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LIFE HISTORY OF THE ENDANGERED CAPE SABLE SEASIDE SPARROW

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ABSTRACT.—Cape Sable Seaside Sparrows (*Ammodramus maritimus mirabilis*) breeding within eastern Everglades National Park were philopatric and moved only short distances between clutches. Incubation required 12 days, nestlings fledged at 9.2 days, and fledgling care ranged from eight to 20 days. The total nest cycle encompassed 34–44 days. Nestlings were fed spiders and insects, primarily Orthoptera, Lepidoptera, and Odonata. Diet varied between years and study sites. With the onset of summer rains, predation rate increased, and nest success decreased. Breeding activity diminished throughout June, coinciding with rising water in nest areas. Our results indicated that the lack of breeding habitat and the onset of summer flooding limit the breeding potential of Cape Sable Seaside Sparrows. *Received 19 October 1996 accepted 5 June 1997.*

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

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

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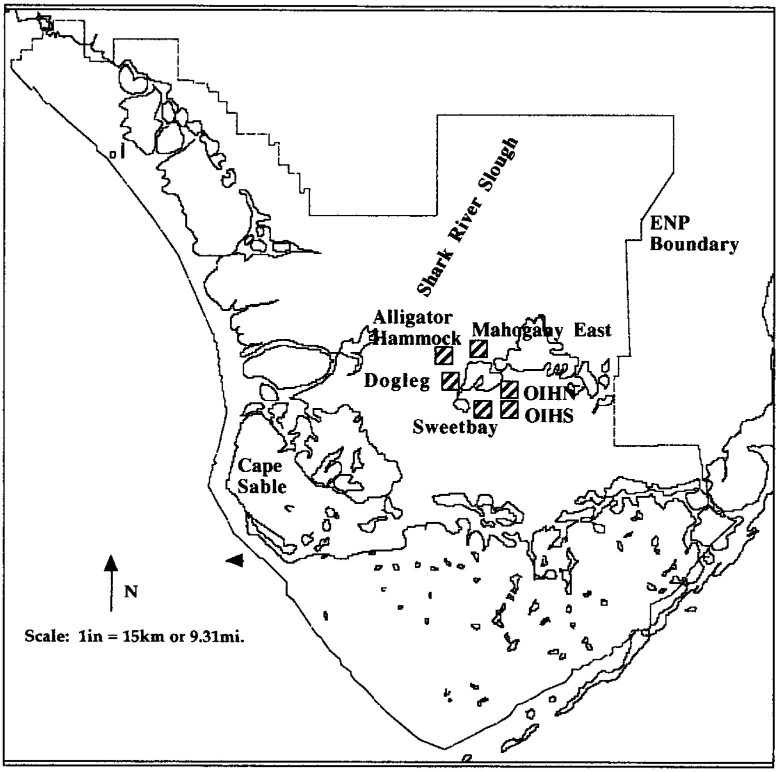

FIG. 1. All study sites were located within eastern Everglades National Park. Each is incorporated within a sub-population of the Cape Sable Seaside Sparrow, southeast of Shark River Slough.

The 1981 surveys indicated that Cape Sable Seaside Sparrows prefer short-hydroperiod freshwater prairies (Bass and Kushlan 1982, Kushlan and Bass 1983). Subsequent, breeding surveys defined two core areas that accounted for over 70% of all individuals (Pimm et al. 1996). One lies east, and the other lies west, of Shark River Slough (Fig. 1). Five areas of lower density and intermittent occupancy adjoin these locations to the east. Since 1993, the western population has declined sharply, while the eastern core population has remained nearly constant (Pimm et al. 1996).

STUDY AREA AND METHODS

We established six study sites (30–60 ha) east of Shark River Slough (Fig. 1). Water inundates all sites from July to December but recedes through most of the sparrows' breeding season (March through June). Muhly grass (*Muhlenbergia filipes*) and sawgrass (*Clad-*

ium jamaicense) dominate the vegetation. Frequent fires and a characteristic hydroperiod maintain the vegetative structure (Kushlan et al. 1982).

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

Observations of morning and late afternoon feedings averaged five hours per nest each week. We photographed adult sparrows holding prey items within 5–10 m of the nest. Comparing these photographs with observer notes corroborated identification of prey. We were unable to classify 25% of the prey items. Most unidentifiable prey items we estimated were less than half the sparrow beak length.

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

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

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

RESULTS

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

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

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

Using the Mayfield method (Mayfield 1975), we calculated a hatching success rate of 88% (N = 14, 28 young from 32 eggs)—a rate common for Seaside Sparrows (Post and Greenlaw 1994). This population laid an average of 3.2 eggs per nest (N = 14, range = 2–4, mode = 3,4). This is consistent with the clutches found by Werner (1975) at Taylor Slough but somewhat smaller than northern populations of Seaside Sparrows (Post et al. 1983, Post and Greenlaw 1994). Each nest, on average, contained three nestlings (range, 2–4, N = 14).

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

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

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

Predation accounted for 78% of all losses of young or eggs. In the first five weeks of the breeding season, a nest succumbed to predators on less

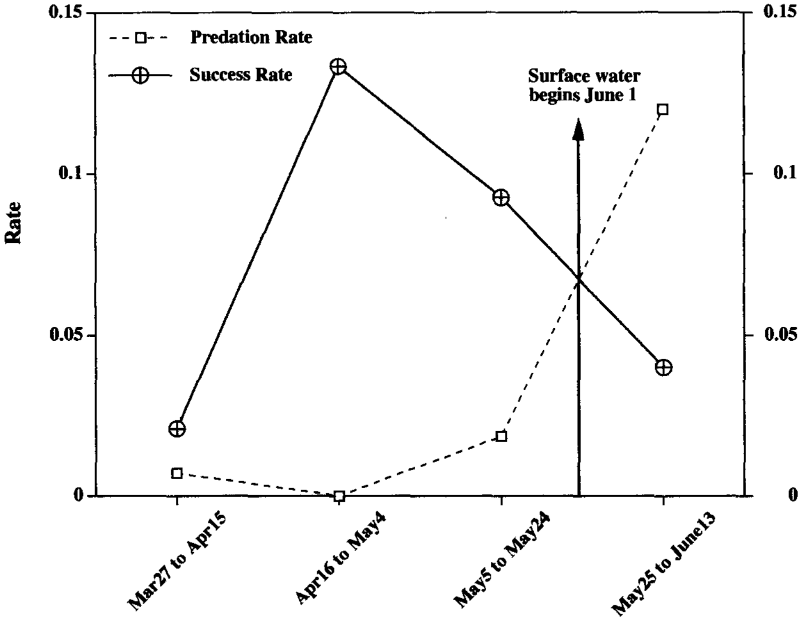

FIG. 2. Predation and success rate for 1996 nests. An increase in nest predation, a decrease in nest success, and the appearance of surface water coincided around June 1, 1996.

than 3% of all the days when eggs or nestlings were present (Fig. 2). Beginning in late May, this rate reached 13%. Thirteen nests were first clutches. Only two of the other six nests (i.e., second and third attempts) successfully fledged young.

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

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

Phenology.—We followed one nest throughout egg laying and incubation. A complete nest found on 22 March did not contain its first egg

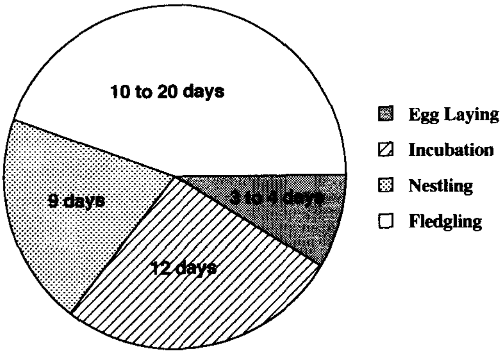

FIG. 3. Cape Sable Seaside Sparrow nest cycle duration encompasses, at the most, 44 days. Thirty-five of those days can be accounted for through previous observations. The remaining 14 are devoted to courtship, nest building, and other activities (e.g., fledgling care, independent feeding).

until 27 March. The female laid the second and last egg on 29 March. She then incubated the eggs for 12 days. This is the first direct observation of Cape Sable Seaside-Sparrow incubation length. An incubation period of 12 days is consistent with other populations of Seaside Sparrows (Post and Greenlaw 1994). It is unclear how common it is for *A. m. mirabilis* females to lay every other day. Post and Greenlaw (1994) indicated that most races of Seaside Sparrows lay one egg per day. Since the average number of eggs laid for this population is 3.2, the number of days devoted to egg laying is likely three or four days.

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

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

Nestling diet.—Six orders of Insecta and one order of Araneida comprised the observed nestling diet. Males brought food to nestlings in 52% and females in 48% of all visits (N = 251). Feedings occurred approximately every 16 minutes (N = 1242) and adults commonly carried more than one insect per trip (average = 1.35; SD = 0.56, N = 260). Since

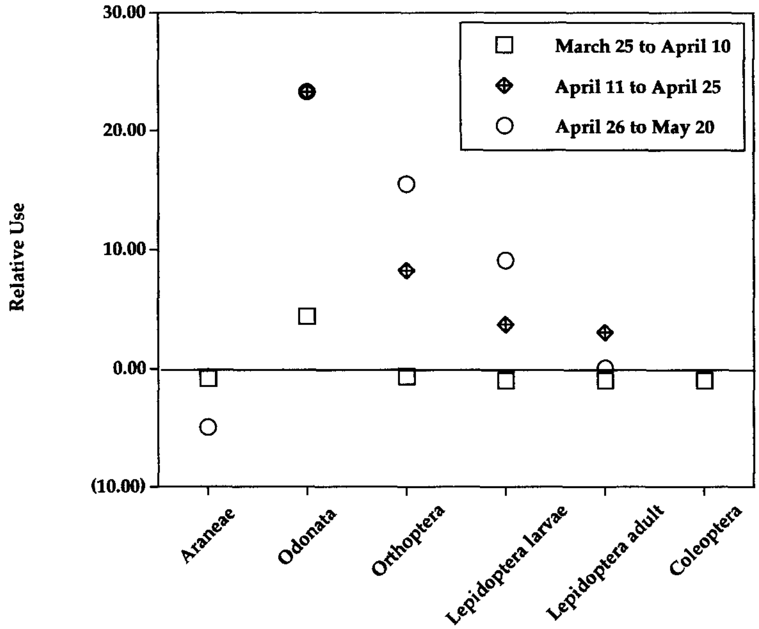

FIG. 4. Relative use of prey items in nestling diet. Availability was based on sweep net samples. Prey use was based on observations made on 1996 nests.

adults often carried only the abdomens of Odonata and Orthoptera, we suspected that they either ate or discarded all other parts before arriving at the nest. Post and Greenlaw (1985) reported that adults of other races presented macerated or mucous-bound food items to nestlings.

Nestling diet included Lepidoptera, Orthoptera, and Odonata to a greater extent than expected by their availability in 1996 (Fig. 4). Conversely, it rarely included Coleoptera and Araneae, despite these orders comprising 88% of the available food items. Relative use of prey items changed over the course of the breeding season. Early in the season (25 March to 10 April), sparrows used only Odonata more frequently than would be expected based on their availability. While disproportionate use of this group persisted to the end of the season, by mid-season (11 April to 25 April) parents also began feeding nestlings Orthoptera and adult Lepidoptera. At the end of the season (26 April to 20 May) the parents switched from Lepidoptera adults to larvae but, continued their disproportionate use of Orthoptera and Odonata.

Nestling diet changed between years ($\chi^2 = 59.1$, df = 4, $P \ll 0.001$, Fig. 5). In 1995, Odonata represented nearly 30% of the nestling diet. In 1996, this number dropped to under 10%. Conversely, Orthoptera ac-

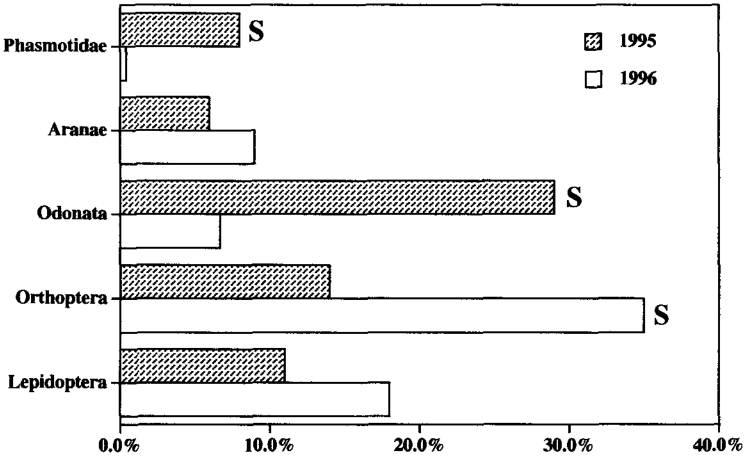

FIG. 5. Composition of nestling diet by insect order. Data collected from first clutch nests in 1995 and 1996. S = significant difference between years.

counted for only 15% of nestling diet in 1995, but exceeded 35% in 1996. Phasmotidae were absent from nestling diets in 1996 but comprised nearly 10% of it in 1995.

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

Seasonal and yearly movements.—Male Cape Sable Seaside Sparrows exhibited a high degree of philopatry—a common trait in all Seaside Sparrow races (Post and Greenlaw 1994). In 1996, three males nested an average of 40 meters away from their 1995 nests. Second clutch nests ranged eight to 95 m from the site of the first clutch nest. Sparrows never reused nests. After nest destruction, we observed males attending a nest within the same territory. Since very few females have been banded, we do not know if the re-nest attempts by these males included the same females as well.

Observations of where *A. m. mirabilis* spends the wet-season (post-breeding) are less detailed. Werner (1975) suggested that rising surface water ended the nesting season but provided no further information. Breeding behavior ceased in two of our study areas when surface water reached the average height of nests above the ground (14 cm). Adults remained within established territories and defended juveniles until surface water appeared. Afterwards, observations of females became rare, and some males disappeared. Those males that remained moved into va-

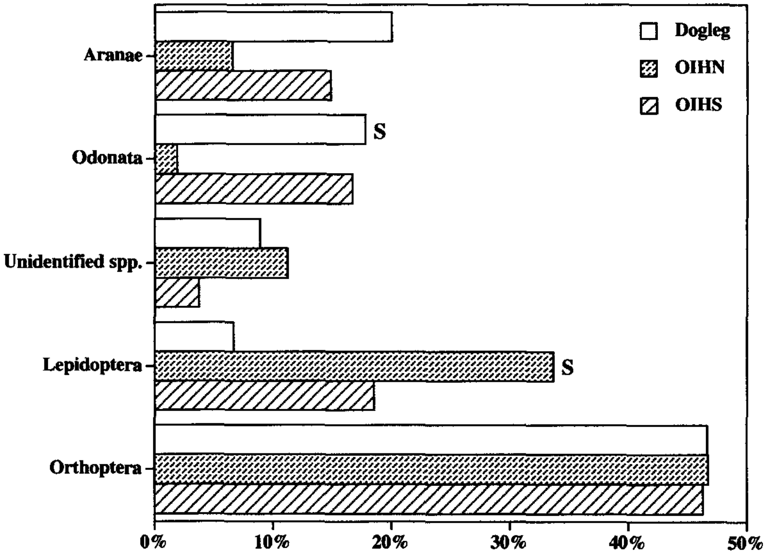

FIG. 6. Between-site differences in composition of nestling diet. S = significant differences between sites.

cant neighboring territories or into taller, denser vegetation. They continued to sing and defend juveniles. Although juveniles tended to associate with a particular male, we observed a group of seven with two banded males outside any nesting territory. Water levels peaked at 18 cm in late June, with a subsequent dry-down occurring in mid-July (down to 4 cm). Breeding activity however, never resumed. We observed sparrows around tree islands and sawgrass sways from late June into July (B. Moody and T. Brooks pers. comm.). Males sang sporadically in open prairies throughout the remainder of the winter.

DISCUSSION

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

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

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

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

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

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

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