the Taylor-Werner mechanism is supported by our data. Sparrows do respond to vegetation cover and cover does increase rapidly over deep soils when compared to increases over shallow soils.

We then expect that measures of how sparrow's respond to time since fire will show similar patterns. Figure 2 also illustrates how soil depth influences the rate at which sparrow density increases according to time since last fire. Among shallow soil locations, there is a positive correlation between mean sparrow density and time since last fire (Figure 2, broken line, $P = 0.007$). However, among deep soil locations there is no correlation (Figure 2, solid line, $P = 0.667$). The slopes of these lines are significantly different ($F = 5.71$, $df = 1$, $P = 0.017$), however mean sparrow density was the same between deep and shallow soil sites ($F = 0.582$, $df = 1$, $P = 0.446$).

When we looked at how soil depth influences the time lag between a burn and sparrow re-occupation, we found 23 survey locations that had experienced one or more fires between 1992 and 1999. Most sites experienced one fire, however four sites experienced two fires and were excluded from consideration. At six sites soil depths were not taken leaving a total of 12 sites for the regression. The number of lag years between when a site burned and when sparrows were again detected was significantly and positively correlated to soil depth (Figure 3) ($R^2 = 0.427$, $P = 0.0211$).

Finally, we expect that maximum sparrow densities will be obtained sooner after fire in shallow soil sites than deep soil sites. When we include only sites with shallow soils, maximum sparrow density is reached eight years post-fire (mean = 1.474, standard deviation = 1.606, $n = 38$). Minimum mean sparrow density was observed at one year post-fire (mean = 0.286, standard deviation = 0.810, $n = 28$). Among sites with deep soils, maximum sparrow density was attained four years sooner than among sites with shallow soils (mean at four years post-fire = 1.347, standard deviation = 1.466, $n = 49$). Minimum mean sparrow density was obtained after 14 years post-fire (mean = 0.333, standard deviation = 1.047, $n = 15$). This yields a ratio of number of years before maximum density to after of 7:3 for shallow soils as compared to a ratio of 1:12 for deep soils. These ratios are significantly different ($\chi^2 = 7.726$, $df = 1$, Fishers Exact $P = 0.0104$) and are weighted in the direction predicted by the Werner-Taylor mechanism.

Discussion

Our results support several predictions from the combined work of Werner (1975) and Taylor (1983). At first glance our results suggest that burning marl prairie every eight or more years should serve to maintain populations of Cape Sable seaside sparrows within eastern ENP. Further, failure to burn after ten or more years appears to drive sparrow densities to very low levels. However, we find ample evidence that there are spatial differences in how marl prairie vegetation, and consequently sparrows, respond to time

since fire. This suggests extreme caution when interpreting the above burn interval recommendations. Specifically, it suggests there are considerable spatial differences in how fire should be managed across the southern Everglades if sparrow populations are to be maintained or restored. At a minimum these spatial differences are driven by variations in soil depth and may include corresponding differences in dominant vegetation.

This spatial difference in response of sparrows to fire has immediate conservation implications. Burning shallow soil sites keeps local sparrow populations at low densities for extended periods exposing them to the vagaries of demography and the environment. If too many shallow soil sites are burned in one year, even if the timing interval is correct, the Cape Sable seaside sparrow may be driven to extinction. However, it remains unclear how spatial differences in soil depth and burn frequency influence sparrow occupancy rates. This interaction is influenced by the topography of this region (i.e., where are the shallow soil sites geographically) and the spatial configuration of occupied sites (i.e., how far is a immigrant source from a burned site).

A burn interval of eight to ten years is at least twice as long as that put forth by Werner (1975) but consistent with the recommendations of Taylor (1983). Werner's study site was situated over what we consider (and Taylor considered) deep soils (14 to 20cm). When Werner's conclusion is viewed as limited in application to only to deep soil sites, it becomes consistent with our results. Among the subset of survey locations

with deep soils, we also observed that maximum sparrow density was obtained four years post fire.

Unlike Werner, we did not observe a significant drop in density after four years post-fire. Instead we found no relationship between time since fire and sparrow density among deep soil sites. Given the consistency of all other evidence supporting the Werner-Taylor mechanism, we suggest that the lack of correlation between time since fire and sparrow density in deep soil sites is in part a by-product of the very quick sparrow re-occupation times in these sites. We were simply unable to detect low sparrow density in burned sites because our records are calculated at too coarse a time interval.

It remains unclear why these sites did not quickly become unsuitable for sparrow occupation as predicted by Figure 1. It is the lack of such a response that provides the right-hand tail of the distribution seen in Figure 2. Thus, we see a 'hump' instead of an increasing relationship between sparrow density and time since fire.

Discerning what habitat changes drive sparrows from previously suitable habitat is perhaps the most neglected portion of the Werner-Taylor mechanism, and of sparrow biology in general. Given the differences in dominant vegetation between the two soil depth groups, it is possible that sawgrass and muhly accumulate and deposit biomass in very different ways and this in turn drives sparrow occupancy patterns post-fire.

Although we have some understanding of how sawgrass recovers from fire and flood (Herndon et al. 1991), the same is not true for muhly grass. Muhly grass simply may not

grow as quickly as sawgrass and thus sites that are dominated by mulhy may not deposit as much litter annually. As this litter layer often serves as the support for nests and cover for juvenile sparrows (Lockwood et al. 1999c, Werner 1975), this difference could easily translate into a lack of suitability for sparrow occupancy.

Since the effects of fire are mediated through soil depths (and possibly vegetation dominance), it may be possible to test more specific predictions of the Werner-Taylor mechanism that have thus far been beyond reach. Instituting controlled burns within occupied habitat of an endangered species is risky. Further, existing fire patterns are homogenous within intensively studied and accessible sparrow habitat within ENP. Soil depth, however, varies considerably and on a much smaller scale than fire. This should make possible the testing of relationships such as how different rates of accumulation of dead vegetation effects sparrow occupancy. Further, our results are restricted to the drier portions of the sparrow's range. Changes in Everglades hydrology have already driven subpopulations of the Cape Sable seaside sparrow to near extinction (Nott et al. 1998). Understanding how hydrology enters into Figure 1 remains of prime importance.

CHAPTER 2.

ESTIMATING DETECTION PROBABILITY FOR THE CAPE SABLE SEASIDE
SPARROW.Introduction

The American Ornithologist Union external peer review committee strongly recommended the estimation of sampling variances for the extensive survey results (Walters et al. 1999). This estimation requires calculation of detection probabilities. Detection probability, or the chance that a male sparrow will be recorded during standard point counts, is influenced by a variety of factors (e.g., weather, observer, and species) all of which decrease the likelihood that a true count of individuals can be taken. These biases should be explicitly incorporated into estimate protocols to avoid inaccuracies in abundance calculations (Barker and Sauer 1995).

Kushlan and Bass (1983) calculated a correction factor of 16 for the extensive survey point counts. This correction accounts for all sparrows present within a 1km² area, males and females. Thus, for every male heard singing it is assumed there are eight others within the 1km cell of that count location and each of these males have one female mate (Curnutt et al. 1998, Kushlan and Bass 1983). These corrected counts are then summed to provide a range-wide estimate of sparrow abundance.

The correction factor of 16 is based on the fraction of total area sampled (a) and detection probability (p), such that $ap = 1/16$ (Walters et al. 1999). Below, we directly calculate p , and variations in p , by conducting fixed-radius point counts within study plots and then comparing these counts to the results from territory mapping (see below for details). The mapping efforts represent the 'true' number of individuals within a 200m radius of the point count location. Once detection probability is calculated, a correction factor can be directly estimated under all conditions explored (e.g., wind speeds, density groups, and time of day).

Methods

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

We mimicked this procedure and conducted fixed-radius point counts from 14 April to 17 July 2000. Locations were 400m apart within seven 600 X 800m plots. Six plots were within subpopulation B and one plot was within subpopulation E (Figure 4).

All individuals heard singing, or sighted, were recorded for seven minutes after arrival at the point count station. We could not simulate the arrival and departure of a helicopter, however traveling by foot through a breeding area has qualitatively similar effects on resident males. [When generally disturbed (i.e. when not defending a nest), males will tend to perch atop sawgrass seedheads and sing.] We varied our start times across study plots such that all time frames between sunrise and 11:00am were covered. During each count we recorded the observer, visibility, water depth (cm) and wind speed. Wind speed was estimated using the Beaufort scale, with adjustments for use in marsh habitat. The Beaufort scale used ranged from zero to four with each increase in scale indicating an increase in wind speed (Table 1).

Table 1. Beaufort scale of wind speed modified for use in marl prairies, Everglades National Park.

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

We began mapping the territories of banded, and unbanded, males on 25 March and continued to update these maps until 17 July 2000. A crew of two or more visited each plot a minimum of one day per week for at least three hours. Observers located

sparrows using spotting scopes or binoculars and the location of their territories were marked using colored survey tape. Some territories were marked after a member of the resident pair was captured in a mist net. Territory location was recorded using a Global Positioning System (GPS) and subsequently recorded on an ArcView map. Point count locations were also recorded using GPS and these locations were overlaid onto the territory maps for each plot. We then counted the number of territories within a 200m radius of each count location based on these maps.

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

Mean detection probability was calculated according to time of day, wind speed, water level, observer, month, and density levels. Start times were categorized into four nominal categories. The first category included start times between 6:00am and 7:00am, the second category included start times between 7:00am and 8:00am, and so on. A final category included all starts after 10:00am. We compared the mean detection probability

between these four start times using ANOVA. Similarly, we compared mean detection probability between observers (seven), and months (four) using AVOVA. We looked for changes in detection probability with water level and wind speeds using simple linear regression. Water depth was measured from soil surface (accuracy of ± 1 cm). All water measurements were taken at the start of each count period.

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

Results

Seven observers conducted a total of 254 point counts. The maximum number of birds detected during any one point count was eight, and the minimum was zero. The maximum number of territories mapped within a 200m radius of a point count location was nine, and the minimum was zero. Detection probability averaged 0.58 (standard error = 0.02) and ranged between zero and 1.67. On 14 occasions more birds were detected than were shown on territory maps. Over-estimates occurred throughout the season and start times with no noticeable pattern. On 11 (4%) occasions no birds were detected in areas that contained more than one mapped territory (i.e. a false negative

occurred). The vast majority (95%) of errors in detection was under-estimates. Visibility very rarely fell below 200m, twice falling to 150m and once to 60m. Thus, during 99% of the counts it was possible to easily see birds within a 200m radius of the count location. Wind speeds varied between zero and four with a modal Beaufort score of one. The earliest start time was 6:48am and the latest was 10:14am. Most counts (84%) were made between 7:00am and 9:00am.

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

Detection probability varied significantly according to observer, time of season (i.e. month), time of day, sparrow density, and wind speeds. Detection probability ranged from 0.378 ($n=8$) for one observer to 0.683 ($n= 36$) for another. Mean detection probability was significantly different between observers (ANOVA $F = 2.57$, $df = 6$, $P = 0.02$). Time of season (month) also had a statistical influence on detection probability (ANOVA $F = 5.90$, $df = 3$, $P = 0.0007$). However, there was no obvious pattern to these differences. The highest mean detection probability recorded was among June counts (0.70, $n = 65$) and the lowest mean detection probability was in July (0.47, $n = 41$). April and May probabilities were 0.51 ($n = 58$) and 0.57 ($n = 92$) respectively.

Mean detection probability declined monotonically with time of day and higher wind speeds. Counts conducted after 10:00am produced the lowest mean detection

probabilities (0.30, $n = 4$). Point counts that started at 9:00am and 8:00am had mean detection probabilities of 0.37 ($n = 30$) and 0.50 ($n = 96$) respectively. The highest mean detectability occurred during counts made between sunrise and 8:00 am (0.70, $n = 114$). These differences were statistically significant (ANOVA $F = 15.4$, $df = 3$, $P < 0.0001$). Detection probability and wind speed were negatively correlated ($F = 30.05$, $df = 2$, $P < 0.0001$). The correspondence of effects for wind speed and start time is not independent. Wind speed tends to increase later in the morning ($F = 43.80$, $df = 3$, $P = < 0.0001$).

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

Discussion

The range of detection probabilities provided here should now be incorporated into an overall estimate of error in the extensive survey. Our results can also be used to increase the accuracy of these population estimates by decreasing detection error. Detection probability can be quite high depending on conditions. An early morning, low wind, count is often better than 60% accurate. However, this probability drops by half as the

morning progresses and the wind increases. To maintain a high rate of accuracy in counts, it is our recommendation that point counts are restricted to time periods before 9:00am and under wind conditions of a Beaufort scale of two or less. Although wind speed tends to increase later in the morning, this is not always the case. We encountered mornings when wind speeds remained low past 9:00am. Thus, discretion in applying this recommendation is necessary, as it may be possible to conduct accurate counts late in the morning on some occasions.

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

We could find no discernable pattern in detection probability during the typical time frame of the extensive survey. This is true despite observing significant differences in detection probability by month. We purposefully excluded juveniles in this calculation despite our recording flocks of juveniles regularly past mid-June. We observed some of these juveniles 'practicing' their song and thus they may be easily mistaken for breeding

males by inexperienced observers. By late June all observers were very familiar with sparrows as they had been finding and following nests since March. They could easily distinguish juveniles by site and sound. This may not be the case for personnel conducting the extensive surveys, if they are not familiar with sparrow behavior. Thus, it is our further recommendation that point counts are not conducted past the first weeks of June as observers may inadvertently include young of the year in their counts.

Because sparrows were absent in the western study population (i.e. the Shark Valley plot) during the 2000 field season (see Chapter four), we can not judge differences across the spatial extent of the sparrow's range. However, there was a discernable difference in detection probability between low- and high-density locations. The low-density locations included here are comparable to densities observed in the Shark Valley plot pre-2000. This study plot is imbedded in what is now one of the most sparsely populated areas of the sparrow's range. In these low-density areas detection probability was high (0.61) indicating that, if sparrows are present, they are likely to be counted. However, there also appears to be a saturation level beyond which observers have a difficult time distinguishing all resident males. Detection probability dropped to 0.49 in locations that held five or more territories. This leads to the slightly counterintuitive result that the extensive survey is likely to under-estimate the number of males within densely populated areas as compared to sparsely populated areas.

CHAPTER 3.

DEMOGRAPHY AND BREEDING BEHAVIOR.

Introduction

Since 1996 we have been finding and monitoring nests of the Cape Sable seaside sparrow. From these nests we can quantify demographic characteristics, breeding behavior, foraging behavior, and document breeding activity within remote subpopulations (i.e. subpopulation A). The information that follows serves two purposes. First, we update various demographic information found in Lockwood et al. (1999b) using nests from the 2000 breeding season. Second, we add basic knowledge to the breeding behavior of this subspecies.

Methods*Study plots*

In 1999 we maintained nine study plots; seven located in subpopulation B, and one each in subpopulations A and E (Figure 4, Table 2). We found this prevented the collection of detailed demographic information by stretching our resources too thin. Thus in 2000, we dropped one study plot from subpopulation B (Sweetbay) and decreased the area of our plots in subpopulations A and E (Table 2). All plots were standardized to 800 X 600m and we placed a 200m grid on each plot to aid in navigation.

Table 2. Study plots by subpopulation and subgroups.

Subpopulation	Subgroup Name	Study Plot Name(s)
A	None	Shark Valley
B	Old Ingraham Highway	Ingraham North Ingraham South Far East
	Main Park Road	Dogleg North Mahogany Alligator Hammock Sweetbay
E	None	Tomato Patch

The plots within subpopulation B can be further sub-divided into two groups based on their location (Table 2). Three plots (Far East, Ingraham North and Ingraham South) are at the end of Old Ingraham Highway, an unmaintained road that runs just south of the Daniel Beard Research Center and the 'hole-in-the-donut'. The remaining three plots (Dogleg, North Mahogany, and Alligator Hammock) are located along Main Park Road just to the north and south of the Mahogany Hammock turnoff. These latter study plots are far more accessible than the former. For this reason, we concentrated our efforts on these three plots after 1 June when rains make the road impassable. This decision represents an effort to collect detailed demographic information on the sparrow, such as mate fidelity, juvenile movements, age at first nesting, and within season total fecundity.

Hydrologic character of plots

From early-April and to late-July, we documented surface water levels within each plot (Figure 5). We did not visit Shark Valley and Tomato Patch as often as the subpopulation B plots, thus the number of surface water depths are fewer in these plots and end on different dates. Figure 5 is not effected by elevation differences. Thus, water depths are equivalent across all three panels.

Shark Valley and the subpopulation B plots were dry in mid-April. The Tomato Patch plot still contained some surface water, but quickly dried down by the next visit in early May. We never recorded surface water depths exceeding five centimeters during our visits to Shark Valley and Tomato Patch. Surface water depths in the subpopulation B plots often rose above 10cm. Our surface water measurements indicate that these plots were dry enough to allow breeding by April (i.e. water levels were below the average height of nests, 16cm), and these conditions continued well into June.

Daily nest survival probabilities

By checking the status of a nest every two to four days after its discovery, we can estimate daily nest survival probabilities using the Mayfield method (Mayfield 1975). We have been calculating annual Mayfield scores since 1996 and detailed descriptions of methods used can be found in Lockwood et al. 1997.

Because unbanded individuals attend many nests, we are thus unable to confirm that later nesting attempts are made by the same individuals. In 1999 we began dividing nests into 'late' and 'early' season attempts. This allows us to determine changes in demographic parameters through time without the need to identify successive clutches by known individuals. All nests found are classed as early-season if they have a hatch day on or before 1 June. All nests found with hatch dates after 1 June are classed as late-season. The 1 June cut-off is the approximate date for the onset of summer rains and thus provides a comparison in nest success between the dry- and wet-season as well.

Observations of breeding and flocking behavior

We conducted behavior sampling of banded individuals, continuously recording their movements and interactions until the individuals moved from sight. Observations were made using binoculars and spotting scopes. We recorded the band combination of the individual resighted, date, and plot where re-sighting took place. These observations were then used to track the associated nest, age (i.e. adult or young of the year juveniles), and parents (if juvenile), and age of the individual.

We continuously recorded the movements and composition of any flocks encountered. We defined a flock as two or more individuals maintaining a proximity to one another of five meters or less, and displaying synchronized behavior such as flushing in one direction. We recorded the size of the flock and distinguished between adults and

juveniles using plumage characters. We recorded the combinations of banded individuals, and the date, plot and duration of observation.

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

Based on the flocking information, we determined association indices for each individual re-sighted more than once. The association index is calculated using the following formula:

$$\text{Index} = N_{AB} / (N_A + N_B + N_{AB})$$

where N_{AB} is the number of occasions when A and B were observed together, N_A is the number of occasions when A was seen without B, and N_B is the number of occasions when B was seen without A (Martin and Bateson 1993). These coefficients vary between zero and one, with a value of one indicating complete association. Values near 0.5 indicate the two individuals were just as likely to be associated as not.

Results

Demography

We found a total of 76 nests during the 2000 breeding season. The first nest was found 13 April and the last nest 17 July. We observed sparrows exhibiting behavior typical of breeding earlier, and later, than these dates. Thus, the breeding season is likely longer than these dates indicate. Because we concentrated our efforts in the subpopulation B plots this year, we found the most nests in these plots (66). We found nine nests in the Tomato Patch plot. This number is smaller than in years past because we decreased the size of this plot by over 50%. Among the Main Park Road nests, we found 49 first, 11 second, and five third clutch nesting attempts. These figures represent confirmed re-nesting attempts made by banded sparrows.

We found 55 early-season and 21 late-season nests. With the exception of the Shark Valley nest (see chapter four), all of the late-season nests were located in the plots along Main Park Road. When we consider only these plots, we found 46 early-season and 20 late-season nests.

The 2000 Mayfield success score was 0.21 indicating that nests had a 21% daily survival probability (Figure 6). The 2000 early-season Mayfield score was 0.28, an almost identical score to that obtained for early-season nests in 1999 (0.30). These scores, however, are somewhat lower than those obtained in all years previous (~ 0.40,

see Lockwood et al. 1999a). The 2000 late-season Mayfield score was 0.14 (Figure 7). This score is based predominately on nests found in the plots along Main Park Road. If we calculate early- and late-season scores for only Main Park Road plots, the Mayfield score for early-season nests becomes 0.30 and the late-season score remains 0.14. These late-season scores are double those found for late-season nests in 1999 (Lockwood et al. 1999b). Thus, nests active in the late-season of 2000 appeared to fare better than late nests of 1999.

We were unable to calculate Mayfield nest success scores for Shark Valley, however we again observed that Tomato Patch nests fared better than nests in the core plots (Figure 8). The Mayfield success score for Tomato Patch nests was 0.38 (early-nests only) whereas the score for core plot nests was 0.26 (early-season nests only). All of these results are consistent with information within Lockwood et al. (1999b).

We can update several demographic parameters given in Lockwood et al. (1999b). We found three nests that were complete but held no eggs. These nests subsequently held eggs two, five and one day thereafter. We documented a laying interval of one egg per day for one female. We found two nests for which we could calculate the length of incubation. One female incubated her clutch for 13 days after the last egg was laid and another incubated for 12 days. Of the 31 nests found with full clutches, the mean clutch size was three. We found 43 nests for which we could calculate the nestling period. The mean nestling period for these nests was 9.1. We documented

three confirmed cases of nestling reduction out of these 43 nests. In each case, one nestling died or disappeared while its nest mates all survived to fledging.

Because we concentrated on the Main Park Road plots this season, we can add new demographic information not provided by Lockwood et al. (1999b). We followed three banded females through three nesting attempts. Over the span of all nesting attempts, these females laid 10, eight, and seven eggs respectively. Thus, on average females lay 8.3 eggs per breeding season. This represents a minimum value, as it is possible one or more of these females made a fourth nesting attempt after we ceased daily search efforts on 26 July or that failed before we found it.

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

In 1997 we began banding nestlings while in their fifth to seventh day in the nest. Subsequently, we have re-sighted several of these individuals in later breeding season. In Lockwood et al. (1999b) we document juvenile dispersal patterns. This year we documented the nesting attempts of 10 individuals banded as nestlings one or two years prior. Of these 10, four nested in the first breeding season after they fledged. The remainder were re-sighted or re-captured in their first breeding season indicating that they may have bred; however we were unable to find their nests. Of the seven individuals that were banded as nestlings in 1998 or 1997, all of them nested in their second breeding season. All 10 banded individuals nested within 1km of the nest from which they fledged.

Breeding behavior

We documented a confirmed case of polygyny in Cape Sable seaside sparrows during the 2000 season. A male banded (Green/Light Green – Green/Aluminum) was confirmed feeding two nestlings no more than two days old on 27 April. The female attending this nest was unbanded. The young from this nest fledged on 7 May. A second nest attended by this same male (male was observed feeding the nestlings) was found 15 May with two nestlings at least five days old. The female attending this nest was also unbanded but was very likely not the same female from the first nest as the nests were ~200m apart. The young from this second clutch fledged on 18 May. Thus, the young from the first nest

fledged approximately two days before the young from the second nest hatched. By back-dating from the date of fledging, we estimate that this second clutch was complete by 28 April. Although this male was not feeding nestlings in two nests at the same time, he paired with a different female and they had a complete second clutch 10 days before the young of the first clutch fledged. Each nest was within the male's territory. However, his territory was approximately 400m diameter; about twice that of other male sparrows.

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

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

Fledglings

We resighted 11 banded fledglings within five different plots, two along Old Ingraham Highway and three along Main Park Road. Nine of these were re-sighted within Main Park Road plots. Thirty-nine nestlings were banded during the 2000 season within the Main Park Road plots, giving a re-sight rate of 23% through the end of July.

Five banded fledglings were observed on multiple occasions, giving a total of 52 re-sighting events. Two banded fledglings were observed on 11 separate occasions, three banded individuals were observed on 6 to 8 occasions, and the remaining individuals were observed only once or twice. The average age at first re-sighting was 42 days since fledging. Two sets of individuals were nest-mates.

The youngest banded fledgling was re-sighted eight days post-fledging. This individual was able to make short 1-2m flights/hops and was observed taking food from a parent on 28 March. The adult was also banded allowing the two individuals to be

unambiguously linked. The feeding took place on the ground with the fledgling concealed within vegetation litter.

The oldest banded fledgling was re-sighted 93 days since it fledged. This individual was capable of flight, perched easily on top of sawgrass seedheads and other sedges/grasses, and regularly vocalized using a short 'seet' or 'chip' note. The plumage was drab green. The white breast patch was visible, however the characteristic spotting and streaking on the breast was absent. The yellow eyestripe could be detected, however it was not as prominent as in adult plumage. This individual was $\frac{3}{4}$ the size of adults and had noticeably shorter tail-feathers. Although these, and other older fledglings, were observed in flocks with adults, they never received food from these adults. This description of plumage, size, vocalization, and interaction with adults is typical of the majority of banded fledglings re-sighted that were from 30 to 90 days old.

Because we did not record the location of these resighted banded fledglings with Global Positioning Systems (GPS), we can not provide precise calculations of movements. However, we did estimate the fledgling's position with respect to grid poles placed every 200m. We never observed a banded fledgling more than one kilometer from the nest from which it fledged, however the fledglings regularly moved several hundred meters between sightings.

Flocks

On 44 occasions we observed flocks of Cape Sable seaside sparrows. The first flock was observed on 2 June; the last on 26 July (last day of fieldwork). Our flock information was gleaned from more than 750 minutes of observations. The average observation period was 20 minutes per flock.

The average flock size was 4.8 individuals (standard deviation = 1.9). Maximum flock size was nine individuals and minimum flock size was set at two by definition. These flocks contained an average of 1.3 adults and 3.5 juveniles. On average one juvenile and one adult per flock were banded. We aged members of the flock based on plumage characteristics derived above.

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

Four banded juveniles were observed in flocks frequently enough to determine association indices. Three of these individuals were most often associated with each other. Banded juvenile 75288 was most often associated with banded juveniles 75291 (0.42) and 75292 (0.33). These latter two banded juveniles are nest-mates. The nest-

mates are most often associated with each other (0.29 and 0.38). The remaining banded juvenile, 75317, was observed in association with five other banded individuals. This fledgling was never observed with the same banded bird more than once. Thus, the association coefficient was 0.125 for each associate.

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

Discussion

Our estimates of daily nest survival probabilities are consistent with information from past years indicating that the 2000 season was normal with respect to reproduction. Further, the results from the 2000 breeding season support demographic information provided in Lockwood et al. (1999b). However, our observations add several missing pieces of demographic information. For example, Cape Sable seaside sparrows have an inter-clutch interval of 20 to 30 days and females can lay at least eight eggs per year.

Further, we now know that sparrows are capable of breeding in their first season as an adult and they appear philopatric to their natal site.

Our observations of breeding behavior also adds to our basic knowledge of this subspecies life history. We appear as the first to document natural polygyny in this subspecies, and species (Post and Greenlaw 1994). Greenlaw and Post (1985) experimentally induced polygyny among populations of seaside sparrows in north Florida and New York. These polygynous males, however, were never observed feeding the young of the secondary nest. Greenlaw and Post (1985) documented that territory quality (as indexed by available food, cover, and nesting sites) varied dramatically between males. This variation could induce a female to become the secondary mate of a male with an unusually 'good' territory if the benefits of being on this territory outweigh the loss in fitness that may result from polygyny (Gowaty 1981). Given the work conducted by Greenlaw and Post (1985) on other races of seaside sparrows, and the fact that we do not observe skewed sex ratios in our study population, we suspect that differences in territory quality very occasionally induce polygyny in the Cape Sable seaside sparrow.

Although we began observing juveniles outside of the nest by late April, observations of flocks did not occur until early June. By June, most of the banded juveniles that composed these flocks fledged 30 or more days prior. Once reaching this age, these juveniles were fully independent and capable of flight. Thus, it appears fledged young will remain largely flightless and close to the nest for several days (up to

eight by our observation). They may remain dependent on one or more of their parents for several days thereafter, even though they are becoming more mobile. By the 30th day out of the nest, these juveniles will begin associating with one another in loose groups with transient membership.

Flocks appear to be loose associations of juveniles typically with a resident adult incidentally incorporated. Flock membership is transient, with no two individuals associated more than 50% of the time. This is true despite flock size remaining relatively constant through time and fledgling movements largely restricted to a one kilometer area. Adults are not related to the juveniles in the flock and do not provide care in the form of food. Juvenile flocks will move through available habitat sticking mostly to dense sawgrass, the edges of tree islands, or open prairie. The former two habitat types are not typically used by adults and are typically much more dense in vegetation.

CHAPTER FOUR.

FATE OF SHARK VALLEY STUDY POPULATION.

Introduction

On 10 April, we began searching the Shark Valley study plot for sparrows. While placing a study grid on the 600 X 800m plot (this required the systematic coverage of the entire plot) no sparrows were seen or heard. Three crewmembers returned to the plot the following day using a tape-recording of the sparrow's song to attract birds (this is the method used to catch birds for banding). Again there were no sparrows encountered. All season we continued periodic searches on the plot using tape-recorded songs and spotting scopes. A total 33 hours were spent searching for sparrows since April 10. Most of this effort was concentrated within the plot, although we also explored areas up to 3km away from the plot boundary.

This search turned up two pairs of sparrows (four unbanded individuals) 2+ kilometers from the camp and well outside of our study plot. These pairs exhibited breeding behavior (e.g., they perched on grass stalks with insects in their bills and gave nest defense calls) during April and May visits. On 6 July we found a nest belonging to one of these pairs. It held three nestlings approximately five days old. An old nest was also found on 6 July. We suspect it to be the first nesting attempt by this same pair due to its proximity.

Based on the time spent searching for sparrows within this study plot, it is certain that the group observed in previous years has disappeared from our study plot. It is unclear if the individuals previously associated with this plot died over the non-breeding season, migrated out of the area, or if some combination of the two events occurred. We have found a total of 10 nests in this plot since 1997, and banded a total of 22 adults and eight nestlings. None of these individuals have been resighted in, or out, of this plot this season, nor did we observe any nesting activity. It remains to be seen if any of these banded individuals will return to this plot next spring.

Resampling Scheme

Beginning in 1997 we sampled the vegetation around all nests of the year. The sampling scheme calls for placing a 1m² quadrat around the nest (once it is no longer active) and estimating the percentage cover of all live vegetation using the Braun-Blanquet scale.

We measured the height of the tallest vegetation in the quadrat and the height of effective cover (i.e. ground vegetation, dead or alive, that is likely to serve as cover for sparrows).

Within each quadrat we also estimated the percentage of dead cover and open or bare ground. We gauged the degree of vegetative clumping using a four point scale where one represents vegetation that shows no clumping and four represents vegetation that grows only in clumps (see Lockwood et al. 1999c for more details on sampling methodology).

We repeated these measurements within quadrats placed 5m from each nest in the four cardinal directions.

In an attempt to document changes in the habitat concomitant with the loss of the Shark Valley population this year, we re-sampled vegetation around the 10 nests found previously. All 10 nests were marked with PVC poles at the end of the season in which they were active. This allowed us to return to each nest and repeat the sampling process. We duplicated the methods summarized above such that the re-samples were taken in the same location as the originals.

Methods

We re-sampled nests from our subpopulation B plots and subpopulation E plot for comparison to Shark Valley (subpopulation A). This comparison allowed us to surmise what changes in vegetation are 'typical' of marl prairies from those that are particular to the Shark Valley plot. These results are not reported to prove cause and effect. The loss of this study population was unplanned, so it is now extremely difficult to prove why it occurred. Further, these results are not intended to explore all possible differences in vegetation succession dynamics across marl prairies. Fire, flood, and soil depth will each effect the rate at which vegetation grows, dies, and propagates. Our plots have very different histories in regard to all three variables. The re-sampling scheme described here was not designed to account for all of these factors and thus can only highlight changes in vegetation within the Shark Valley plot that are unusual compared to vegetation in the other plots.

For each quadrat, we calculated the difference in percent cover, heights and vegetation clumping scores between the original and the later sampling periods. This produces two 'populations' of differences for each variable, one original set and one re-sample set. We can then compare the means of these sets for each variable across subpopulation plots using ANOVA. We compared changes in the clumping score using Chi-Square. Large negative mean differences indicated a decrease in cover, height or clumping through time. Large positive mean differences indicated an increase in these estimates through time. We re-sampled nests one, two and three years after they were originally sampled. We expected that the magnitude of the mean differences to increase as the time between sampling sessions increased. Thus, the number of years between samples is considered a co-factor in each ANOVA test.

Results

Our results highlighted two unusual habitat changes that occurred in the Shark Valley plot as compared to plots in other subpopulations. First, the degree of vegetative clumping in Shark Valley dropped through time whereas clumping scores in the other subpopulation either stayed nearly the same (subpopulation B) or increased (subpopulation E). Statistically the differences in clumping scores significantly varied across subpopulation ($\chi^2 = 18.8$, $df = 10$, $P = 0.04$). There were far lower clumping

scores (i.e. vegetation growing as mostly single stems) in the resampled Shark Valley nests than expected based on a comparison with resampled nests in the other plots.

Second, the percentage bare ground in Shark Valley increased significantly relative to the other subpopulations (ANOVA $F = 19.2$, $df = 2$, $P < 0.0001$). The mean difference between the original and later Braun-Blanquet estimates of bare ground was 1.9. We scored most quadrats with 10 to 25% bare ground in the original samples. During re-sampling, we scored the same quadrats as having 50 to 75% bare ground. The other subpopulations showed no notable differences in percent bare ground. There was also a significant year effect for changes in percentage bare ground (ANOVA $F = 17.17$, $df = 1$, $P < 0.001$). However, this effect was in the opposite direction than we expected; mean differences in percent bareground decreased as the time since resampling increased. Thus, one year differences were much larger than two and three year differences among Shark Valley nests (slope = -1.5, $R^2 = 0.53$). There was not a similar effect for the nests found in other subpopulations (subpopulation A slope = -0.7, $R^2 = 0.23$; subpopulation E slope = 0.02, $R^2 = 0.005$). Finally, time and subpopulation had an interaction effect on mean difference in bare ground (ANOVA $F = 6.1$, $df = 2$, $P = 0.001$).

Discussion

Although these results are very limited in scope they point to changes in two habitat factors that may have influenced the fate of this study population. Cape Sable seaside

sparrows require vegetation that is structurally clumped and has a sufficiently high stem density to support a nest (Lockwood et al. 1999c). Sparrows place their nests within, and near the base of, clusters of grasses. Nest material (mostly dead sawgrass leaves) are woven into these grasses thus providing support for the nest (Lockwood et al. 1997, 1999c, Werner 1975). The density of grasses around the nest may also provide cover for the nest, concealing it from predators. Thus, a decrease in density of grasses, or vegetation clumping, likely removes the structure necessary for nest placement and concealment.

It is not clear if high 1999-2000 wet-season water levels and rapid dry-down rates caused these changes in vegetation. The vegetation in this plot likely suffered the effects of the sustained high water events of 1993 and 1995 (for more details see Nott et al. 1998). The 1993 and 1995 high water events were characterized by the growth of large mats of periphyton that, after dry-down, crushed most live vegetation (Nott et al. 1998). The changes we observed may have been the final consequence of this event. Because we did not witness a similar growth of periphyton during the 1999-2000 wet-season, there was little evidence that periphyton mats had crushed the vegetation around nests.

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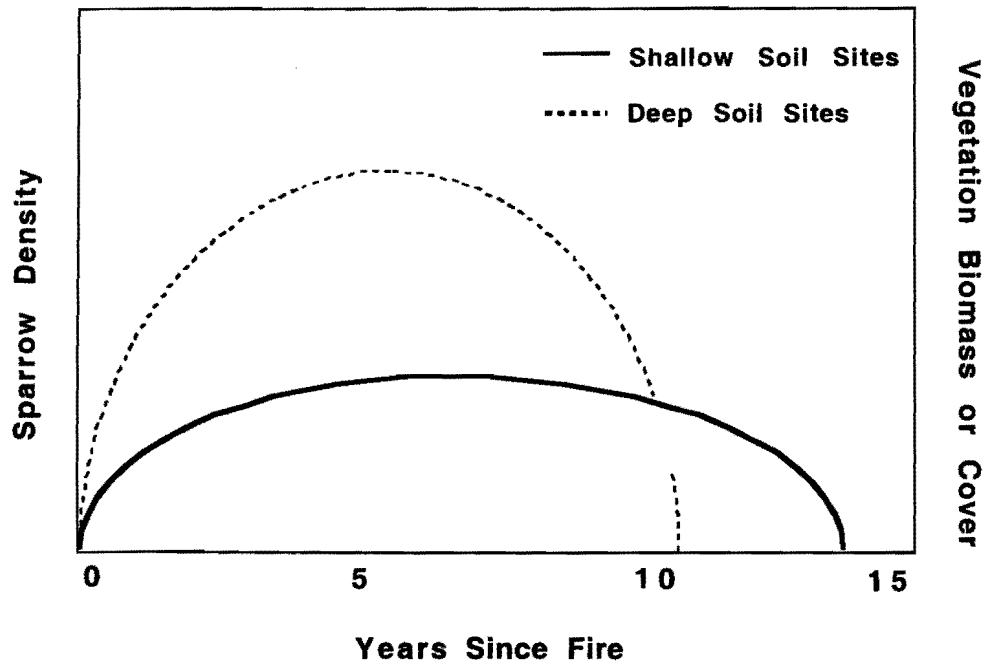


Figure 1. Relationship between soil depth, vegetation cover, sparrow density and years since fire as developed by Werner (1975) and Taylor (1983).

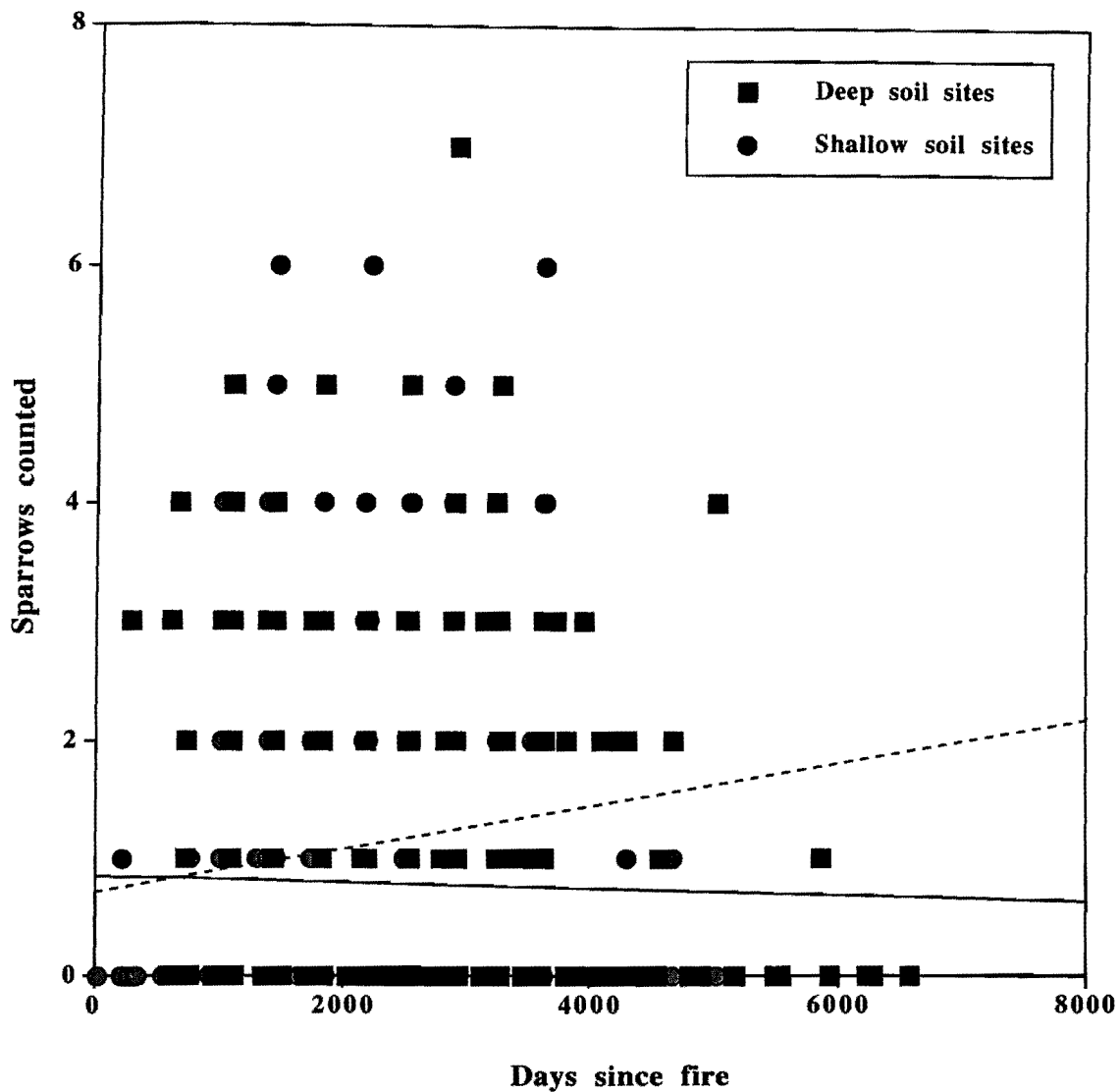


Figure 2. Number of Cape Sable seaside sparrows recorded according to days since count location last burned. Solid line is a simple linear regression using only deep soil sites. Broken line is a simple linear regression using only shallow soil sites.

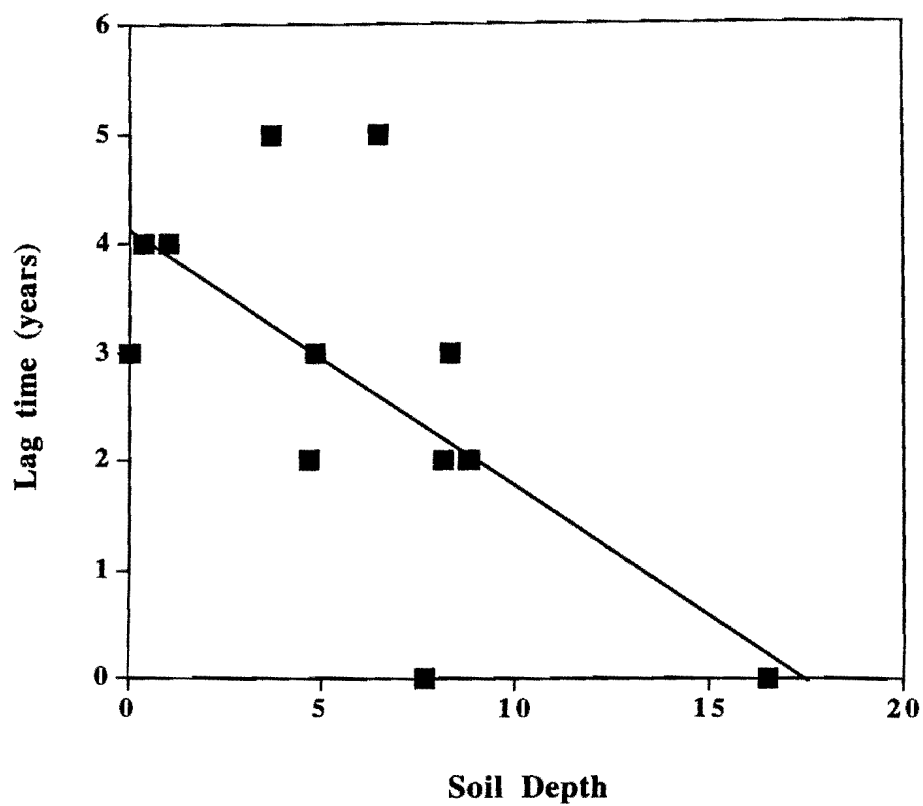


Figure 3. Number of years until sparrows re-occupy burned sites as a function of soil depth.

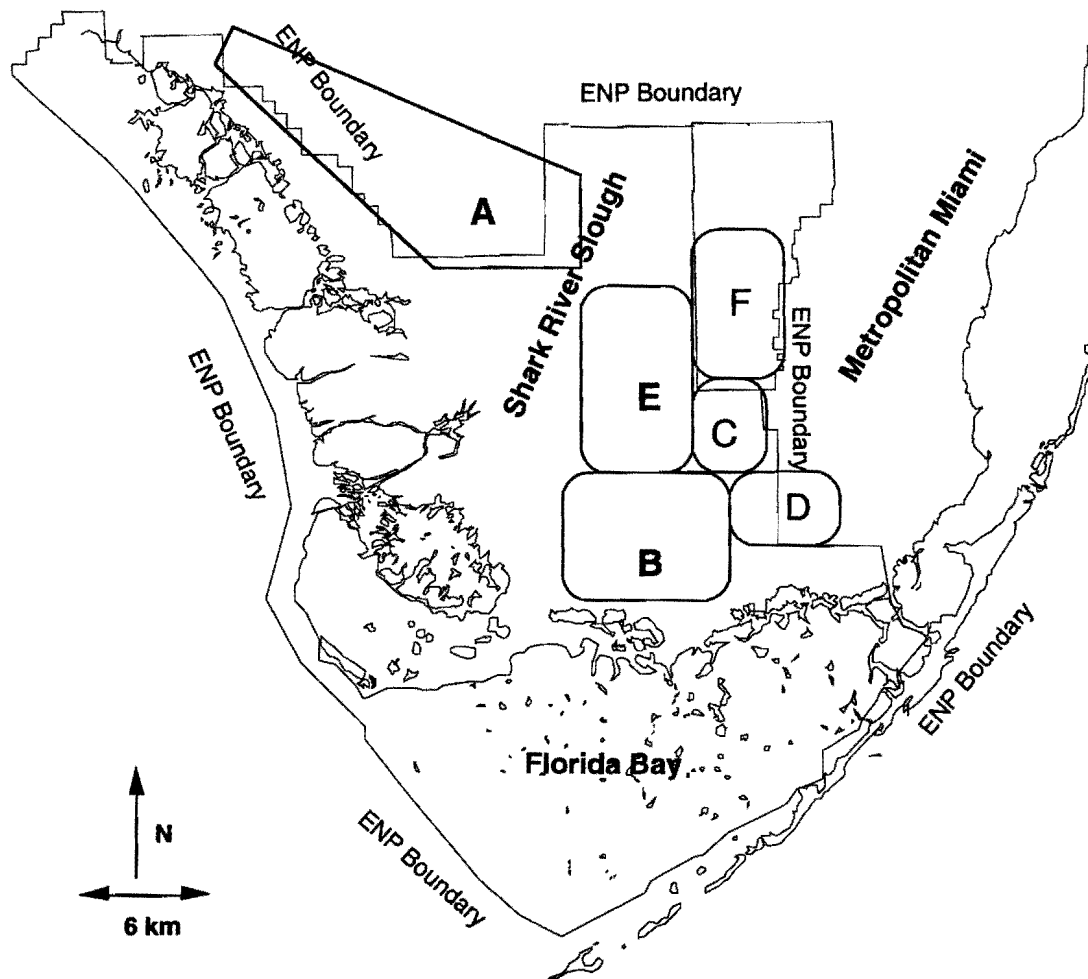


Figure 4. Everglades National Park with Cape Sable seaside sparrow subpopulations shown. Subpopulations in which we have established study plots are shown in bold type.

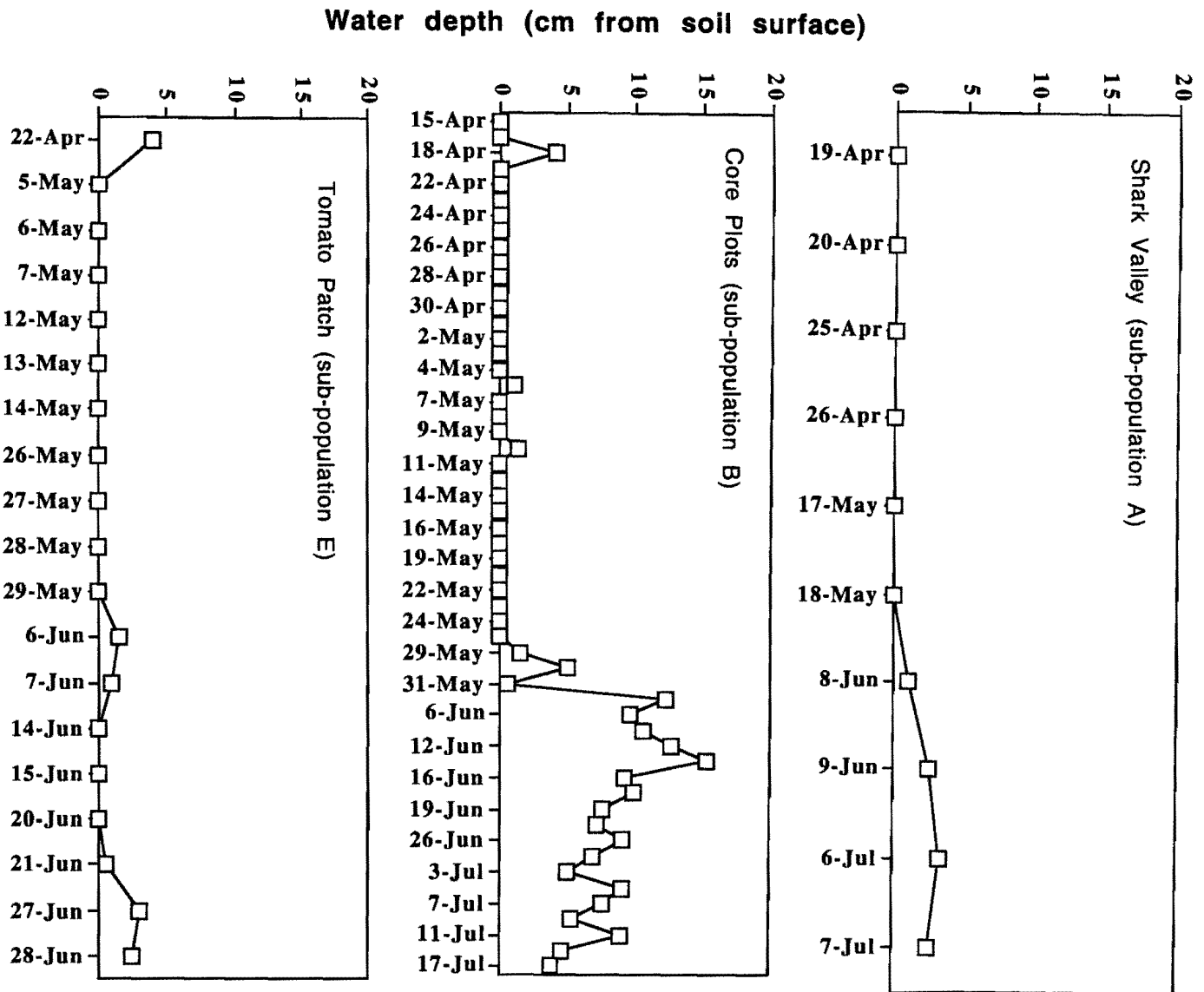


Figure 5. Surface water depths recorded at each of our study plots. Information from plots is grouped according to subpopulation. Water depths taken within the core plots (subpopulation B) were averaged to obtain a mean value per day.

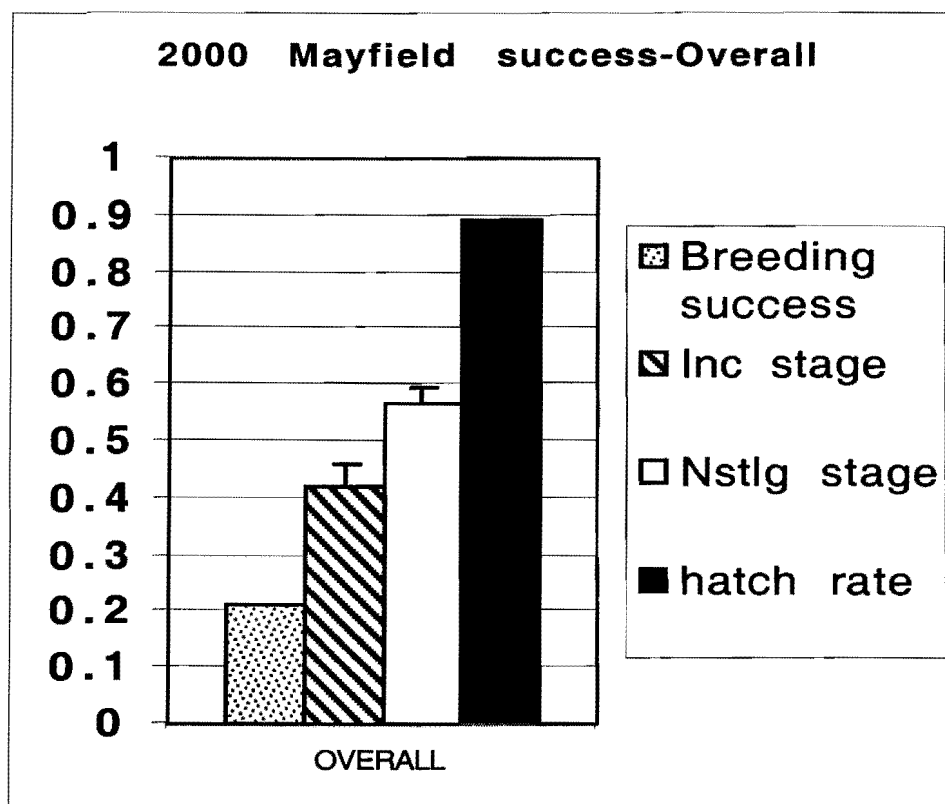


Figure 6. Mayfield success scores for the 2000 breeding season. Error bars represent 95% confidence intervals. Scores are based on information gathered from April through July.

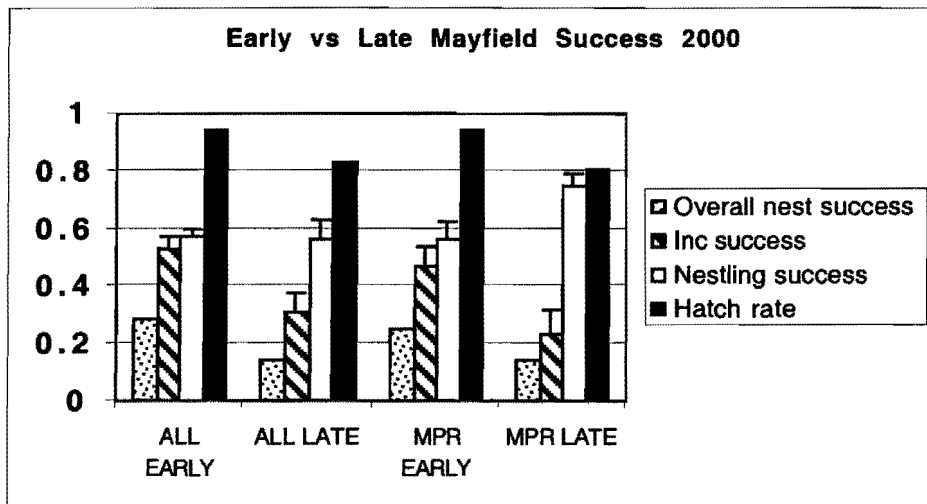


Figure 7. Mayfield success scores for early-season and late-season nests. Since the majority of late-season nest information comes from the Main Park Road (MPR) sites, we re-calculated these scores using only these nests. Error bars represent 95% confidence intervals.

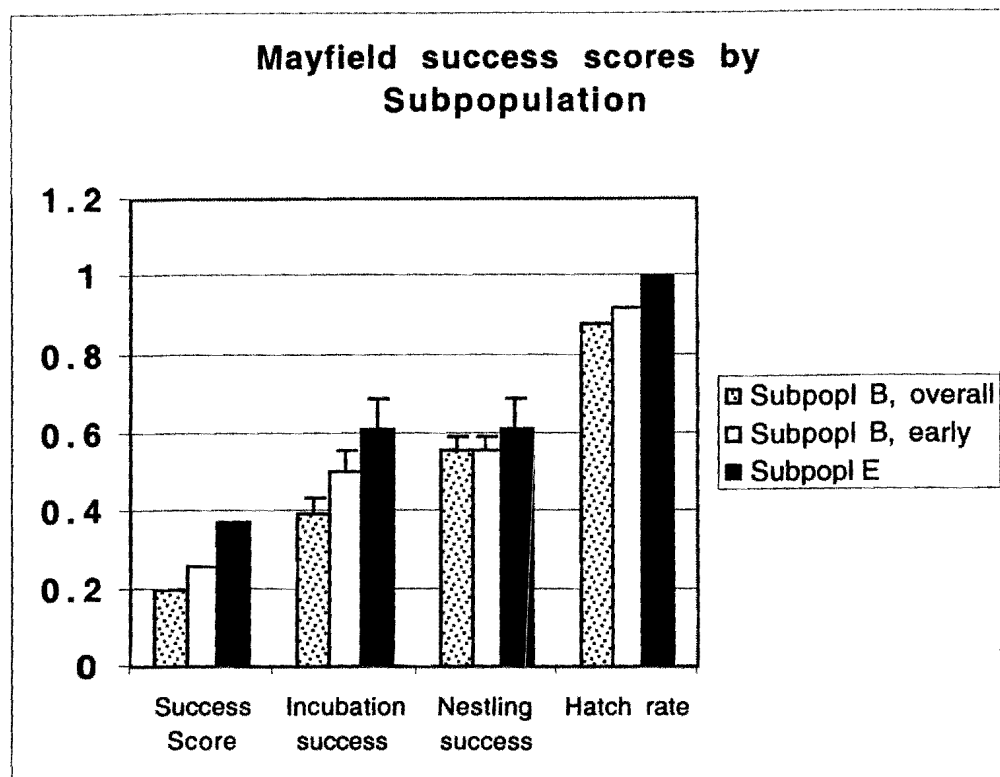


Figure 8. Mayfield success scores divided by subpopulation. Because all nests found within the subpopulation E were early-season, we re-calculated the subpopulation B scores using only early nests for comparison. Error bars represent 95% confidence intervals.

