

DEMOGRAPHY OF THE CAPE SABLE SEASIDE SPARROW (*AMMODRAMUS*
MIRITAMUS MIRABILIS).

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INTRODUCTION

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

The Cape Sable seaside sparrow lives within the Everglades ecosystem of extreme south Florida (Werner and Woolfenden 1982, Kushlan and Bass 1982). This 'river of grass' is characterized by a slow overland flow of water originating at Lake Okeechobe in the north and terminating into Florida Bay in the south. The primary drainage system of the Everglades is a slough (Shark River Slough Fig.1) flanked by

expanses of marl prairie. Water inundates these prairies when the slough overflows (Curnutt et al. 1998). Under natural conditions, these periods of inundation occur from the onset of summer rains in early June until the beginning of the dry-season in January (Curnutt et al. 1998). During the dry months of February through May, Cape Sable seaside sparrows build their nests low in these marl prairies (Werner 1975, Werner and Woolfenden 1981, Lockwood et al. 1997).

Beginning in the 1940s, a series of canals and spillways built within the Everglades began altering this overland flow of water. Management diverted water from the eastern Everglades to control flooding around the growing urban population of greater Miami (Nott et al. 1998, Fennema et al. 1994). The legacy of these efforts is that flows now drain into the western portion of Shark River Slough leaving the eastern marl prairies in a dry state far longer than under natural conditions. Conversely, the western marl prairies are flooded more often (Curnutt et al. 1998). Nott et al. (1998) provide evidence that these alterations in flow patterns (i.e. hydrology) have contributed to the observed sparrow population declines in the western marl prairies. Further, Curnutt et al. (1998) attribute the declines within extreme eastern Everglades to frequent fires due to over-drying. Our study researched how Cape Sable seaside sparrow demography changes under varying hydrological conditions.

STUDY AREAS

The sparrow's current range lies entirely within federally protected lands in south Florida.

Most individuals live within Everglades National Park (ENP); a small segment live within Big Cypress National Preserve (Kushlan and Bass 1982). The population can be separated into six spatially distinct 'patches' or sub-populations (A – E, Fig. 1). The western (A) and eastern (C, D, and F) sub-populations have experienced large declines in abundance since the first range-wide survey in 1981 (Curnutt et al. 1998).

Sub-population A held half the known population in the 1981 survey (Kushlan and Bass 1982), however this population has suffered greater than 50% declines since 1992 (Curnutt et al. 1998). Sub-populations B and E have remained largely stable in numbers since 1981 (Curnutt et al. 1998). Sub-population B now holds the vast majority of sparrows and is often referred to as the population 'core'.

Most of our study plots established within Everglades National Park were chosen for their accessibility. We have seven study plots within sub-population B. All of these plots lie along the one maintained road (Main Park Road) and the one unmaintained road (Old Ingraham Highway) that pass through portions of the sparrow's range. In 1997 and 1998 we established new study plot within sub-population A and E respectively (Table 1). Daily visits to these plots require overnight stays and helicopter transport. Thus, these plots are visited half as often as the others. The constraint of efficiently gathering

information with the least amount of expense and personal risk prohibited establishment of more study plots within sub-populations C, D, and F.

TABLE 1. CAPE SABLE SEASIDE SPARROW STUDY PLOTS: NAME, SUB-POPULATION, AREA AND YEAR ESTABLISHED.

Study Plot Name	Sub-population	Approximate Area (km ²)	Year Established
Alligator Hammock	B	0.48km ²	1994
Dogleg	B	0.48km ²	1993
Sweetbay	B	0.24km ²	1993
Ingraham North	B	0.48km ²	1993
Ingraham South	B	0.48km ²	1993
North Mahogany	B	0.24km ²	1995
Far East	B	0.48km ²	1997
Shark Valley	A	0.48km ²	1997
East Side	E	3.75km ²	1998

MONITORING METHODS

Each year we search for sparrow nests from mid-March until early-June. In the 1995, 1996, and 1999 seasons we continued searching for nests until August. In the two seasons (1997, 1998) we did not continue past June, a separate radio telemetry project worked from early-June until the following March (Dean and Morrison 1998). We incorporate results from this study where appropriate.

To find nests we use behavioral cues (e.g., adults delivering food or giving defensive calls) and random search-and-flush techniques (Bibby et al. 1992). Nest are checked every second or third day until fledging or failure. On each nest visit, we record

nestlings per nest using ANOVA. If significant differences are found, we use Fisher's protected least square difference (PLSD) to do post-hoc pairwise comparisons between means.

The above information also estimates nesting success according to Mayfield techniques (Mayfield 1975, Johnson 1979). Because adults are banded with a unique combination of color bands (see below), we also follow an individual's multiple nesting attempts. We divided all nests found according to their date of hatching. All nests that have a hatch date before 1 June are termed 'early-season' and all nests that have a hatch date after 1 June are called 'late-season'. The 1 June cut-off is the approximate time of year when the summer rains begin (Olmstead et al. 1980). Such classification allows us to compare Mayfield nest success rates between years as well as before and after the onset of summer rains.

We record all evidence of nest failure, including the presence of standing water in the nest and destroyed eggs or nestlings. We record apparent predation events as the unexplained loss of all nest contents between nest checks (Schaub et al. 1992).

Calculation of predation rate for specific time periods throughout the breeding season are based on these records (Schaub et al. 1992, Lockwood et al. 1997). Predation rate is calculated as the number of predation events divided by the number of nests with eggs or young present. These rates are calculated over 10- to 14-day intervals starting each year from the day that the first nest was found.

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

Because Lockwood et al. (1997) present preliminary evidence of increased predation rates with increases in water level, we test for a similar effect using regression techniques. We use hydrological information from an ENP monitoring station. This hydrological station (P46) is located within ~2km of all sub-population B plots. The P46 water levels function as the independent variable; predation rates calculated for the seven sub-population B plots are assigned as the dependent variable. Each data point represents a particular unit of time encompassing the 1995 to 1999 breeding seasons. We then fit several lines to these data and chose the best fit based on which regression technique produced the highest R^2 value.

We capture and band adult Cape Sable seaside sparrows using mist-nets and play-back recordings of their song (Bibby et al. 1992). Male sparrows are territorial and respond to a tape-recording of their song by flying toward the source (a recorder placed

under the mist net). Females will respond to taped play-back of songs or they can be flushed into a net. Adult sparrows are sexed based on behavior (e.g., only males will sing) or morphologically (e.g., presence of a brood patch or cloacal protuberance). It is possible to distinguish hatch-year (HY) and after-hatch-year (AHY) individuals based on plumage differences (e.g., HY birds have short flight feathers). In 1997 we began banding nestlings on the fifth to seventh day in the nest.

All banded individuals are given a USFWS aluminum band and three celluloid color bands. The combination of color and aluminum bands allows us to indentify individuals throughout the breeding season and in subsequent years. We began searching for previously banded individuals in March of each year, marking the territories of any resighted or recaptured birds with colored surveyors tape. We use resight-recapture information to generate a survivorship estimates for males using the Cormack-Jolly-Seber statistical model from the program MARK (White and Burnham 1997). Finally, we calculate the proportion of individuals that are resighted or recaptured each year and compared these return rate values across years, sub-populations, sexes, and ages.

The locations of banded, recaptured and resighted individuals are recorded in Universal Transverse Mercator (UTM) Easting and Northing coordinates using a Global Positioning System (GPS). The accuracy of the GPS varied from 1 to 20m. Recording the locations of banded individuals each year allows us to calculate breeding dispersal

distances (i.e. the distance breeding individuals move from year to year) and natal dispersal distances (i.e. the distance juveniles move from their place of birth to the next breeding season). Dispersal distances are calculated using the following formula. Given two points X (E_x ; N_x) and Y (E_y ; N_y), where E and N are respectively the Easting and Northing coordinates, then:

$$\text{Distance (X, Y)} = D(X,Y) = \sqrt{(E_x - E_y)^2 + (N_x - N_y)^2}$$

We use Student's t-test to compare dispersal distances between adult and juvenile sparrows.

RESULTS

Fecundity

We found 259 Cape Sable seaside sparrow nests between 1995 and 1999. Ten of these nests were found in sub-population A, 218 in sub-population B, and 31 in sub-population E. Three nests were found in 1995, 19 in 1996, 33 in 1997, 60 in 1998, and 140 in 1999. Most nests (74%) were found from 15 March to 31 May. We found 68 nests in June and July (26%).

Although fecundity has several different definitions (Clobert and Lebreton 1991), there are three measures commonly calculated for birds: the number of nests produced in one breeding season, number of young produced per nest, and number of fledglings

produced per egg laid. Below we describe each measure for the Cape Sable seaside sparrow.

The first fecundity measure is the number of nests produced per breeding season. The average length of the breeding season and the length of one nest cycle (i.e. phenology) influence this value. The earliest Cape Sable seaside sparrow nest was found on 20 March 1997. This nest had two eggs, but was lost to predation seven days later. Werner (1975) reports observing young from a nest initiated in late-February. The latest date we have found the first nest of the season was 17 April 1995. As this was the first year in which we searched for nests, this date likely reflects under-sampling early in the season. In 1999, we found three nests on 10 July with one of these nests eventually fledging young on 26 July. Werner (1975) reports observing nests with eggs as late as 26 July and Dean and Morrison (1998) report catching recently fledged young as late as September. T. Dean reports a nest successfully fledging young as late as 2 August 1998 (T. Dean pers. com.). Thus, Cape Sable seaside sparrows can nest from March until at least early August (122 to 142 days).

The number of clutches produced in one breeding season depends upon how much time individuals devote to pair bonding, nest building, egg laying, incubation, nestling care, and fledgling care. Most of our observations concern egg laying, incubation and the nestling period. We recorded the timing of egg laying at seven nests. Of these, six females laid eggs every day until the clutch was complete. We observed

five nests from initiation of the clutch to hatching. The average incubation period for these nests was 11.5d (± 0.61 d). We observed 24 nests from hatching to fledging. The average nestling period length for these nests was 9.62d (± 0.84 d). We have found one nest that was clearly in the process of being built. This nest was found on 4 April 1996 as a loosely woven grass circle without any discernable sides or bottom. When next visited (18 April 1996) it held three eggs that subsequently hatched on 25 April 1996. Assuming a 12-day incubation period and three-day laying period, this nest first held eggs seven days after its discovery. We have found two nests that appeared complete (i.e. clearly had sides, bottom and cup) but did not contain eggs until five and eight days after discovery. Thus, we estimate that Cape Sable seaside sparrows require 30 to 35 days to build a nest, lay eggs, incubate, and fledge young.

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

How many re-nesting attempts have we actually observed in one breeding season? Of the 259 nests found in our study, 29 were known second clutches, four were known third clutches, and one was a known fourth clutch. The proportion of nests found that are second clutch attempts is consistent across sub-populations. Of the 218 nests found in sub-population B, 24 (11%) are second clutch attempts. Of the 31 nests found in sub-population E, four (13%) are second clutches. Only one out of 10 nests found in sub-population A was a confirmed second clutch (10%). All third and fourth clutch attempts were documented within sub-population B.

The second component of fecundity is the number of young produced in one breeding attempt. Cape Sable seaside sparrows lay an average of 3.24 eggs per nest (± 0.64 , $N = 173$ nests). This average varies by year (ANOVA $F = 2.962$, $df = 4$, $P = 0.0225$). All significant differences in the post-hoc Fisher's PLSD tests are between the 1999 average number of eggs per nest and all other years. We recorded 2.98 eggs per nest in 1999 (± 0.408 , $N = 43$ nests), a value significantly lower than averages in 1997, 1998 and 1995. There was no difference in the number of eggs laid per nest across sub-populations (ANOVA $F = 1.414$, $df = 2$, $P = 0.247$). Cape Sable seaside sparrows average of 2.86 nestlings per nest (± 0.82 , $N = 184$ nests). This also varies according to year (ANOVA $F = 6.476$, $df = 4$, $P = <0.0001$). Again, post-hoc comparisons between years reveals that the number of nestlings per nest decreased in 1999. Nests held an

average of 2.47 nestlings (± 0.78 , $N = 53$ nests) in 1999, a value significantly lower than in 1997, 1998, and 1995. The number of nestlings per nest did not vary according to sub-population (ANOVA $F = 0.212$, $df = 2$, $P = 0.8090$).

Finally, fecundity can be measured as the number of fledglings produced per egg laid, often calculated using the Mayfield method (Mayfield 1975, Johnson 1979).

Mayfield nest success rates varied from year to year (Table 2), but showed an overall value of 0.41. Thus, 41% of all eggs laid from March to early-June will survive to fledging.. When we re-calculate overall Mayfield success rates for early- versus

TABLE 2. MAYFIELD NESTING SUCCESS CALCULATIONS FOR CAPE SABLE SEASIDE SPARROW NESTS FOUND MARCH TO JUNE FROM 1995 TO 1999.

Year	Breeding success (Mayfield 1975)	Incubation success	Incubation 95% conf. interval	Nestling success	Nestling 95% conf. interval	Hatch rate
1995	0.2433	0.2433	0.2095	1.0000	0.0000	1.0000
1996	0.4336	0.6912	0.0422	0.6673	0.0430	0.9400
1997	0.3216	0.3785	0.0565	0.8802	0.0198	0.9655
1998	0.5217	0.9158	0.0145	0.7097	0.0212	0.8026
1999	0.3160	0.7795	0.0235	0.4729	0.0351	0.8571
total	0.4110	0.6832	0.0164	0.6620	0.0144	0.909

late-season nests, we see a large drop from 40% to 13% (Table 3). This decrease is largely due to increased predation pressure. Thirty percent of early nests are lost to predation whereas 67% of late nests are lost.

TABLE 3. EARLY VERSUS LATE SEASON MAYFIELD NESTING SUCCESS RATES.

Time of breeding season	Breeding success (Mayfield 1975)	Incubation success	Incubatio n 95% conf. interval	Nestling success	Nestling 95% conf. interval	Hatch rate
overall--early (n=185)	0.4002	0.6671	0.0174	0.6600	0.0145	0.909
overall-late (n=91)	0.1271	0.2748	0.0327	0.5782	0.0296	0.800

Lockwood et al. (1997) find circumstantial evidence that higher water levels increase the rate at which Cape Sable seaside sparrow nests are lost to predation. To test if the observed temporal variations in predation pressure are due to differences in hydrology, we look for correlations in predation rate and water levels. Using all nests found within sub-population B study plots, we calculated predation rates over 10- and 14-day intervals and compared them to the average water levels at the P46 hydrological monitoring station. Predation rates varied from 0 to 0.118 with an average value of 0.0342 (± 0.038). The average water level at the P46 hydrological station varied from 5.46cm MSL to 53.36cm MSL with an average of 31.8cm MSL (± 13.48 cm). When we plot predation rate within the sub-population B plots against water levels at the P46 station, an exponential regression provides the best fit ($R^2 = 0.459$; Fig. 2). Most of the points in the upper left corner of Fig. 2 (i.e. have high predation rates and water levels) represent time periods occurring after 1 June. This substantiates our assertion that predation pressure increases after the onset of summer rains. However, not all points in

the upper left corner of Fig. 2 are late-season nests. High water levels, no matter when they occur, increase predation pressure within sub-population B study plots.

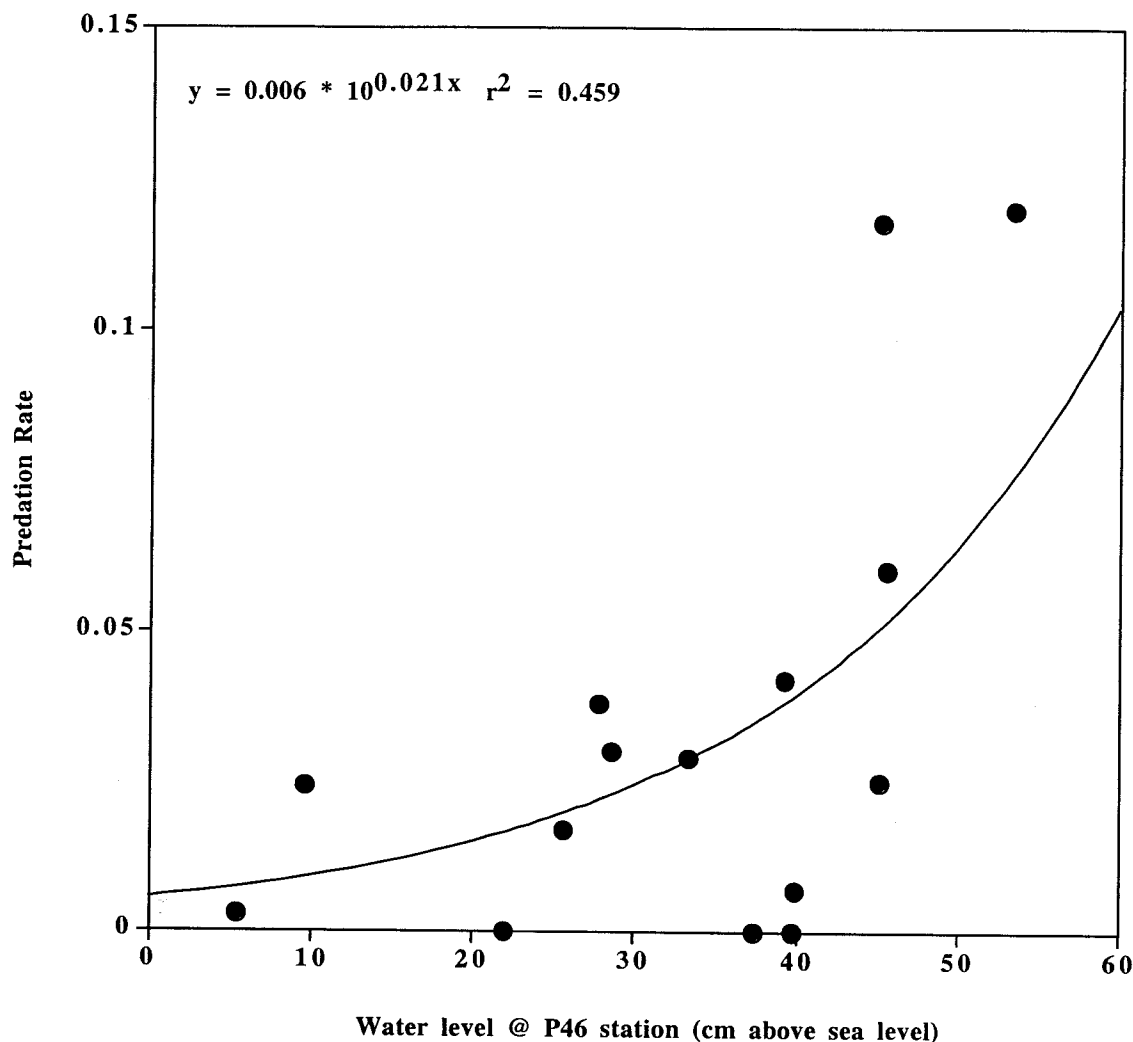


FIGURE 2. PREDATION RATE PLOTTED AGAINST WATER LEVELS AT THE ENP P46 HYDROLOGICAL MONITORING STATION. EACH POINT REPRESENTS EITHER A 10 OR 14 DAY PERIOD DURING THE 1995-99 BREEDING SEASONS. AN EXPONENTIAL REGRESSION PROVIDED THE BEST FIT FOR THESE POINTS.

Comparing Mayfield nest success rates across space, shows that sub-population E has by far the highest success rate at 50% whereas sub-populations A and B have success rates of 17% and 24% respectively (Table 4). Most of the differences in Mayfield nest

success rates between sub-populations is due to differential predation pressure.

Sub-population B shows the highest proportion of nests lost to predation at 44%.

Sub-population A and E have lost 12% and 13% of all nests found to predation respectively. These proportions are significantly different (Fisher's Exact $X^2 = 12.04$, $df = 2$, $P = 0.0024$). Thus, nesting success varies across the spatial extent of the sparrow population largely because of variations in predation pressure.

TABLE 4. MAYFIELD NESTING SUCCESS RATES LISTED BY SUB-POPULATION.

Sub-population	Breeding success (Mayfield 1975)	Incubation success	Incubation 95% conf. interval	Nestling success	Nestling 95% conf. interval	Hatch rate
B	0.2358	0.4293	0.0194	0.6220	0.0144	0.883
E	0.5077	0.8174	0.0331	0.7832	0.0305	0.793
A	0.1744	0.3009	0.1281	0.5795	0.1141	1.000

How high can water levels rise before they are detrimental to Cape Sable seaside sparrow nesting? The answer may depends in part on the prevalence of predators, but it also depends on how high sparrows will build their nests from the ground. The average height that Cape Sable seaside sparrows place their nests from the ground (i.e. from soil surface to bottom of the nest structure) varies through time and, to some extent, through space. The average height that nests sit off the ground within sub-population A is 16cm (± 6 cm, $N = 10$), within sub-population B is 18cm (± 7 cm, $N = 212$), and within sub-population E is 19cm (± 8 cm, $N = 30$). There are no discernable differences

between these values (ANOVA $F = 0.551$, $df = 2$, $P = 0.577$). However, the variance around each of these averages is relatively high (one standard deviation is roughly equal to at least 1/3 of the average). Although we can not detect spatial differences across large scales, on smaller scales the height of nests off the ground is highly variable.

We next pool the nests and look for differences between years and through the breeding season. The average height that a nest sits off the ground increases after the onset of summer rains in early June (Student's $t = -4.34$, $df = 223$, $P < 0.001$). Nests that hatch young before 1 June sit an average of 17cm off the ground (± 7 cm, $N = 160$) whereas nests that hatch young after 1 June sit an average of 21cm off the ground (± 7 cm, $N = 69$). Similarly, the average height that nests are built off the ground varies from year to year (ANOVA $F = 4.8$, $df = 3$, $P = 0.0029$). During the 1996 and 1997 breeding seasons, Cape Sable seaside sparrows built nests lower to the ground (16cm and 15cm respectively) than during the 1998 and 1999 breeding season (20cm and 18cm respectively).

Survival

We have banded 265 adult (AHY) Cape Sable seaside sparrows between 1994 and 1998. The number of AHY individuals banded ranged from 20 to 80 per year. We recaptured or resighted 193 of these 265 individuals in subsequent years. Using program MARK (White and Burnham 1997) we derive survival models for adult males (females have a

different catch rate and thus should be treated separately). A Cormack–Jolly–Seber model that assumes constant survivorship and recapture probability provides the best fit to our data. From this, survival rate is estimated at 0.66 (standard error = 0.06) and recapture is 0.65 (standard error = 0.08). Thus, 66% of all adult males in our sampled population survive between years.

This statistical model efficiently derives survivorship estimates while accounting for the various pitfalls of using mark–recapture information (Brownie et al. 1985, Seber 1986). However, it poorly distinguishing differences in survival rates and recapture rates when sample sizes are low or mark–recapture efforts have been underway for less than four years. This being the state of our data, we can not compare survival models between HY and AHY individuals, between males and females, or between sub–populations.

Return rates, or the proportion of individuals resighted or recaptured from year to year, are also poor estimators of survival rates for a variety of reasons (Begon 1979). Yet, they do allow a glimpse into demographic differences between various groups of individuals within the population (e.g., HY vs. AHY, males vs. females, etc.).

Table 5 provides the proportion of individuals from yearly cohorts that return in subsequent years. From 28% to 48% of AHY individuals return one year after banding; 20% to 37% returned two years post–banding and only 5% returned four years after banding. One individual, resighted for four consecutive years, constitutes our oldest known Cape Sable seaside sparrow.

TABLE 5. RETURN RATE OF BANDED ADULT (AHY) LISTED BY YEAR BANDED.

	Year Banded	Total # of AHY banded	1995 returns	1996 returns	1997 returns	1998 returns	1999 returns
	1994	20	9	4	1	2	1
% returning			45	20	5	10	5
	1995	60		20	22	13	7
% returning				33	37	22	12
	1996	45			13	11	4
% returning					29	24	9
	1997	80				38	25
% returning						48	31
	1998	60					23
% returning							38

We have banded 213 juvenile (HY) sparrows; most in the nest. We can only calculate a return rate for HY individuals up to two years post-banding. Return rates for HY individuals ranges from 15% to 20%; nearly half that of the equivalent return rate of AHY individuals (Table 6).

TABLE 6. RETURN RATES OF YOUNG (HY) BIRDS LISTED ACCORDING TO YEAR BANDED.

	Year banded	# of HY banded	1998 returns	1999 returns
	1997	82	13	11
% returning			16	13
	1998	128		25
% returning				20

If we divide banded individuals according to gender, males and females show similar overall return rates. Males return at a rate between 26% and 52%. Females return

at a rate between 25% and 45% (Table 7). We do not have enough banding information from the various sub-populations for a spatial comparison of return rates.

TABLE 7. MALE VERSUS FEMALE RETURN RATES LISTED BY YEAR BANDED.

	Year Banded	# of males banded	# of females banded	1998 returns		1999 returns	
				male	female	male	female
	1997	58	22	30	8	15	10
% returning				52	36	26	45
	1998	44	16			19	4
% returning						43	25

Return rates can give rough estimates of survival if adjusted for known pitfalls in utilizing resight-recapture methods. For example, every year a proportion of banded individuals survive but are not observed by our field crew. Some of these individuals will be resighted or recaptured in subsequent years. If we assume these 'missed' birds were alive in years they were not re-sighted, return rates increase to 55% one year post-banding (Table 8). Return rates remain high (between 25% and 45%) two years post-banding, but quickly drop back to levels similar to unadjusted return rates for individuals returning three and four years post-banding.

A second adjustment involves eliminating individuals banded in areas not carefully monitored in subsequent years. If we re-calculate return rates only within areas visited consistently from 1994 to 1998, return rates reach 62% for individuals returning after one year post-banding and 50% two years postbanding (Table 9). Return rates

remain relatively high for individuals returning three years after banding (maximum of 32%), but then drop after four years post-banding.

TABLE 8. RETURN RATE OF ADULT (AHY) BIRDS ADJUSTED ASSUMING THAT INDIVIDUALS 'MISSED' IN SOME YEARS WERE ACTUALLY ALIVE IN THOSE YEARS.

	Year banded	# of AHY banded	1995 returns	1996 returns	1997 returns	1998 returns	1999 returns
	1994	20	10	5	2	2	1
% returning			50	25	10	10	5
	1995	60		33	27	19	7
% returning				55	45	32	12
	1996	45			19	14	4
% returning					42	31	9
	1997	80				38	25
% returning						48	31
	1998	60					23
% returning							38

TABLE 9. RETURN RATES OF ADULTS (AHY) BANDED ONLY WITHIN INTENSIVELY SEARCHED AREAS.

	Year banded	# of AHY banded	1995 returns	1996 returns	1997 returns	1998 returns	1999 returns
	1994	20	10	5	2	2	1
% returning			50	25	10	10	5
	1995	60		33	27	19	7
% returning				55	45	32	12
	1996	45			16	13	3
% returning					62	50	12
	1997	80				32	22
% returning						46	31
	1998	60					21
% returning							41

Dispersal

By following banded individuals from one breeding season to the next, we can calculate breeding dispersal distances for adult (AHY) individuals. Adult Cape Sable seaside sparrows will defend a territory an average of 212m ($\pm$ 131m, N = 30) from the location of a territory established within two previous years. The distribution of these dispersal distances is leptokurtotic with most individuals moving less than 300m (Fig. 3). Dispersal distances increase over longer time intervals. Banded adults return an average of 957m from the location of their territory three years prior.

Because we limit the spatial extent of our re-sight efforts, we are not likely to detect dispersal movements over medium to long distances. Dean and Morrison (1998) utilized radio-transmitters to document Cape Sable seaside sparrow movements over the non-breeding season. They report individuals maintaining a home range of 13ha and a rate of travel of 6.4m/hr. Non-breeding season dispersal distributions were leptokurtotic with most individuals moving 100m to 150m, and all but two individuals moving less than 370m, between consecutive sightings. Dean and Morrison (1998) recorded longer range movements, sometimes up to 7km, however these movements were rare and most of these individuals returned to their breeding territories by the end of the non-breeding season (Dean and Morrison 1998). We have never resighted or recaptured a banded individual from one sub-population within another. Collectively, these observations

indicate that adult Cape Sable seaside sparrows are quite sedentary throughout the year and thus adult immigration and emigration rates are low.

Natal dispersal is defined as the distance a HY individual will move from their place of hatching to the site in which they settle during their first breeding season. [These sites may or may not be breeding territories.] Individuals banded as nestlings were resighted or recaptured an average of 577 ($\pm 98\text{m}$, $N = 15$) from their place of hatching (Fig. 3). This value is significantly different than that observed for equivalent time frames in adults (i.e. one and two year movements; $t = -4.729$, $df = 42$, $P < 0.0001$). In contrast to the distribution of AHY dispersal distances (left-skewed), HY birds move longer average distances thus producing a more even distribution of dispersal distances (Fig. 3). We have not collected information on HY individuals over enough years to calculate longer interval movements.

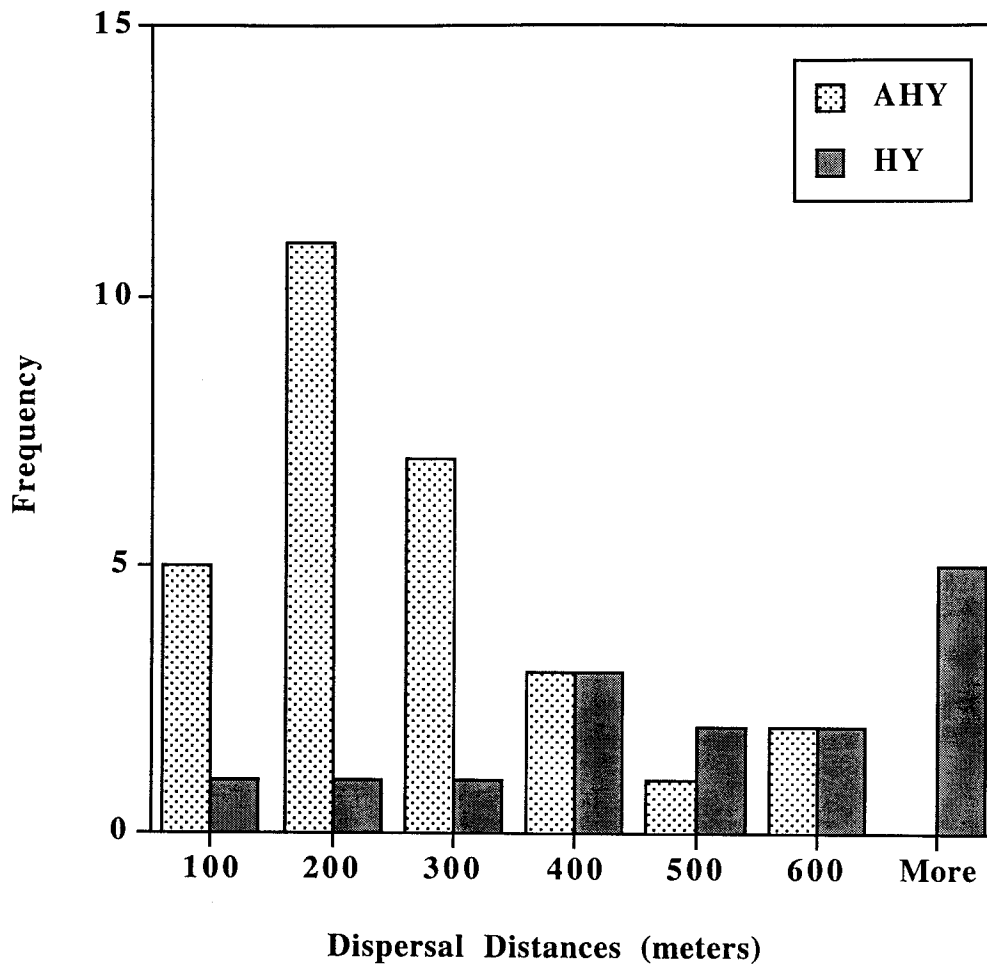


FIGURE 3. DISPERSAL DISTANCES FOR JUVENILE (HY) AND ADULT (AHY) CAPE SABLE SEASIDE SPARROWS.

DISCUSSION

Cape Sable seaside sparrows are highly sedentary and extremely faithful to particular breeding locations. The individuals occupying various sub-populations rarely move between them. These traits make the Cape Sable seaside sparrow extremely dependent on the marl prairies they inhabit. One individual is not likely to stray outside a 1 to 2km

area within its approximately three to four year lifespan (Dean and Morrison 1998 and here). This small expanse of marl prairie must provide a year-long food supply, sufficient cover from predators, and appropriate nesting habitat.

Cape Sable seaside sparrows are unlikely to live past three years of age; at least 40% of the population dying each year. These survival estimates are typical of small land birds (Ricklefs 1973, Perrins and Birkhead 1983). Observed return rates of 40% to 50% in the first two years post-banding are consistent with other races of seaside sparrows (Post and Greenlaw 1994). Juveniles are much less likely to return from year to year. This is also typical of land birds (Ricklefs 1973). Typically low survivorship in this first year of life (Sullivan 1989, Ricklefs 1973) plus the tendency of young sparrows to disperse over longer distances influence these low juvenile (HY) return rates. Since juveniles fly longer distances, it is this segment of the population that probably accounts for movements between sub-populations.

Cape Sable seaside sparrow fecundity reaches its maximum potential early in the breeding season (March to June). Because sparrows only produce 2 to 3 young per nesting attempt, these early-season nest successes just replace breeding adults but do not increase the population. Successful late-season nesting attempts are critical for the recovery of this sub-species. This is especially true in years, such as 1999, when early-season per nest fecundity levels were significantly lower than normal.

Unlike other races of seaside sparrows, Cape Sable seaside sparrows exist within a non-tidal ecosystem and thus nesting success is not influenced by tidal flooding events (Post and Greenlaw 1994, Marshall and Reinert 1990). Whereas unusually high tides cause mass loss of active nests in these other races, (Marshall and Reinert 1990) hydrological influences on nesting success come from annual variations in the summer rains and management decisions regarding water releases into Everglades National Park.

Cape Sable seaside sparrows place their nests near the ground making them extremely vulnerable to high water events. However, the height of nests from the ground varies through the breeding season, from year to year, and across small spatial scales. This variation renders inexact predictions concerning what water levels will cause mass loss of active nests. However, we can make general predictions. The highest recorded average height of nests off the ground is 21cm (late-season nest average). If we add one standard deviation to this value, we can estimate that at locations where water levels rise above 29cm, 95% of all active Cape Sable seaside sparrow nests will flood and fail. Water management decisions that reflect this fundamental aspect of Cape Sable seaside sparrow biology will increase the probability that this sub-species will recover.

Predation pressure is also influenced by hydrological patterns. The higher the water level the higher the probability that a sparrow nest will be lost to predation. Most nest losses in our study we attribute to snakes because the nest structure is undisturbed. (The other assumed predator, the rat, often leaves feces and dishevel the nests a bit.)

Some evidence implicates the cottonmouth (*Agkistrodon piscivorus*) in predation events. These snakes are common in sub-population B study plots. One incubating nest was checked and found empty with a 3cm diameter hole on each side. Another nest was found empty with a cottonmouth underneath it. T. Dean reports finding a cottonmouth with an adult radio-collared sparrow in its stomach (T. Dean pers. com). If cottonmouths are the principle predators of sparrow nests, this may explain the correlation between high water levels and predation rate. Cottonmouths bask in the sun during the day, but are most active at night especially after heavy rain (Behler and King 1988).

Predation of nests is a natural event, especially for a ground-nesting species that constructs an open-cup nest such as the Cape Sable seaside sparrow (Martin and Li 1992, Bosque and Bosque 1995). Further, the implicated predator is native to the Everglades and has likely co-evolved with the sparrow. It is not clear what management action could be taken to reduce predation pressure on late-season nests. The correlation between high water and predation has only been documented for sub-population B nests. Other sub-populations, in particular sub-population E, may not suffer from predators in the same manner. Continued study of these more remote sub-populations and on the identity of nest predators may provide insights into the role of predator control in recovery plans.

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