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BIOLOGY OF THE SEASIDE SPARROW IN THE EVERGLADES REGION OF FLORIDA

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SYNOPSIS. The biology of Seaside Sparrows (*Ammodramus maritimus*) breeding in the Everglades region of Florida is reviewed. The population in this area has been described as a morphologically distinct subspecies (the Cape Sable Seaside Sparrow, *A. m. mirabilis*). It is isolated from the other races of the Seaside Sparrow, the closest of which, the Scott's Seaside Sparrow (*A. m. peninsulae*), is found in tidal marshes on the Gulf coast, 300 km north. Despite plumage differences between the Cape Sable and Scott's Seaside Sparrows, the behavior and ecology of the two forms are similar. The salient difference between the Everglades subspecies and its relatives is in habitat use: unlike other Seaside Sparrows, most of which live in salt marshes, the Cape Sable Seaside Sparrow is now completely confined to freshwater marshes.

The distributional history of the Cape Sable Seaside Sparrow is fragmentary, largely because of the difficulty of reaching the isolated areas where they live. Populations have frequently disappeared, and the same or other populations have been rediscovered in widely separated areas, often many years later. These long-range shifts in distribution, if real, appear to have been in response to the fluctuations that characterize the temporally unpredictable environment of the Everglades. Agencies such as fire and hurricanes have caused short-term shifts in population distributions, and also long-term modifications of sparrow habitat.

Since the seminal research of Harold Werner, initiated in 1970, several studies have been conducted in an attempt to determine the number of sparrows remaining, and to gather information about their demography. The population was first surveyed in 1981, at which time it was estimated that 2000-3000 male sparrows remained. These "extensive" surveys were reinitiated in 1992, but, unfortunately, the preliminary (1981) survey techniques were not modified in such a way as to make their results statistically meaningful. The results of the surveys allow conclusions to be made about population density changes in specific areas; however, because of invalid assumptions about the behavior of the sparrow, the results cannot be extrapolated to form reliable estimates of total population size, or changes in population size.

Data collected so far on a limited number of birds indicate that *mirabilis* has high reproductive success: 64% of nests produce fledglings. The subspecies also appears to have high reproductive potential: females can potentially produce nine fledglings per year. In addition, survival rates are high: on average, at least 70% of adults survive from year to year. Preliminary radiotelemetry studies indicate that juvenile sparrows may disperse long distances from their natal territories. If we accept the hypothesis that the sparrow is decreasing over its entire range, the question then arises: if its reproduction and survival are high, and if juveniles disperse widely, why is the sparrow decreasing? This question can only be answered when better survey data are available, and after more detailed demographic and dispersal information have been gathered.

Based on the survey results, the main Cape Sable Seaside Sparrow population now lives in hair grass (marl) prairie east of Shark River Slough. Although current researchers hypothesize that hair grass prairie is the "preferred" habitat of the subspecies, information about habitats that have been used in the past suggests that hair grass prairie is simply the habitat into which the sparrow has most recently been forced. Management decisions to enhance the recovery of the Cape Sable Seaside Sparrow are based on the results of the extensive surveys, and on the corollary assumption that hair grass is the optimum habitat for the subspecies. For the most part, recovery efforts since 1975 have focused on controlling environmental factors (water level fluctuations) that affect sparrows in this one habitat type.

The Seaside Sparrow (*Ammodramus maritimus*) occurs in relatively small, localized populations along the Atlantic and Gulf coasts of the United States, from New Hampshire to Texas (Werner and Woolfenden 1983, Post and Greenlaw 1994). Most breeding birds inhabit salt and brackish marshes associated with tidal areas, and are thus confined to a narrow coastal zone. Some have moved farther inland, to colonize freshwater marshes, as, for example, on the Hudson River in New York (Bull 1964), the St Johns River in central Florida (Nicholson 1929) and Taylor Slough of the Everglades region (Ogden 1972). Despite their use of freshwater habitats, the biology of the inland populations appears to differ little from that of birds living in tidal marshes, where the species is presumed to have evolved (Beecher 1955, Werner and Woolfenden 1983, Post and Greenlaw 1994).

The Seaside Sparrow has been studied over most of its range (reviewed by Post and Greenlaw 1994). Detailed ecological studies, many of marked populations, have been conducted or are ongoing in Massachusetts (Marshall and Reinert 1990), Rhode Island (DeRagon 1988), New York (Post and Greenlaw 1982, Post 1974, Greenlaw and Post 1985, Merriam 1983), New Jersey (Woolfenden 1956), South Carolina (Post in prep.), and Florida (Trost 1968, Sharp 1970, Werner 1975, Sykes 1980, Kushlan and Bass 1983, Kushlan et al. 1982, Werner and Woolfenden 1983, McDonald 1989, Post et al 1983, Lockwood 1997, Pimm et al. in prep.)

Largely because of the alteration of coastal wetlands by humans, the species has disappeared from some parts of its range (Kale 1983, Kushlan and Bass 1983, McDonald 1988, Greenlaw 1992). Two Florida subspecies, the Dusky Seaside Sparrow (*A. m. nigrescens*) and the Smyrna Seaside Sparrow (*A. m. pelonota*), have recently become extinct (Kale 1996). Other subspecies distributed along the Gulf of Mexico are also classified as endangered, threatened or of special concern by governmental agencies (*A. m. mirabilis*, *A. m. sennetti*, *A. m. juncicola*, *A. m. fisheri* (Kale 1996).

Seven allopatric races have been described from Florida alone (American Ornithologists' Union 1957). The distribution and habitat use of these forms are described by Kale (1983). The Cape Sable Seaside Sparrow, *mirabilis*, is the most isolated of the seven Florida populations. The distance between *mirabilis* and populations of its geographically closest relative, the Scott's Seaside Sparrow (*A. m. peninsulae*), is 300 km. *Mirabilis* is lighter in coloration than *peninsulae*; much of the black of the latter's dorsal plumage is replaced in the former by yellowish olive. There appear to be no major differences between the ecology and behavior of the two forms (Post and Greenlaw 1994). See Post et al. (1983), McDonald (1983, 1989), Greenlaw and Post (1985) for descriptions of the behavior and ecology of Scott's Seaside Sparrow.

Like the St Johns population of the Dusky Seaside Sparrow (*Ammodramus maritimus nigrescens*), the Cape Sable Seaside Sparrow occupies inland freshwater marshes. As in the case of *nigrescens*, the Cape Sable subspecies is a focus of concern because of wide-scale alterations of its habitat. Most changes have been caused by humans: introductions of exotic plants, unnatural water regimes, large-scale fires. The complex interactions of these factors make the conservation

and management of the Cape Sable Seaside Sparrow particularly difficult (Kushlan et al 1982, Post 1983, Post and Greenlaw 1994, Curnutt 1996).

The life history of the species has been reviewed recently (Post and Greenlaw 1994). The purpose of this paper is to review the biology of the southernmost subspecies, the Cape Sable Seaside Sparrow (*A. m. mirabilis*) in more detail by: 1) reviewing published and unpublished information; 2) examining this information in light of what is known about the species as a whole; 3) discuss gaps in our knowledge of *mirabilis*.

Distribution. The Cape Sable subspecies is limited to the southern tip of Florida (Collier, Monroe and Dade Counties) in a roughly rectangular area of 700 km-sq. As discussed by Werner and Woolfenden (1983), the climate of the area is similar to the tropical wet-and-dry climate of Trewartha et al. (1967). Historical information about the distribution of the sparrow demonstrates that it 1) was widespread, and occupied several habitat types, although it took many years for ornithologists to discover new populations in the difficult terrain occupied by the sparrows, 2) Once found, breeding groups ("colonies") were difficult to relocate, as they seemed to move often and over long distances. These apparent shifts in range took place either gradually, in response to successional changes, or abruptly as a result of catastrophic habitat changes. Several widely-spaced populations have been reported existing at the same time, and specific localities may hold sparrows for a few years, the birds then disappear, and the same or another group reappears elsewhere.

The Cape Sable Seaside Sparrow was described in 1918 (Howell 1919). Initially it was thought to be restricted to brackish or salt marshes in the Cape Sable area, although it is possible that at the time of its discovery it also occupied other areas and habitats throughout extreme southern Florida. Since 1928 the subspecies has been documented as occurring regularly in three other areas of the Everglades region: 1. Southern Big Cypress (Nicholson 1928); 2. Ochopee area (Anderson 1942); 3. Taylor Slough and the eastern side of Shark River Slough (Ogden 1972). The history of these populations is outlined in detail by Kushlan et al. (1982) and by Kushlan and Bass (1983). Since 1992, surveys have been conducted over most of the subspecies' range, but details of the current status of the various populations have not yet been published.

POPULATION ESTIMATES

History. Based on surveys conducted in 1974-1975, Werner (1978) made the first estimate of the entire *mirabilis* population. Extrapolating to the area of known occurrence from population densities that he found on measured plots on Taylor Slough, he estimated the total population to be 2000 to 3000 birds. This estimate assumed that the Taylor Slough birds made up 95% of the subspecies' numbers.

Bass and Kushlan (1983), employed by Everglades National Park, conducted an extensive, systematic survey in 1981, using fixed-radius point-counts (see Hutto et al. 1986). In these, they assumed that the sparrows were uniformly distributed, and that the population density of each sample plot accurately reflected that which prevailed in the entire 1 km-sq. Therefore, for each male heard singing within a 200-m radius (12.57 ha), seven other males were assumed to be in the

100 ha in which the sample was made. These authors based their estimate on a larger area than did Werner. In addition to Taylor Slough, they included the relatively large Big Cypress area, which Werner did not consider to have a significant number of Seaside Sparrows six years earlier. They also surveyed Cape Sable and the Ochopee area. The 1981 survey consisted of 864 grid intersections. A total of 416 birds were seen at 32% of the intersections. Kushlan and Bass (1983) estimated the *mirabilis* population to be composed of 6600 birds (3300 males and 3300 females). These authors speculated that this population estimate represented a high point in a fluctuating population cycle, which was related primarily to the occurrence of fires.

In 1992, after a ten-year hiatus, the surveys were resumed by Everglades National Park, in cooperation with personnel from the University of Tennessee (UTK; Curnutt et al. 1998). The surveyors used the same sampling procedures as Kushlan and Bass (1983). But, as the 1981 survey method of Kushlan and Bass (1983) had not controlled for a possible interaction between breeding period and location, the UTK team instituted a stratified random sampling scheme (Curnutt et al. 1998).

Curnutt et al. (1998) tested the reliability of the survey technique by comparing the number of birds known to be present on measured census plots with those estimated to be present from point counts. Their results indicated that the point counts underestimate actual numbers present by 36%. The authors considered this to be an unrealistic deviation, however, as the census plots they used for comparison had been chosen for other studies, which required a relatively high density of breeding males. If the calibration plots had been chosen at random, they theorized, lower numbers of birds would have been present, which would have more closely reflected the actual situation, in which many survey points had zero values.

Results of recent surveys. Unfortunately, due to logistic constraints, not all of the original 864 grid intersections have been sampled in each of the seven years that the surveys have been conducted since 1981. In addition, a number of new sample plots have been added, apparently to compensate for those that were not sampled, due either to logistics, or because the original sample plots were invaded by trees. Taking the 1981 study plots as a baseline, the censused (not extrapolated) population has shown some variation (Table 1). The surveys did not cover all potential breeding habitat of *mirabilis*, therefore it is not possible to provide a complete estimate of total population size.

Table 1. Number of male Cape Sable Seaside Sparrows recorded in 1981 and succeeding years on the same plots. Sample plots that were invaded by trees (N = 30) were excluded for all years.

Year	No. of Points	Percentage of 1981 points	No. of males
1981	813	100	387
1992	757	93	368
1993	618	76	189
1994	181	22	survey incomplete
1995	505	62	159
1996	497	61	no data available
1997	486	60	225
1998	553	68	160

Although in succeeding years the surveys did not cover all the original (1981) sample plots, it is possible to analyze the data using plots which were covered in two years, and for which in at least one year one bird was located. Plots that were noted as having trees were eliminated from the analysis. No birds were noted in plots that had been invaded by trees. This method of comparison uses the presence of the birds as an index of suitability. The question is then reduced to one of asking whether the *mirabilis* population changed between any two census years in the areas where males were recorded.

First, I ask whether the population density remained the same between 1981 and 1992. In each year a total of 315 points was sampled. An average of 1.23 males was recorded per point in 1981, as compared with 1.17 males per point in 1992. There is no significant difference between these means (ANOVA; $F = 0.446$; $P = 0.505$; $df\ 1 / 628$).

It is then asked whether the population densities that were found in 1998 were the same as those found 1992. For these two years, 195 points held at least one male in at least one year. The average number counted per point in 1992 was 1.71, versus 0.84 in 1998, a highly significant difference ($F = 45.78$; $P < 0.001$; $df\ 1 / 388$).

The next comparison is between the two most recent surveys. A mean of 1.86 males was recorded at 121 points in 1997, compared with 1.32 males per point for the same sampling areas in 1998. In this case, I reject the hypothesis that population density remained the same: there was a highly significant difference in the number of males recorded between the two years ($F = 9.68$; $P = 0.002$; $df\ 1 / 241$).

From the above preliminary analysis, it is concluded that although the population densities remained unchanged over 11 years (1981-1992), they changed between 1992 and 1998.

A similar analysis was then conducted separately for each of two main population areas. First, the question is asked whether the population density of the main group east of Shark Slough (B)

remained the same between 1992 and 1998. For the two years, 94 points were occupied at least once each. The mean number found per point in 1992 was 1.89, compared with 1.14 for 1998, a significant difference ($F = 112.90$; $P < 0.001$; $df\ 1/168$).

Second, the same analysis was conducted for the main group of birds found west of Shark River Slough (area A). For 85 points which were occupied by males in at least one of the two years, the 1992 density was 1.51 males per point, as compared with 0.22 males per point in 1998, a significant difference ($F = 14.16$, $P < 0.001$; $df\ 1 / 186$).

Finally, I examined whether population density remained the same in area A between 1997 and 1998. The average density in 1998 was 1.17, and in 1999, 0.42. Only a small number of plots (12) were shared between the two years, reducing the power of the test. A comparison suggests that there was no significant change in population density in area A between 1997 and 1998 ($F = 4.22$; $P > 0.05$; $df\ 1 / 22$).

Discussion. Unfortunately, many of the original (1981) survey points have been omitted over the years (Table 1). Different areas were censused in different years, and there were no within-year replications of surveys. It is still possible to analyze variation between years, however, as long as the same plots are compared; this appears to be the only data set amenable to statistical analysis. Pimm (1995) also recognized the problem of uneven survey coverage, and tested for internal consistency. He calculated changes that occurred between years on the same plots, and then applied these percentages to the census totals for all plots. He then used these results to predict the actual survey estimates. He found close agreement between the observed and predicted values. I performed a similar calculation for years for which I had data, and also found a good fit. Comparing 1981 with 1992, the population decreased by 5% on plots that were surveyed in both years. For all plots, the comparable figure was 1%. For 1992 to 1993, the estimated decrease was 49%, compared with a 50% reduction for all plots that were surveyed.

The analysis given in the previous section suggests that the Cape Sable Seaside Sparrow populations remained stable over an eleven-year period (1981-1992). Between 1992 and 1998, however, densities decreased significantly in the entire survey area: a reduction of 51% in male density on all plots. During the latter period, the population density on plots west of Shark River Slough has decreased by 85%, compared to a 40% decrease east of Shark River Slough. For the area of greatest concern, that west of Shark River, male density appeared to have stabilized after 1997.

The only inferences that can be made from comparisons between years relate to changes in male density within groups of specific sample plots. For reasons discussed below, estimating total Seaside Sparrow population sizes from point samples is misleading (see for example, Curnutt et al. 1988).

Survey-based estimates of total population. The current method of estimating the total population size of *mirabilis* is based on the following implicit assumptions.

First, to determine male population densities at sample points, the investigators assume that (1) During a 10-min visit to each fixed-radius sample plot (radius=200 m; area=12.6 ha; Kushlan and Bass 1983, Curnutt et al. 1998), all breeding males are detected. (2) Birds are distributed

randomly (not clustered). (3) During survey period, males remain in separate areas (singing areas do not overlap).

To estimate the total population size from male density estimates, it is assumed that: (4) Each male that is detected has one female on his activity space. (5) The habitat found in each circular sample plot (12.6 ha) is representative of the 87.4 ha surrounding it. (6) Singing males are uniformly distributed: the density determined for the sample plot prevails over the 100 ha; i.e., on average, the activity spaces of males are distributed in the same way over the 100 ha. (7) In any given year, breeding birds are potentially located only at sites that are actually sampled; plots at unsampled grid intersections have no singing males. (8) Breeding Seaside Sparrows occur only in the surveyed region.

Since 1992, an additional implicit assumption has been made in regard to allocation of sampling effort: (9) Areas that are flooded are assumed to have no breeding birds, and these areas may not be surveyed.

The complete results of the surveys have not yet been published, but the most recent estimates for the entire male *mirabilis* population have been provided by the US Army Corps of Engineers (1998; Table 2)

Table 2. Population estimates of male Cape Sable Seaside Sparrows in the Everglades region, 1981- 1998 for each geographical area.

Area	1981	1992	1993	1994	1995	1996	1997	1998
A	2688	2608	432	80 + *	240	272	272	192
B	2352	3184	2464	2224	2128	1888	2832	1808
C	432	3	0	- **	0	48	48	80
D	400	7	96	- **	0	80	48	48
E	672	37	320	112	352	208	832	912
F	112	2	0	- **	0	16	16	16
TOTAL	6656	6576	3312	2416 +*	2720	2512	4048	3056

*Survey incomplete; ** No survey

The results of the surveys show wide fluctuations between years within the different areas. The overall male population size is believed to have remained stable between 1981 and 1992. In 1992, 93% of the 1981 sample plots were revisited (Table 1). Between 1992 and 1993, the population estimate fell by 50%. Many of the areas were not surveyed in 1993, however, apparently because of unusually high water (Table 1; see Curnutt and Pimm 1993).

In 1993, only 27 males (extrapolated to 432; table 2) were recorded in area A (west of Shark River). By 1995, the A population had fallen to about 200 males, at about which level it has remained through the 1998 survey.

During 1994-1996, the overall population estimate remained about the same: 2400-2700 males. Between 1996 and 1997, the total population increased, and then decreased the next year. Most of these fluctuations were due to variation in the size of the B population, which decreased by 11% (1995-1996), increased by 50% (1996-1997), and then decreased by 36%. As discussed later, the wide fluctuations in the estimated size of population B appear to be due to either sampling error or to movements of males.

Discussion. Most of the assumptions of the population estimate technique are untested, or are contradicted by published information on the species' biology.

1. Assumption: all males are recorded. The sampling procedure does not account for seasonal or diurnal variation in males' behavior. For example, singing decreases rapidly within 2 h after dawn. Reduction in song rate is particularly pronounced in tropical climates (J.S. Greenlaw, pers. comm.). Singing rates are high before the arrival of a female on territory, decrease during the pair establishment period, increase when the female is incubating, and decrease again when the male is feeding young (Post 1974, Post and Greenlaw 1984). The problem of recording false zero values is discussed by Pimm (1995), who suggested making repeated measures per plot.

In addition, *mirabilis* has an extended breeding period (February-August; Werner and Woolfenden 1983). Most surveys have been conducted from late April to early June. This leaves unsampled two 5-6 week periods, one at each tail of the breeding period.

2. Assumption: males are distributed randomly. Some studies of the species have demonstrated that territorial males are clustered in space; that is, large areas of habitat are unoccupied, while in the same area and habitat breeding sparrows occur at population densities of up to 20 pairs per ha (Post 1970a). Uneven dispersion of breeding pairs over apparently homogeneous habitat, and absence from apparently suitable microhabitat, has led to descriptions of the species as colonial or semicolonial (e.g., Audubon 1831, Nicholson 1928, Tomkins 1941, Stimson 1968, Werner 1975, Kushlan et al. 1982, Austin 1983, Kushlan and Bass 1983). Pimm (1996) also commented on the non-random distribution of sparrows on his marked study plots. Extrapolation from point counts underestimates population sizes in areas where sparrows are clumped (Curnutt et al 1998).

3. Assumption: activity spaces do not overlap. When feeding, Seaside Sparrows range widely outside their nidic territories, and may make foraging flights of over 1 km. This leads to a pattern of overlapping activity spaces. This behavior has been reported for birds occupying tidal areas (Tomkins 1941, Woolfenden 1956, Post 1974, Post et al. 1983, Greenlaw and Post 1985), as well as non-tidal areas (Werner 1975, Sykes 1980).

4. Assumption: each male is mated. The proportion of unmated male Seaside Sparrows varies widely (23-60 %; Greenlaw and Post 1985, Post and Greenlaw 1994). At Taylor Slough in 1974, 12% of males remained unmated through breeding season; 11% in 1975 (Werner and Woolfenden 1983). The variation in incidence of unmated males between populations appears to be related to habitat suitability (Post et al. 1983, Greenlaw and Post 1985).

5. Assumption: Habitat is uniform. Extensive vegetative studies in the Everglades (reviewed in Kushlan 1990, Gunderson 1994), including analysis of *mirabilis* territories (Werner 1975), demonstrate that three-dimensional variation of habitat structures that would be of significance to Seaside Sparrows occurs over short distances, e.g., within 10 m intervals (Post et al 1983). Although it is possible that a randomly chosen plot is representative of large proportion of the habitat contained within the entire 100 ha, this should be verified on a cases by case basis.
6. Assumption: males are uniformly distributed. It is assumed that male density recorded on the sample plot is the same over the entire 100 ha. As discussed under assumption 2, this is not supported by published studies of this species (Nicholson 1928, Tomkins 1941, Woolfenden 1956, Stimson 1968, Werner 1975, Kushlan et al. 1982, Austin 1983, Kushlan and Bass 1983).
7. Plots that are not sampled have no singing males. This assumption has been necessitated by failure to cover all of the sample plots (see Table 1)
8. Assumption: only areas that are surveyed have Seaside Sparrow breeding populations. This assumption can only be tested by increasing the area of coverage of the surveys. The history of the intermittent disappearance and rediscovery of sparrows in different areas of southern Florida argues against the validity of this assumption (Kushlan and Bass 1983, Werner and Woolfenden 1983). The subspecies also displays an opportunistic response to the geographical-habitat array (Curnutt 1996), and may abandon and later recolonize specific areas, depending on water levels (Werner 1975, Werner and Woolfenden 1983, Lockwood 1996).
9. Flooded areas have no breeding birds. For several reasons, this assumption needs to be tested. Each plot is visited only once per year. It is possible that any bird remaining on its activity space during a flood occurring early in the breeding season will wait until waters recede and then nest, or move to higher ground, or build its nest higher (Tomkins 1941). Seaside Sparrows nests in tidal areas are frequently flooded, often several times in a season. Pairs that are flooded out immediately resume retesting (Post 1974; Greenlaw 1983, 1992; DeRagon 1988; Marshall and Reinert 1990). It is also possible that birds unable to breed due to lack of proper substrate merely move to the nearest available suitable site (Post 1974).

HABITAT USE

General. The species is a habitat specialist that occupies tidal marshes or nearby freshwater marshes (Kale 1983, Robbins 1983), but with a discontinuous local distribution (Greenlaw 1983, 1992). The physiognomy of vegetation used by the species is varied, and reflects opportunism in using available substrates (Greenlaw 1983, Post et al. 1983), although the response is predictable between regions (Greenlaw 1992). Requirements shared by most breeding populations are: first, elevated nest sites that provide protection from periodic tidal and storm flooding; second, nearby openings in vegetation, such as pannes, pools and creek edges, that allow birds to forage on open

mud, and at the bases of rooted vegetation. For all populations for which habitat use has been described, there is a remarkable similarity in habitat structure: an interspersed of homogeneous stands of a tall and a short graminoids, and open mud or shallow water areas. The species of vegetation varies widely, and does not appear to be critical in the distribution of the species (see habitat photographs in Post 1970a,b; 1981; Post et al. 1983; Post and Greenlaw 1994; Sykes 1980; for *mirabilis* alone, see figure 2 in Werner and Woolfenden 1983). Optimum habitats contain contiguous nesting and feeding sites; otherwise, birds commute between nest-centered territories and distant feeding areas (Tomkins 1941, Woolfenden 1956, Post 1974).

Seaside Sparrows on the southeastern Atlantic coast and on the Gulf of Mexico breed in habitats with the same vegetative structure as those on the northeastern Atlantic coast, although plant diversity is greater in the southern marshes. Salt-meadow grass (*Spartina patens*) is replaced by two other fine-textured grasses, saltgrass (*Distichlis spicata*) and drop-seed (*Sporobolus virginicus*), and by several taller, coarse-textured species such as switch grass (*Spartina bakeri*) and black needle-rush (*Juncus roemerianus*). Low areas are dominated by smooth cordgrass, cattails (*Typha*) or sawgrass (*Cladium jamaicense*). Southern Florida Seaside Sparrows (*mirabilis*) inhabit hair grass (*Muhlenbergia*) prairie and sawgrass prairie (Werner and Woolfenden 1983, Kushlan and Bass 1983). The St. Johns segment of the now extinct east central Florida group (*nigrescens*) also occupied freshwater prairie that was structurally similar to hair grass prairie, but which was dominated by switch grass. The Merritt Island segment of this race occupied salt marsh habitat similar to that used by other southeastern populations (Nicholson 1928, Sykes 1980).

History of habitat use by *mirabilis*. The Cape Sable subspecies was first described as occupying brackish marshes ("salt grass", *Distichlis spicata*), and adjacent, presumably less saline marshes dominated by "switch grass" (*Spartina bakeri*; synonymous with *Spartina patens juncea*); see Stimson (1968). Nicholson (1928) described the Cape Sable Seaside Sparrow as nesting in a variety of habitats in the Cape Sable region: brackish marshes composed mainly of switch grass mixed with smaller patches of salt grass, and shallow ponds. The sparrow population in the Cape Sable area was destroyed or displaced by the hurricane of 1935 (Stimson 1968). Some researchers have suggested that the hurricane caused a wide-scale shift from switch grass to more salt-tolerant plants, and that the sparrows left the area because of a shift in plant communities from grasses to halophytic forbs (*Salicornia* and *Batis*; see Werner and Woolfenden 1983).

Within the last two decades (Werner and Woolfenden 1983), Cape Sable Seaside Sparrows have been described as living in four distinct habitat types: 1) clumped *Spartina* prairies, 2) unclumped *Spartina* prairies, 3) sparse *Cladium* prairies, 4) *Muhlenbergia* prairies. In addition to these four habitat types, Kushlan and Bass (1983) describe a "mixed prairie habitat". From their descriptions, this appears to correspond to sparse *Cladium* prairie.

Spartina prairies were widespread on coastal marl fringing the mangrove zone, in the western part of the sparrow's range. *Spartina* prairies, both clumped and unclumped, have been reduced in extent, due primarily to changes in salinity and to invasion of mangroves and other woody vegetation (Kushlan and Bass 1983, Werner and Woolfenden 1983).

Sparse *Cladium* prairie is widespread from Gum Slough east to Shark River Slough. In the 1950's, this habitat supported the most extensive known population of the sparrow. The sparrows

were rare there in 1970-1975, but surveys in the late 1970's again found them widespread in the same area (Bass in Werner and Woolfenden 1983). The fluctuations in the population sizes of sparrows living in sparse *Cladium* prairie is believed to be related to the effects of fire (Werner and Woolfenden 1983)

Besides those living in sparse *Cladium* prairie (mixed prairies of Kushlan and Bass 1983), the majority of the surviving sparrows now nest in *Muhlenbergia* prairie, mainly on marl in areas east of Shark River Slough. Before Ogden's (1972) rediscovery of Seaside Sparrows in the Taylor Slough area, and Werner's (1975) research, *Muhlenbergia* was not reported as a nesting substrate, and Davis (1943) did not mention the species as a component of the marl prairies where the sparrow now occurs. Conversely, hair grass may have been present but confused with other graminoids (Olmstead et al 1980). It has been claimed that the vast *Muhlenbergia* prairies now existing east of Shark River have been propagated by man-influenced reduction in water levels, coupled with the destruction of shallow organic soils by drought fires (Craighead 1974, Werner and Woolfenden 1983). The question has therefore been raised whether the population east of Shark River Slough was formerly as large as it is now (Werner and Woolfenden 1983).

Recent research. During the 1981 surveys, the researchers recorded the vegetation at each of 864 grid intersections. The percentages of all habitat types that were found at the intersections were compared with the percentages of the respective habitats in which male sparrows were recorded. Data were recorded for 416 males. Four areas were surveyed: Taylor Slough (396 sites, 46% of the sample sites), Big Cypress (441, 51%), Ochopee (22, 3%), Cape Sable (5, < 1%).

Of the total number of birds, 60% were in Taylor Slough and 40% were in Big Cypress. No males were found in the other two areas. The surveyors (Kushlan and Bass 1983; Table 3) found that 32% of the sample points were occupied by at least one male. Half of the intersections that were covered by *Muhlenbergia* prairie had sparrows, as did half of the sparse *Cladium* prairie. Only 13% of the *Spartina* marsh that was sampled had sparrows. Pure (dense) stands of *Cladium* were not utilized at all.

Table 3. Habitat use of Cape Sable Seaside Sparrows, based on Kushlan and Bass (1983).

Habitat type	Number of sites sampled (percent)	Number of sites occupied (percent)
<i>Muhlenbergia</i> prairie	371 (43)	186 (50)
Sparse <i>cladium</i>	164 (19)	82 (50)
<i>Spartina</i> marsh	61 (7)	8 (13)
<i>Cladium</i> marsh	175 (20)	0
Other	93 (11)	2 (2)
Total	864 (100)	278 (32)

Food availability as a factor in habitat distribution. At Cape Sable the most important food items for *mirabilis* (15 stomachs, 26 March-5 April 1926) were beetles (35.5% of volume), spiders (14.5%), Heteroptera (bugs; 9.9%) and Hymenoptera (8.3%). The numerically most important groups were ground-inhabiting taxa such as ground beetles (Carabidae), variegated mud-loving beetles (Heteroceridae), and checkered beetles (Cleridae). Several stomachs also contained amphipods and mollusk fragments (Post and Greenlaw 1994). Sweep net samples of vegetation in *mirabilis* nesting habitat (Werner 1975) indicate that most prey items found in stomachs were probably taken from the ground rather than from the vegetation column.

Although sparrows were distributed non-randomly on his study plots, Pimm (1996), using sweep-nets, found few differences in insect fauna between sites that were occupied and unoccupied by sparrows. In 1996, Pimm reported that the main insect groups taken were Orthoptera, Lepidoptera and Odonata. Diet varied between years and sites, which reflected the patchy distribution of the insects, as well as the opportunistic foraging of the sparrows (Pimm 1996). Recent studies of food use have been based on observations of items being carried in adults' bills; apparently, it has not been possible to actually sample food brought to young (Lockwood et al. 1997).

Determining diet by observing from a distance food brought to young may give a biased picture of food intake (Merriam 1983). For example, using this method for Seaside Sparrows in New York, Post (1974) overestimated the importance of large prey such as Lepidoptera and Trichoptera by 73%, and underestimated the importance of Diptera by 27% (Merriam 1983). Adults delivering food to nests often carry multiple items, which have been macerated, making it difficult to identify individual items (Merriam 1983, Post et al 1983). Until young are seven days old, small items (volume < 0.01 cc) make up the bulk of the nestling diet (Merriam 1983).

The method used to determine diet of nestlings appears to be biased in favor of larger items. For example, Homoptera and Hemiptera are abundant in most Seaside Sparrow habitats, but are not reported as food by Lockwood et al (1997). Although ground-inhabiting insects, mainly beetles, may be abundant, and have been reported as the main prey of adult *mirabilis* (Post and Greenlaw 1994), Lockwood et al. (1997) did not identify any as being brought to nestling. These discrepancies indicate that the sampling techniques used to identify the food that is delivered, and to determine the availability of food, need to be modified (see Merriam 1983 and Post et al 1983, for methods used to sample foraging sites in shallow water and mud microhabitats).

Discussion. Based on information from other populations, and from earlier studies of the Cape Sable Seaside Sparrow, it is possible that *Muhlenbergia* prairie is not the preferred habitat of the subspecies. The Everglades Seaside Sparrows may have been primarily adapted to the brackish switch grass (*Spartina bakeri* = *S. patens juncea*) and salt grass (*Distichlis spicata*) of the coastal (southwestern) part of its range (Stimson 1968). The structure of this habitat appears to have been similar to that occupied by other subspecies (*peninsulae*, *nigrescens*, *macgillivraii*) After the hurricane of 1935, populations of sparrows were found nesting in similar habitat north of Cape Sable, along the western mangrove fringe, north to Ochopee.

Early ornithologists did not find sparrows nesting in *Muhlenbergia* prairie, and this grass appears to be a recent invader of many areas of the Everglades (Davis 1943, Atwater 1954, Gunderson 1994). It is possible that, because of degradation of the coastal and interior *Spartina*

prairies that were once occupied by the sparrows, the subspecies is now occupying the remaining vegetation (*Muhlenbergia*) that is most similar in structure to *Spartina*. Recent studies (Lockwood et al. 1997, Curnutt 1998) state that *Muhlenbergia* prairie is the preferred habitat of the subspecies. Examined from an historical perspective, however, *Muhlenbergia* prairie may be regarded as simply the most suitable habitat into which the Cape Sable Seaside Sparrows has most recently been forced.

Population density by itself cannot be used as an index of habitat suitability: Seaside Sparrow densities vary widely even within the same habitat, and reproductive potential is density-independent (Post 1974, Greenlaw and Post 1985). It is improper to refer to habitat as "preferred" on the basis of correlational patterns alone (Wiens 1989). Density is most likely to be decoupled from a strong association with habitat in environments that are temporally unpredictable, spatially patchy, and strongly seasonal, and in species that are ecological generalists and that have a high reproductive capacity (Van Horne 1983).

If higher population densities of sparrows are found in a specific area, this finding might support a preliminary hypothesis that the habitat is preferred. It then must be shown that components of fitness are consistently higher for the birds that occupy this habitat. Comparisons should be made with other populations in other habitats during the same period. As yet, no data are available about the reproductive potential or the survivorship of contemporaneous populations of Seaside Sparrows in different habitats in the same region. It is possible that hair grass prairie may represent a "suboptimal" refugia for the subspecies. Recent findings that sparrows occupying this habitat have low annual survival support this hypothesis (Pimm 1995).

A similar situation, that of a remnant population existing in a suboptimal habitat, may have existed during the final decline of the Dusky Seaside Sparrow. This subspecies nested in salt marshes on Merritt Island. It disappeared from Merritt Island after the salt marshes were diked. After it was almost extinct there, in 1968 Sharp (1969, 1970) found about 895 males in *Spartina bakeri* prairie near the St. Johns River. The birds on the St Johns lasted another 12 years. Some information was gathered about the breeding biology of the Merritt Island birds (Trost 1960, Sykes 198), but little was learned about the prairie-nesting sparrows (Baker 1973, 1978).

DEMOGRAPHY

Population viability analysis models predict population changes, and estimate the probability of extinction based on projected environmental changes (Shaffer 1990). Most modeling efforts have been severely hampered by lack of accurate demographic data: measures of fecundity and survivorship, as well as estimates of variation of these rates (Derrickson et al. 1998). Predictions of population viability based on "estimates" of demographic features must be viewed with considerable skepticism (Caughley 1994).

Adult survival estimates. The annual survival of the Cape Sable Seaside Sparrow appears to vary between cohorts, and perhaps between study sites (Werner 1975, Pimm 1995). Based on data for 16 males, Werner estimated maximum annual disappearance (losses from mortality or

emigration) as 12%. Based on additional information from the same study population, Kushlan et al. (1982) provide an annual adult survival estimate of 90%.

Using an estimation method presumably similar to that of Werner and Kushlan, and data on 18 birds followed over two years, Pimm (1995) estimated a minimum adult male survival rate of 50%. From 1994 to 1996, Pimm (1996) banded 122 sparrows. Only 29% of these were seen or caught by the end of the 1996 research season. He reported that adults that had nested in a given area had an annual survival rate of 100%, while those that did not nest had an annual survival of 38% (Pimm 1996). Sample sizes were not given. An annual report submitted to Everglades National Park (Pimm 1997) listed chapter 8, which "reports on the bird's annual survivorship".⁽¹⁾

Discussion. Over two years, Post et al. (1983) studied a color-marked population of Seaside Sparrows nesting at Gulf Hammock, Florida, and estimated annual adult male survival at 86%. Additional annual survival estimates for different cohorts from this population are above 80%. Some individuals have survived for nine years (Post and Greenlaw 1994, McDonald and Post, unpubl.). Adult male Seaside Sparrows in New York have an estimated annual survival of 53-60%, depending on cohort (Post and Greenlaw 1994).

Non-migratory temperate zone passerines have annual survival rates averaging about 55% (reviewed by Greenberg 1980, Dobson 1990, Karr et al. 1990). It has been widely held that a latitudinal gradient in survivorship exists, with survival rates increasing toward the equator (Fogden 1972, Ricklefs 1973, Snow and Lill 1974). The only standardized study that has addressed this question has found, however, that survivorship for small birds in the tropics is about the same as that for temperate zone species (54% vs 55%, Karr et al. 1990). These authors considered species occupying forested areas only.

As yet, little has been published about the survivorship of New World species that occupy open country, in either the tropics or subtropics. The following examples suggest that some open-country species which breed at lower latitudes have comparatively high survival rates: in Puerto Rico, the minimum annual adult survival rate of male Yellow-shouldered Blackbirds (*Agelaius xanthomus*) is 74% (Post 1981). In coastal South Carolina, the minimum annual survival of male Boat-tailed Grackles (*Quiscalus major*) is 85-88% (Post 1992). Also in Florida, the minimum annual survival of resident Grasshopper Sparrows (*Ammodramus savannarum floridanus*) has been estimated at 60% (Delany et al. 1993). The latter estimate is particularly relevant, as the Grasshopper Sparrow is closely related to the Seaside Sparrow. Grasshopper Sparrows nest in dry grasslands. Adults attending nests may have higher mortality from ground predators than do marsh-nesting Seaside Sparrows, although the few studies comparing the reproductive success of marsh and field-nesting species provide contradictory results (Ricklefs 1969, Post 1986).

It is therefore likely that the average annual adult survival rate of Seaside Sparrows nesting in the Everglades region is at least 70%, which is intermediate to the estimates of Werner (1975), Kushlan et al. (1982) and Pimm (1995).

Footnote

1. This section was not included in copies of the annual report that we received from the US Fish and Wildlife Service.

REPRODUCTIVE OUTPUT

Length of the nesting cycle. Female Seaside Sparrows may initiate as many as four clutches per season. The length of each cycle varies according to the female's mating status, number of previous clutches, season, resource availability, and male parental investment (Post and Greenlaw 1982). The factor which contributes most to the variation in the length of the cycle is the amount of time that the female spends caring for fledglings. In some cases, males alone have fed young while they were still in the nest, during which time females have started new clutches (Marshall and Reinert 1990). Because of the difficulty of observing female behavior, only a few *mirabilis* cycles have been measured directly. Estimates of cycle length vary from 31 to 49 d.

Based on nests found early in the 1996 season, which were probably first nests, Pimm (1996) calculated the average length of the *mirabilis* nest cycle (courtship, egg laying and incubation) as 43 days (sample size and range not indicated). Based on a nest found 27 March 1996, Lockwood et al. (1997) calculated a nesting cycle of 34 d. The mating status of the pair was not known. Werner (1975) measured three cycles. In one case, a female that changed mates fledged the succeeding brood in 48 d. The third successive brood of this female fledged less than 37 d later. Another pair fledged a successive brood in 38 d. Werner (1975) and Werner and Woolfenden (1983) documented one instance of brood overlap, the second brood fledging exactly 31 days after the first.

The core period of each Seaside Sparrow nesting cycle is 24 days: four days for deposition of eggs, 12 days for incubation (incubation may start with the laying of the penultimate egg), and 9 days during which young are in the nest (Werner 1975, Post and Greenlaw 1994). I assume that once young have fledged, the female is immediately free to begin renesting. It has been found that males may feed fledglings alone, and that females may initiate a new clutch before the old one has fledged (Marshall and Reinert 1990, Werner and Woolfenden 1983). Nest construction usually requires 3-4 d. Therefore it is possible that the renesting of a mated pair can occur in 31 days or less, which agrees with Werner and Woolfenden's (1975) and Marshall and Reinert's (1990) observations. If the birds are not yet mated, I estimate that bonding will take at least 5 d. For new pairs, therefore, the first nest cycle may require at least 35 d. If females are physiologically capable of producing four clutches per season, and if nest mortality rates are low, most pairs should be able to produce at least three broods within a 125-d period.

Reproductive success. Two published papers (Werner and Woolfenden 1983, Lockwood 1997), and two unpublished reports include information on the reproductive success of the Cape Sable Seaside Sparrow (Werner 1975, Fenn 1997). Summary analyses contained in the reports combine data from different years, and from different study areas, which makes it difficult to assess sources of variation. Fortunately, Fenn et al. (1997) included an appendix which categorizes each nest history by year and location. Werner (1975) did not use Mayfield's (1975) correction method. For reasons discussed below, I do not use the Mayfield method for subsequent years. The results of the analysis (Table 4) show that total nesting success over the four study periods was relatively high: 64% of eggs, and 70% of nests, produced fledglings. The comparable means (each of the four periods given equal weight) are 64% and 69%.

Table 4. Estimated reproductive success of Seaside Sparrows in the Everglades region, 1975-1997. Data from Werner (1975), Fenn et al. (1997), and Lockwood (1998).

Year	(1) Eggs (no. nests)	(2) Young (no. nests)	(3) Fledglings (no. nests)	Percent (2)/(1)	Percent (3)/(2)	Percent (3)/(1)
1974-1975	55 (16)	41 (15)	34 (11)	75 (94)	83 (73)	62 (69)
1995	15 (4)	11 (3)	11 (3)	73 (75)	100 (100)	73 (75)
1996	60 (19)	46 (16)	33 (12)	77 (84)	72 (75)	55 (64)
1997	111 (33)	83 (25)	74 (22)	75 (76)	89 (88)	67 (67)
1998	166 (53)	147 (51)	* (40)	89 (96)	- (78)	- (76)
Mean **	-	-	-	78 (85)	86 (83)	64 (70)

* data not provided.

** each year given equal weight.

During the entire cycle, success for individual nest contents (eggs through fledglings) varied from 55% (1996) to 73% (1995). Success during the incubation stage (percentage of eggs that produced nestlings) varied little between periods (73%-77%). Most of the between-year variation in total nest success may be accounted for by losses occurring during the nestling stage: success of individual nestlings ranged from 72% (1996) to 100% (1995).

Variation in RS between study sites. The largest number of nests were found in 1997, and enough were found to allow comparisons between study plots. (Nest-exposure days are not available for study plot, so it is necessary to use uncorrected estimators anyway). The results (Table 5) indicate that total egg success in each plot ranged from 53% to 100%. Total nest success during the egg stage was 50-100%. Although the range in success between study plots is high, this is undoubtedly related to the small sample size in two plots. In all plots, however, total nest success was relatively high, and was related to good survival during the nestling stage. One plot, Sweet Bay (14 eggs, 4 nests) had no losses. All mortality to nestlings occurred in one plot, Far East (7 young lost from 3 nests).

Table 5. Estimates of Seaside Sparrow nest success on different study plots in the Everglades region, 1997. Only plots with four or more nests are included. Data from Fenn (1997).

Study plot	(1) Eggs (no. nests)	(2) Young (no. nests)	(3) Fledglings (no. nests)	Percent (2)/(1)	Percent (3)/(2)	Percent (3)/(1)
Sweet Bay	14 (4)	14 (4)	14 (4)	100 (100)	100 (100)	100 (100)
Ingraham	32 (10)	17 (5)	17 (5)	53 (50)	100 (100)	53 (50)
Far East	30 (9)	24 (8)	17 (6)	80 (89)	57 (75)	57 (67)
Shark Valley	13 (4)	11 (3)	11 (3)	85 (75)	100 (100)	85 (75)

Unfortunately, it appears that most nests were found late in the egg stage, or in the nestling stage. The analysis for egg survival is based on seven losses occurring during only 90 days of exposure. In this case the estimator appears to be biased due to the loss of many nests late in the egg stage, and the coincidental concentration of visits in this period (see Appendix A of Fenn 1997). The Mayfield method should be used whenever possible, but it is not recommended for samples based on small numbers of nest-visitations, or when losses are extremely high. The total sample contained 33 nests with eggs (396 potential nest-days), whereas data are available for only 90 nest-days (23%). For this reason, it is more realistic to use an uncorrected estimator of nest success (Table 4)

Sources of mortality. In most studies of nesting biology, sources of mortality are difficult to determine. Both Werner (1975), Lockwood (1997) and Fenn et al. (1997) were able to infer causes of mortality to nest contents in some cases. At Taylor Slough 4/55 eggs were depredated, (7%); 9/55 (16%) failed to hatch. Predation was confirmed during the nestling stage (7 young lost); Werner listed no other causes of mortality for nestlings. Lockwood et al. (1997) Reported 2 of 36 egg failed to hatch, 2 eggs were flooded, 3 young were flooded, and 1 nestling presumably starved. Predation was not subdivided according to stage of cycle, but overall, 78% of all losses of young and eggs were attributed to predation. Lockwood (1998) reported that predation accounted for 92% of all nest losses in 1998. No nests were lost to floods, and no other sources of mortality were listed.

Based on 1996-97 data, Lockwood et al (1998) found peaks in the seasonal pattern of predation, which were correlated with rise in water level. No such peaks were found in the 1998 nesting season, which was attributed to lack of surface water (Lockwood et al 1998). The species of predators were not determined, although snakes are mentioned as possibilities. It is not explained how high water can lead to increased snake activity. It has been shown, however, that rodent movements in the Everglades are affected by fluctuations in water levels (Smith and Vrieze 1979). Nest survival and habitat selection of Seaside Sparrows in other areas of Florida are affected by rice rats (*Oryzomys palustris*; Post 1981).

Based on Ricklefs' (1969) method, average daily mortality rates can be calculated from the proportion of nests that survive any given portion of the nest cycle. I calculated these based on a mean of the four study periods for which complete data are available (Table 4). The daily mortality rate for individual eggs during the 12 d egg period (m_e) was 2.39%; the daily mortality rate for individual young during the 9 d nestling period (m_n) was 1.68%; during the 21 d cycle the daily mortality rate for an individual was 2.13%. Based on the proportion of nests that survived during the whole period, the daily mortality rate of whole nests (M) was 1.77%. Partial (within-brood) mortality rates were greater than whole-brood losses ($m > M$). At the same time, partial mortality during the egg stage outweighed that during the nestling stage ($m_e > m_n$). This pattern indicates that 1) partial losses occurring during the nestling period were most important, and 2) that compared with partial losses, whole nest losses were relatively unimportant. This mortality pattern resembles that of species nesting in the humid tropics, and, of the species studied, is most similar to that of the Yellow-faced Grassquit (*Tiaris olivacea*; Ricklefs 1969). In this species partial losses from factors such as starvation are less important than those due to hatching failure. Mortality related to partial losses is about the same as that resulting from whole-nest losses (predation or storm flooding).

Discussion. A preliminary analysis of daily mortality rates indicates that most mortality to Cape Sable Seaside Sparrow nests resulted from partial losses to nest contents. Relatively little loss can be assigned to total nest destruction, as might result from flooding or from predation. In addition, daily mortality rates are higher during the egg stage than during the nestling stage. Such a pattern indicates that most mortality may be due to hatching failure, and relatively little may be caused by starvation, bad weather, or parasitism. This pattern of mortality is different from that found for Seaside Sparrows at Gulf Hammock, Florida, where most mortality was related to whole-nest losses resulting from predation. It is also different from New York, where tidal flooding and predation were the main mortality factors (Post et al. 1983).

The reproductive potential (number of young/female/year) of the Cape Sable Seaside Sparrow is yet to be determined. However, most of the measurements that are used to estimate reproductive potential are higher for this subspecies than for any other population. The mean clutch size of *mirabilis* is 3.5 (Post and Greenlaw 1994), compared with a clutch size of 3.1 in *peninsulae* (Gulf Hammock, Florida) and 3.1 for *macgillivraii* (southeastern Atlantic coast; Post and Greenlaw 1994). Based on the average of four data sets (Table 4), the reproductive success (percentage of eggs that produce fledglings) of *mirabilis* is estimated as 64%, which is much higher than that reported for Seaside Sparrows at Gulf Hammock, Florida (3%) and higher even than that in New York (35%; Post et al 1983).

Length of breeding season in *mirabilis* may exceed 150 days (Werner and Woolfenden 1983), as compared with 103 days for Seaside Sparrows in northern Florida (Post et al 1983). If the first nesting cycle requires 35-40 days, and each succeeding cycle requires 31-36 days (see above, under length of nesting cycle), and assuming that reproductive success is 64% for each nesting attempt, it is possible for a completely successful female to produce nine fledglings per season.

DISPERSAL

The spacing behavior of breeding Seaside Sparrow has been studied extensively (Woolfenden 1956, Post 1972, Werner 1975, Greenlaw and Post 1985). Little information is available about the use of space outside the nesting period. Seaside Sparrows forage in relatively dense vegetation, and adults do not form flocks. After the breeding period, the primary song, which is the principal means of locating birds in the summer, is rarely given, at least until completion of molt (November). Several other vocalizations are given during the winter, such as a contact call, *seep*, and an alarm vocalization, *tuck* (Post and Greenlaw 1974). In winter, most other vocalizations are rarely heard, and if uttered, usually only in the context of roost-entering; e.g., *zuck* and *tchi* (Post unpubl.).

Werner (1975) documented short-distance movements by juvenile Cape Sable Seaside Sparrows. In 1974, a male established a territory 400 m from the site where he was banded as a fledgling; a female was caught 940 m from its original banding point. Werner stated that postbreeding emigration of fledglings probably provided the principal mechanism of dispersal.

In the winter (wet season) of 1996-1997, Balent et al. (1998) relocated 14 color-banded individuals that had been captured in the spring of 1995 or 1996, presumably on their breeding territories. The mean distance between the original point of capture and the resighting point was 277 m (range 77-986 m). These results indicated that at least some Cape Sable Seaside Sparrows did not make long range movements. Rather than moving long distances, the birds appeared to shift microhabitats, moving from open prairie to the edges of small tree islands and hammocks, and to sawgrass swales. Few birds were relocated, they suggested, because of the difficulty of detection in these habitats. They did note, however, that the number of sparrows in their study areas decreased during October-December, perhaps suggesting a movement out of the marl prairies. Coinciding with the start of the breeding period (February), sparrow numbers appeared to increase again on their study sites. In winter, the authors searched widely in other habitats outside the marl prairies, but found no Cape Sable Seaside Sparrows. From these results, they concluded that *mirabilis* is dependent on marl prairie throughout the year.

Recent results from radio telemetry studies of Cape Sable Seaside Sparrows indicate that juveniles may disperse up to 7 km after the nesting season; movements appear to halt when individuals meet a habitat barrier such as a hammock (T. Dean, unpubl.). This researcher also found a male that nested in one area, and then moved during the same breeding season to establish a new territory about 3 km away.

Discussion.

Nonmigratory populations of Seaside Sparrows nesting in regions that have extreme tides are not sedentary, but undertake short-range seasonal movements. (Post and Greenlaw 1994.) Seaside Sparrows that breed in these areas usually nest in high marshes (Cooper 1983), most of which occur at the heads of estuaries. After breeding, individuals move down the estuaries, usually occupying areas of tall *Spartina alterniflora*, where seeds and insects are plentiful (Davis and Gray 1966, Post et al. 1994). In early spring, the birds return to the upper estuary, where nest sites are less vulnerable to flooding (Tomkins 1941, Post 1974).

Juvenile Northern Seaside Sparrows leave their natal territories soon after fledging, gathering in loose flock in feeding areas located in tall *Spartina alterniflora*. Marked juveniles have been found 2.5 km from their hatching sites. One juvenile was recaptured in a feeding area 65 km from its hatching point. (Post and Greenlaw 1994). Greenlaw (*in* Kushlan et al 1982) reported an individual that had dispersed 8 km. Sharp (*in* Kushlan et al 1982) pointed out the importance of post-breeding emigration of juveniles as a means of population maintenance in habitats which undergo periodic perturbations.

The limited amount of data indicate that Seaside Sparrows nesting in non-tidal areas disperse relatively long distances. Six of 13 Dusky Seaside Sparrows nesting in brackish impoundments on Merritt Island, Florida, moved 1.2 km between years; one moved about 1.6 km within the same nesting season (Sykes 1980). It is not known what proportion of these movements represented permanent shifts in activity spaces, or were simply long-range foraging flights. In the non-breeding season, Sykes also found Dusky Seaside Sparrows 8-32 km outside their known breeding range; Sharp (*in* Kushlan et al 1982.) felt that such movements were in response to habitat degradation. Similarly, Dusky Seaside Sparrows nesting on freshwater *Spartina* prairie were reported to move up to 1.6 km from their original banding site (Baker 1978).

The Seaside Sparrow is believed to have evolved in estuarine areas (Beecher 1955, Werner and Woolfenden 1983). Individuals that occupy tidal areas respond to seasonal changes in water levels by moving relatively long distances. It seems reasonable to assume that individuals of the Cape Sable subspecies have retained sufficient behavioral flexibility to respond appropriately to short-term habitat variations, whether predictable ones such as water level changes, or unpredictable ones, such as those caused by hurricanes and fires. Woolfenden (1956) noted an influx of adult sparrows in New Jersey in the middle of the breeding season, and speculated that it involved birds that had been displaced from their territories in another marsh. Kushlan et al. (1982) cited instances of population densities increasing in unburned areas after a fire, suggesting that the sparrows reoccupied suitable habitat soon after being displaced. As emphasized by Kushlan et al., if the movement patterns of adults are restricted, then the ability of the population to compensate for severe, short-term habitat alterations is jeopardized.

Natal dispersal is the most significant geographical movement of individuals, but little information exists on dispersal in birds. Our inability to track dispersal prevents us from understanding population dynamics at the landscape level (Faaborg et al. 1998). Based on their failure to find marked individuals farther than 1 km from their summer territories, Balent et al. (1998) concluded that the Cape Sable Seaside Sparrows that they studied were sedentary throughout the year. Their sampling methods were flawed, however, as they did not correct for the attenuation of bird numbers as distance from the capture point increased ("bird spreading"; see Ostrand et al. 1998). This and other studies of the Seaside Sparrow have not yet provided sufficient information on dispersal for an understanding of metapopulation dynamics.

RECOVERY OF THE CAPE SABLE SEASIDE SPARROW

Sixteen years ago, Kushlan et al. (1982) assessed the status of the Cape Sable Seaside Sparrow, and concluded that "the sparrow was probably never abundant but was, apparently, and remains, widespread in southern Florida". These authors proposed continued vigilance and some habitat management as a means of maintaining the current status of the subspecies. I reviewed the management plan (Post 1983), and concurred in this conclusion, but noted that in light its relatively high reproductive potential and high survival rate, statements about the subspecies' decline seemed contradictory. It was also pointed out that though the management plan was thorough, it was not innovative enough. For example, it did not consider the potential of captive-rearing, although this approach had proven feasible during the recovery efforts for the Dusky Seaside Sparrow (Post and Antonio 1981). The plan also did not mention field intervention techniques, such as use of predator-baffles to protect nests, which also had been developed and tested as methods to improve the reproductive output of Dusky Seaside Sparrows (Post and Greenlaw 1989).

Unfortunately, although a preliminary survey protocol had been established in 1981, for ten years governmental agencies were unable to continue monitoring the Cape Sable Seaside Sparrow populations. It is not known whether the Everglades National Park continued prescribed burning, as recommended by Werner (1975), Taylor (1983), and Kushlan et al. (1982). The recovery plan outlined by Kushlan et al. listed 17 research goals, none of which appear to have been addressed until 1992.

The basis for recent management decisions has been the "extensive survey" (see Curnutt et al. 1998). The census techniques used to estimate population density are essentially unchanged from those used in 1981. The resulting estimates, therefore, are based on unproven assumptions. When surveys were reinitiated in 1992, it would have been advisable to design statistically meaningful sampling techniques; for example, estimates of population density based on replications and on distance sampling (reviewed by Buckland et al. 1993), calibrated by habitat type. Because the sampling techniques are flawed, they cannot be used to accurately estimate population sizes of Cape Sable Seaside Sparrows.

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