

# Endangered Cape Sable Seaside Sparrow Survival

REBECCA L. BOULTON,<sup>1</sup> *Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, NJ 08901, USA*

JULIE L. LOCKWOOD, *Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, NJ 08901, USA*

MICHELLE J. DAVIS, *Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, NJ 08901, USA*

ARTUR PEDZIWLK, *Nicholas School of the Environment, Duke University, Durham, NC 27708, USA*

KELLY A. BOADWAY, *Nicholas School of the Environment, Duke University, Durham, NC 27708, USA*

JOSHUA J. T. BOADWAY, *Nicholas School of the Environment, Duke University, Durham, NC 27708, USA*

DAVID OKINES, *Nicholas School of the Environment, Duke University, Durham, NC 27708, USA*

STUART L. PIMM, *Nicholas School of the Environment, Duke University, Durham, NC 27708, USA*

**ABSTRACT** We investigated survival for male, female, and first-year Cape Sable seaside sparrows (*Ammodramus maritimus mirabilis*, hereafter sparrows), a federally endangered bird restricted to the Florida Everglades, USA. Accurate estimates of survival are critical to improve management decisions and population estimates for this and other threatened species. We used Program MARK to evaluate effects of age, sex, population membership, temporal variation, and ground-water levels on annual survival from mark-recapture data collected across 3 sparrow populations from 1997 to 2007. We found little evidence that annual survival rates differed between the populations or across ground-water levels, but we found high variability between years for both adult and juvenile survival. Our results revealed female sparrows experienced 14–19% lower survival than males. Sparrows experienced much lower survival during their first year of life and were short-lived (2–3 yr). Our results highlight sparrows' susceptibility to population declines and suggest that management actions aimed at increasing survival may be effective for this species' management. (JOURNAL OF WILDLIFE MANAGEMENT 73(4):530–537; 2009)

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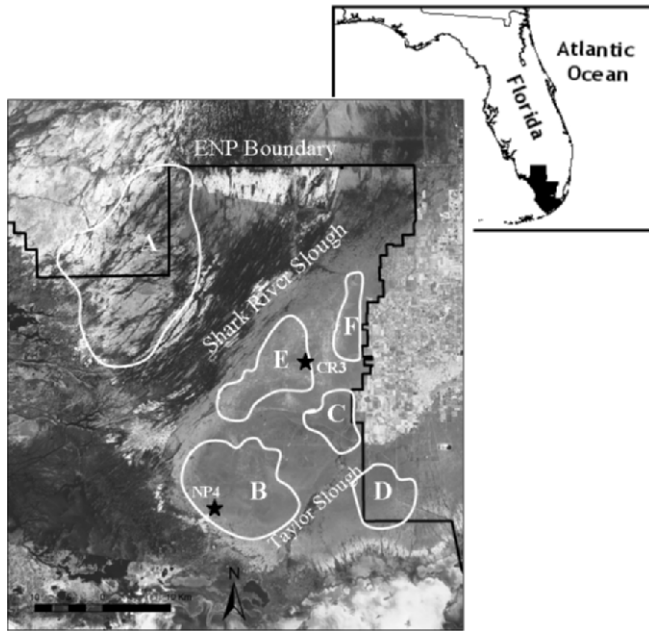
Florida's Everglades (USA), a freshwater marsh stretching from Lake Okeechobee south toward Florida Bay and the Gulf of Mexico, is a wetland of global importance (Davis and Ogden 1994). Historically, seasonal floods would cause the area to be inundated by shallow, slow-moving water stretching up to 90 km wide. Seasonal flooding creates a spectrum of hydroperiods (annual period of water inundation) responsible for the diverse vegetation communities of the Everglades. The construction of levees, canals, and pumping stations have altered Everglades' water flows leading the United States government to list nearly 40 species native to the ecosystem as endangered or threatened (Nott et al. 1998, Armentano et al. 2006). Restoration of water flows to pre-drainage conditions, while maintaining ecological processes and viable populations of all native species, has become a major focus of Everglades' management (South Florida Ecosystem Restoration Task Force 2000).

Bordering Shark River Slough, the main drainage system for the southern Everglades, is a complex mosaic of wet prairie, sawgrass (*Cladium mariscus jamaicense*), tree islands, and tropical hammock communities. Water management practices have directly influenced southern freshwater prairies surrounding Shark River Slough and, consequently, available habitat for the federally endangered Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*, hereafter sparrow), which is restricted to these prairies. Reduced water flows through the eastern Slough have shortened hydroperiods, increasing drought and fire severity in the eastern

sparrow habitat, while unseasonable pulses of water to the west extended hydroperiods and reversed natural drying patterns in the western sparrow habitat (Pimm et al. 2002, Davis et al. 2005). One measure of Everglades restoration success is a viable population of Cape Sable seaside sparrows, and thus the fate of this subspecies has become an indicator to evaluate success of alternative restoration options (DeAngelis et al. 1998, Curnutt et al. 2000, Fuller et al. 2008).

During restoration implementation, it is important for managers to understand which of the sparrow's demographic parameters are more likely to respond to restoration efforts and contribute significantly to the populations' growth. Simple demographic models in the past have considered nest success and duration of the sparrow's breeding season as two of the most important demographic parameters (Lockwood et al. 2001). Recent modeling suggests factors increasing mortality of both adult and juvenile sparrows may also pose an extinction risk (Elder and Nott 2007). However, reliability of this and any related model (e.g., Fuller et al. 2008) is largely determined by the accuracy and variance estimate of the demographic parameters they utilize (Ludwig 1999). Until now, there has been insufficient data to permit robust analyses of sparrow survival estimates, particularly with respect to the possible impact of water levels, sex, and age. Our research objectives were to 1) determine whether survival varied between populations, varied by age or sex class, 2) examine annual variation in adult and juvenile survival, 3) examine the degree to which nonbreeding and breeding-season water levels influence annual survival rates, and 4) demonstrate the value of long-

<sup>1</sup> E-mail: [rlboulton@gmail.com](mailto:rlboulton@gmail.com)



**Figure 1.** Map of extant Cape Sable seaside sparrow populations (A–F) and water-monitoring stations (denoted by stars) used to collect water-level data from 1997 to 2007, Everglades National Park (ENP), Florida, USA.

term research to understand survival of Cape Sable seaside sparrows.

## STUDY AREA

We conducted our research within the boundaries of Everglades National Park and Big Cypress National Preserve (USA), the places that hold almost all the Cape Sable seaside sparrows (Pimm et al. 2002). We established study plots in 3 of the 6 extant sparrow populations: 6 0.5-km<sup>2</sup> plots within population B, 1 0.5-km<sup>2</sup> plot in population A, and 1 2-km<sup>2</sup> plot within population E (Fig. 1). Cape Sable seaside sparrow populations are restricted to the short-hydroperiod (<7 months standing water) freshwater marl prairies, dominated by muhly grass (*Muhlenbergia capillaris filipes*), sawgrass, beak rushes (*Rhynchospora* spp.), and Florida little bluestem (*Schizachyrium rhizomatum*) in the southern Everglades ecosystem (Pimm et al. 2002). The region was semitropical, with a hot, humid wet season (Jun–Oct) and a mild dry season (Nov–May). Average rainfall ranged from 160 cm to 185 cm and fell mainly during the wet season as intense thunderstorms and severe tropical storms (Miami weather station 2000–2006; Everglades National Park Everdata 2007).

We established 6 plots from 1993 to 1994 in the central population B, east of southeastern Shark River Slough. This population was relatively stable, holding the largest distribution and highest sparrow density (Cassey et al. 2007). We also situated plots outside population B in 2 smaller, peripheral populations that experienced different hydrologic flows. In 1997, we established one plot in population A, which was the only sparrow population west of Shark River Slough. This plot was by far the wettest due to the diversion of water into this area that once flowed

eastward into northeastern Shark River Slough (Davis et al. 2005). We also established a plot in population E during 1998, east of mid-Shark River Slough, in an area that experienced shorter hydroperiods than population A. Intensive monitoring of this plot did not occur until 2002, when a fire burned the southern section of the plot and it became part of a long-term demography study (La Puma et al. 2007). Both populations A and E were isolated and required helicopter access. For further detail of the plots see Pimm et al. (2002).

## METHODS

### Capture, Marking, and Monitoring

We searched for Cape Sable seaside sparrows across the study plots during each breeding season (Apr–Jun). Throughout the breeding season, a team of 2–4 people searched within each study plot, using playback calls of male territory song to catch sparrows opportunistically in mist nets (single 6–12 m). We marked each sparrow with a unique color band combination plus an individually numbered United States Fish and Wildlife Service aluminum band. We determined sex of each breeding adult either by presence of a brood patch for females, a large cloacal protuberance for males, or the bird's behavior prior to capture (only M sing). It is not possible to reliably age adult sparrows based on plumage; thus, we aged sparrows as adults (after hatch yr, >1 yr old) or juveniles. Although we refer to juveniles in the analyses below, we banded most of these individuals as nestlings (96% nestlings, 4% fledglings). At each plot, we resighted color-marked individuals during visits to capture unbanded sparrows. We also systematically resighted sparrows throughout the breeding season using a spotting-scope.

Although we made every effort to capture females, we captured no females until the 1996 breeding season. We supplemented the above procedure by capturing females in close proximity to their active nests. Implementation of this capture method began in 1997 when intensive nest searching commenced in population B. Using sparrow behavioral cues (i.e., nestling feeding, aggressive chipping), 2–4 people systematically searched all territories across the plots every 2–4 weeks from April to early July to locate nests. Nest-searching activity occurred from 1997 to 2001 in the 6 plots within population B and from 2002 to 2007 in population E. We visited nests every 2–3 days (and on the day of fledging) to confirm whether the nest successfully fledged or failed (Baiser et al. 2008). We individually color-banded all nestlings surviving until 4–6 days after hatching. We removed from the data set all individuals banded in nests known to have failed.

### Survival Analysis

We estimated apparent survival ( $\Phi$ ) and recapture probabilities ( $p$ ) using the standard Cormack–Jolly–Seber (CJS) model in Program MARK 5.1 (White and Burnham 1999). We constructed all models using a logit-link function. Data for each analysis consisted of capture histories obtained from the 3-month breeding season of each year, pooled into one

capture occasion per individual. We examined effects of population membership, sex, and age on annual survival and recapture estimates, in which we modeled each covariate as a group effect and year as the time-dependent variation in the data.

Many environmental variables can cause temporal variation in survival estimates and only long-term data sets allow examination of this variation. Attempting to understand the cause of temporal variation in survival estimates is essential, particularly for endangered species when trying to mediate species recovery. We evaluated the effect of ground-water levels, the central component of the Everglades ecosystem, on annual sparrow survival. We obtained water-level data from United States Geological Survey water-monitoring station NP46 situated close to population B study plots (Fig. 1). We used water-level data from NP46 for 3 reasons: 1) we marked no sparrows in E early in the sampling period, 2) >73% of marked sparrows were located within B, and 3) water levels at NP46 reflected variation at CR3 the closest water station to population E (Pearson's correlation  $n = 10$ : nonbreeding season  $r = 0.841$ ,  $P = 0.002$ ; breeding season  $r = 0.863$ ,  $P = 0.001$ ). We divided each year into 2 periods, the nonbreeding season (1 Aug–14 Mar;  $\text{Water}_{\text{NBS}}$ ) and breeding season (15 Mar–31 Jul;  $\text{Water}_{\text{BS}}$ ). We calculated water levels across these periods using the daily average water level (m) above and below ground level (ground level set to zero). We chose these 2 water covariates because they represent 2 behavioral periods in the sparrow's life-cycle and biologically we anticipated that stress associated with variation in water levels at either time could affect adult survival. Although our recapture period took place throughout the breeding season we used water levels from this period because stressful conditions (e.g., flooding or drought) incurred during breeding may influence future survival (Visser and Lessells 2001, Hanssen et al. 2005). We only considered the effect of these water-level covariates on survival parameters, because we had no reason to expect water levels would affect recapture rates.

We assessed goodness-of-fit of global models using the bootstrap procedure in Program MARK ( $n = 500$  replicates). The global model was the most parameterized, not necessarily the fully saturated model. Simulated results provided an estimate of the over-dispersion parameter ( $\hat{c}$ ), which we calculated as the observed model  $\hat{c}$  of the original data divided by the mean simulated  $\hat{c}$ .

We used this variance inflation factor to correct for over-dispersion, if detected. We fit a time-since-marking model to our most general model (ad data only) to test for the presence of transient individuals, that is, birds who are marked and released and then who permanently emigrate from the population and, thus, cannot be resighted (Pradel et al. 1997). Based on these analyses, we found no evidence of transience in our data and do not present these results here. Our annual samples were not instantaneous, because our sampling periods extended over several months. O'Brien et al. (2005) illustrated that violating this assumption by increasing recapture periods actually increased precision in

survival estimates and that bias is minimal if survival is relatively constant throughout the recapture period and if recapture rates are  $>0.2$ . Based on detailed nest monitoring, we have no evidence that within-breeding-season survival of sparrows is low and our recapture rate was  $>0.4$  (see below). However, we present an analysis using both 1-month and 3-month recapture duration to test whether survival estimates were biased by recapture duration.

We based model selection on a quasi Akaike's Information Criterion ( $\text{QAIC}_c$ ), corrected for small sample sizes and over-dispersion using the  $\hat{c}$  adjustment from our bootstrap simulations (Burnham and Anderson 2002). We used Akaike weights and the difference ( $\Delta\text{QAIC}_c$ ) between  $\text{QAIC}_c$  for each model and that for the model with the smallest  $\text{QAIC}_c$  from the set of candidate models when examining the relative support for each model. By definition, the best-fit model has a  $\Delta\text{QAIC}_c$  value of zero, but we considered other models if  $\Delta\text{QAIC}_c \leq 2$ .

### Data Sets and Candidate Models

The overall Cape Sable seaside sparrow project had research objectives and study sites that changed somewhat across the years. Therefore, to adequately examine the effect of sex, population membership, age, and annual variation on survival we used different subsets of our mark-recapture data. To achieve a standardized capture effort we used data from 1997, because throughout the earlier years of the project (1994–1996) we were still establishing methodologies and study sites.

To establish if it was reasonable to pool across the 2 larger populations (B and E) we examined population-specific survival for adult males from 2002 to 2007, resulting in 6 sampling occasions. Using the design matrix tool in MARK, we investigated whether survival varied with population or year (time;  $t$ ) and recapture probability with population membership. We estimated overall survival for population A to allow comparison between small and large sparrow populations. We had few data from population A, which only allowed us to run a constant survival and recapture model. For estimating survival in population A, we used all available data (i.e., both ad M and F from 1997 to 2007) resulting in 11 sampling occasions.

There was no evidence that sparrow survival rates differed between populations B and E (see below). Therefore, we pooled all adult sparrows of known sex from these populations to examine sex and annual variation in survival and recapture probabilities, using data from 1997 to 2007 (11 sampling occasions). To evaluate whether water levels explained any observed variation in temporal survival probabilities we fit linear water-level covariates to survival parameters.

We estimated survival probability for all sparrows captured and marked for the first time as nestlings or fledglings. Juvenile survival included probability that a banded sparrow nestling survived the remaining 4–6 days in the nest, that fledged individuals survived the 8–20-day period when they were still dependant on adults for food and predator protection, and that independent juveniles survived to their



**Table 1.** Models used in Program MARK to determine effect of population membership on apparent survival and recapture probabilities of adult male Cape Sable seaside sparrows from populations B and E (2002–2007), Everglades National Park, Florida, USA. Only the top 5 mark–recapture models are shown.

Model no.	Model structure <sup>b</sup>	Model statistic <sup>a</sup>				
		Qdev	K	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	w <sub>i</sub>
1	Φ (t) <i>p</i> (group)	63.92	7	560.62	0.00	0.74
2	Φ (c) <i>p</i> (group)	75.87	3	564.32	3.70	0.12
3 (global)	Φ (t + group + group × t) <i>p</i> (group)	57.53	12	564.80	4.18	0.09
4	Φ (group) <i>p</i> (group)	75.72	4	566.21	5.59	0.05
5	Φ (t) <i>p</i> (c)	78.93	6	573.55	12.93	<0.01

<sup>a</sup> Model statistics: deviance (Qdev), no. of parameters (*K*), quasi Akaike's Information Criterion (QAIC<sub>c</sub>), difference in QAIC<sub>c</sub> (ΔQAIC<sub>c</sub>), and QAIC<sub>c</sub> wt (*w<sub>i</sub>*).

<sup>b</sup> Model structure: Φ = probability of apparent survival; *p* = probability of recapture; group = sparrow population B and population E; t = time; c = constant.

first breeding season. We used banding and resight information from populations B and E 1998–2007, thus resulting in 10 sampling occasions. We built 2 age-class models that allowed a juvenile age-class to span one sampling occasion after capture (first-yr survival) and one adult age-class. We compared these age models with the standard CJS models with no age effects.

## RESULTS

Using adult sparrows from population E (2002–2007), we found that bias in survival estimates did not increase with recapture period duration. Between 67% and 82% of all individual resights occurred in the first 1-month recapture period. With a 1-month recapture period, overall survival estimates were 0.60 (95% CI = 0.52–0.68). Using a 3-month recapture period, we estimated overall survival to be 0.59 (95% CI = 0.52–0.66). As predicted, recapture estimates were lower with a 1-month recapture period (0.67, 95% CI = 0.54–0.78) compared with the 3-month recapture period (0.90, 95% CI = 0.79–0.96).

### Populations and Survival

We obtained 421 captures and resights, representing 239 individuals within populations B and E (146 from population B and 93 from E; resight individuals = 60 from population B and 56 from E). The global model Φ (group × t) *p* (group) fit the data well (goodness-of-fit: *P* = 0.39). We found little evidence of over-dispersion but used the  $\hat{c}$  adjustment of 1.08 in our analysis to make parameter estimates as robust and valid as possible. The best model was one that included time-dependence in survival and a difference in recapture rates between the 2 populations (Table 1). Apparent survival estimates (95% CI) using this model varied across years: 2002 = 0.75 (0.58–0.87); 2003 = 0.60 (0.45–0.74); 2004 = 0.69 (0.55–0.81); 2005 = 0.44 (0.33–0.56); and 2006 = 0.66 (0.49–0.79). Probability of recapture was 0.91 (95% CI = 0.78–0.97) for population E and 0.60 (95% CI = 0.48–0.72) for population B. The higher recapture probability for population E during this

**Table 2.** Models used in Program MARK to examine effect of water levels and annual variation on apparent survival and recapture probabilities of adult Cape Sable seaside sparrows from populations B and E (1997–2007), Everglades National Park, Florida, USA. Only the top 5 mark–recapture models are shown with the global model.

Model no.	Model structure <sup>b</sup>	Model statistic <sup>a</sup>				
		Qdev	K	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	w <sub>i</sub>
1	Φ (Water <sub>NBS</sub> + sex + Water <sub>NBS</sub> × sex) <i>p</i> (c)	255.51	5	1,492.00	0.00	0.34
2	Φ (Water <sub>NBS</sub> + sex + Water <sub>NBS</sub> × sex) <i>p</i> (sex)	254.84	6	1,493.36	1.36	0.17
3	Φ (t + sex) <i>p</i> (c)	242.86	12	1,493.63	1.63	0.15
4	Φ (t + sex) <i>p</i> (sex)	241.18	13	1,494.02	2.02	0.13
5	Φ (Water <sub>NBS</sub> + sex) <i>p</i> (c)	261.38	4	1,495.85	3.85	0.05
Global	Φ (t + sex + t × sex) <i>p</i> (sex)	227.09	22	1,498.68	6.68	0.01

<sup>a</sup> Model statistics: deviance (Qdev), no. of parameters (*K*), quasi Akaike's Information Criterion (QAIC<sub>c</sub>), difference in QAIC<sub>c</sub> (ΔQAIC<sub>c</sub>), and QAIC<sub>c</sub> wt (*w<sub>i</sub>*).

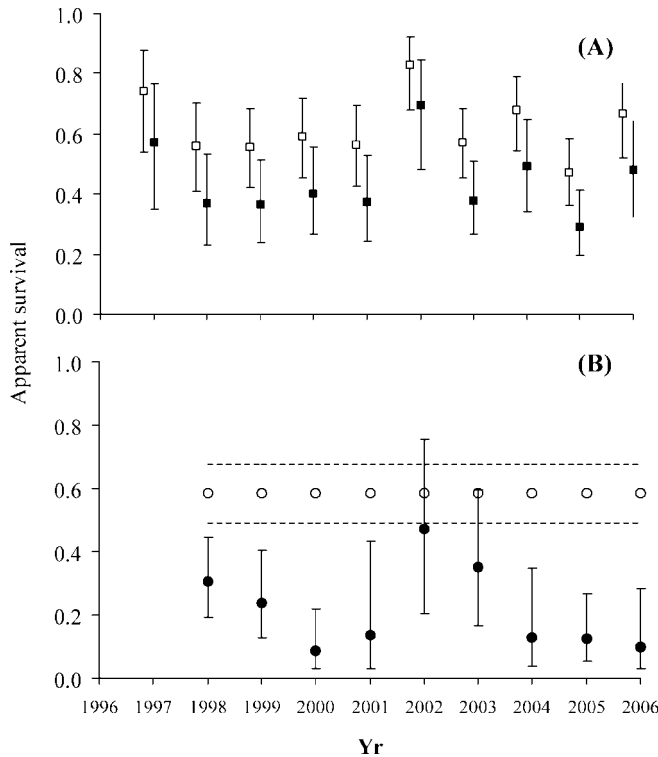
<sup>b</sup> Model structure: Φ = probability of apparent survival; *p* = probability of recapture; t = time; c = constant; sex = M or F; Water<sub>NBS</sub> = average ground-water level (m) during the nonbreeding season.

period may be explained by a greater investment in nest monitoring extending the recapture period in this population.

We obtained 81 captures and resights, representing 52 individuals in population A. The constant model Φ (c) *p* (c) fit the data well (goodness-of-fit: *P* = 0.66) and we found no evidence of over-dispersion ( $\hat{c}$  = 0.99). Population A experienced an overall survival rate of 0.56 (95% CI = 0.41–0.70) and recapture rate of 0.54 (95% CI = 0.32–0.74).

### Sex and Survival

We obtained 947 captures and resights, representing 550 adults (389 M and 161 F; resight individuals = 200 M and 51 F) across populations E and B. The global model Φ (sex × t) *p* (sex) fit the data well (goodness-of-fit: *P* = 0.41) and over-dispersion of the data was minimal ( $\hat{c}$  adjustment = 1.09). The best model from our candidate set for survival included the covariate nonbreeding-season water levels and the interaction of nonbreeding-season water levels with sparrow sex (Table 2). However, we interpret these results with caution because the 95% confidence interval for Water<sub>NBS</sub> overlapped zero (−3.80–13.26) and the 2 models without the nonbreeding-season water covariate were within approximately 2 ΔQAIC<sub>c</sub> units of the best model (Table 2). In other words, models that included a water covariate failed to improve fit to the data any more than a model including annual variation in survival. In addition, nonbreeding-season water levels had a positive effect on female survival but a negative effect for males (intercept β = −0.89, Water<sub>NBS</sub> β = 4.73, sex β = 2.38, Water<sub>NBS</sub> × sex β = −12.68). Male (range Φ = 0.47–0.83) and female (range Φ = 0.29–0.69) survival estimates varied considerably across the sampling period, with females recording 14–19% lower survival than males (Fig. 2A). There were negligible differences in recaptures rates between males (*p* = 0.65,



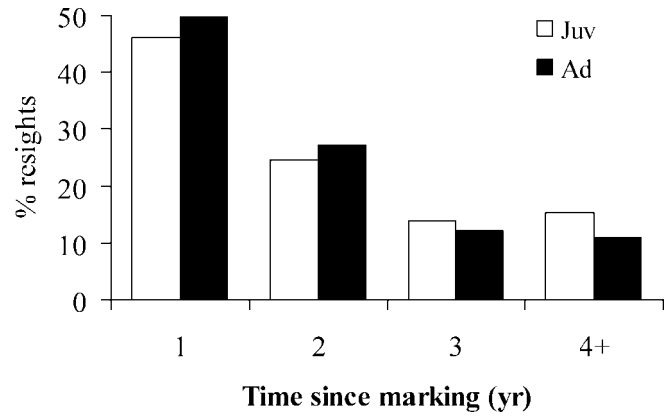
**Figure 2.** Annual variation in apparent survival rates ( $\bar{x} \pm 95\%$  CI) for Cape Sable seaside sparrows marked as (A) adult males ( $\square$ ) and females ( $\blacksquare$ ) from populations B and E, Florida, USA, 1997–2007; we derived annual survival estimates from model  $\Phi(t + \text{sex})p(c)$  (Table 2) and (B) juvenile ( $\bullet$ ) and adults ( $\circ$ ) marked as juveniles from populations B and E, 1998–2007; we derived annual survival estimates from the model  $\Phi(a2 - t/c)p(c)$  (Table 3).

95% CI = 0.58–0.71; Model 2, Table 2) and females ( $p = 0.58$ , 95% CI = 0.42–0.73).

### Age and Survival

We obtained 598 captures and resights using marked juveniles only, representing 498 individuals (resight individuals = 27 F, 28 M, and 10 unknown sex) within populations B and E. Raw data for these return rates showed that only 13% of juveniles returned to the study sites and were resighted at least once, after >12 months since marking. In comparison, we resighted 45% of the 494 adults banded in populations B and E during 1998–2007 at least once since marking. Using only known-aged birds, (i.e., banded as juv) we saw a maximum age of 8 years for males and 4 years for females. We saw most resighted sparrows in the first or second year since marking (Fig. 3).

The global model  $\Phi(a2 - t/t)p(a2 - c/c)$  provided an adequate fit to the data (goodness-of-fit:  $P = 0.36$ ) and there was only slight over-dispersion ( $\hat{c}$  adjustment = 1.07). Due to data sparseness, we constrained recapture rates to be constant. There was obvious age-structure in the survival estimates with models that pooled survival for juveniles, and their subsequent transition into adults received little support ( $\Delta\text{QAIC}_c > 21$ ). The 2 best models ( $\Delta\text{QAIC}_c < 0.05$ ; Table 3) both revealed annual variation in juvenile first-year survival with considerably higher after-first-year survival (ad >1 yr old;  $\Phi_{ad} = 0.58$ , 95% CI = 0.49–0.68; see Fig. 2B).



**Figure 3.** Percentage of resighted individuals (juv  $n = 65$ ; ad  $n = 221$ ) seen alive (max. time since marking) in Cape Sable seaside sparrow populations B and E during the period 1998–2007, Florida, USA. We resighted most (>70%) individuals (both juv and ad) in the first 2 years since marking.

The worst survival for juveniles was in 2000, with a survival estimate of just 0.09 (95% CI = 0.03–0.22), whereas the best survival was in 2002, with a survival of 0.47 (95% CI = 0.21–0.76; see Fig. 2B). Models 1 and 2 indicate equivocal support for age-structuring in the recapture estimates. Model 1 does not include age-structure ( $p = 0.47$ , 95% CI = 0.35–0.58), whereas Model 2 supports slightly higher recapture rates for juveniles ( $p_{juv} = 0.54$ , 95% CI = 0.38–0.70) compared to adults ( $p_{ad} = 0.40$ , 95% CI = 0.27–0.54). Although we had few resights for this data set we attempted to model the water covariate  $\text{Water}_{\text{NBS}}$  for the 2 best models; however, these models provided little support for explaining annual variation in survival estimates ( $\Delta\text{QAIC}_c > 3.5$ ). We did not include the covariate  $\text{Water}_{\text{BS}}$  because we banded most juveniles late in the breeding season.

**Table 3.** Models used in Program MARK to determine age-specific effects on apparent survival and recapture probabilities of Cape Sable seaside sparrows marked as juveniles from populations B and E (1998–2007), Everglades National Park, Florida, USA. Only the top 5 mark-recapture models are shown with the global model.

Model no.	Model structure <sup>b</sup>	Model statistic <sup>a</sup>				
		Qdev	K	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	w <sub>i</sub>
1	$\Phi(a2 - t/c)p(c)$	106.78	11	620.13	0.00	0.42
2	$\Phi(a2 - t/c)p(a2 - c/c)$	104.74	12	620.18	0.04	0.41
3	$\Phi(a2 - c/c)p(c)$	126.28	3	623.21	3.08	0.09
4	$\Phi(a2 - c/c)p(a2 - c/c)$	124.87	4	623.83	3.70	0.07
5	$\Phi(a2 - t/t)p(c)$	100.90	18	628.99	8.86	0.01
Global	$\Phi(a2 - t/t)p(a2 - c/c)$	99.79	19	630.01	9.88	<0.01

<sup>a</sup> Model statistics: deviance (Qdev), no. of parameters (K), quasi Akaike's Information Criterion (QAIC<sub>c</sub>), difference in QAIC<sub>c</sub> (ΔQAIC<sub>c</sub>), and QAIC<sub>c</sub> wt (w<sub>i</sub>).

<sup>b</sup> Model structure:  $\Phi$  = probability of apparent survival; t = time; c = constant; p = probability of recapture; a2 = indicates a 2 age-class model structure, with one juv age-class spanning 1 yr and one ad age-class (i.e.,  $\Phi(a2 - t/c)$  specifies time-varying  $\Phi$  for a juv age-class and constant  $\Phi$  for ad age-class).

## DISCUSSION

Compared to other demographic parameters, survival is often difficult to estimate due to cryptic behavior and difficulties in marking and monitoring individuals (Murray and Patterson 2006). Inaccessibility and the secretive nature of Cape Sable seaside sparrows previously produced survival estimates based on small sample sizes and largely anecdotal interpretation of data (88% survival, Werner 1975; 90% survival, Kushlan et al. 1982). Our long-term data set and robust analysis expands on the simple male survival analysis presented by Lockwood et al. (2001; 1994–1998  $\Phi$  0.66  $\pm$  SE 0.06). We accurately estimated annual adult survival and increased knowledge concerning sex, age, and population survival; all are important components of the sparrow's life-history.

Our estimate of annual adult survival rates fall within the range recorded for other Emberizid sparrows (Karr et al. 1990, Perkins and Vickery 2001, Sandercock and Jaramillo 2002, Morrison et al. 2004). Indeed, Sandercock and Jaramillo (2002) found moderate annual survival rates (0.35–0.56) within Emberizidae species regardless of their ecology. Because many sparrow species are monomorphic during winter capture periods, both sexes are often lumped during analyses (Sandercock and Jaramillo 2002, Thatcher et al. 2006). By capturing our sparrows in the breeding season we could reliably sex adults and ascertain lower survival rates for female sparrows. Although authors allude to the possibility of lower survival for female sparrows and its possible implication for population growth, all models to date have used one adult survival parameter (Lockwood et al. 2001, Pimm et al. 2002, Elder and Nott 2007). Differential mortality between sexes can cause skewed adult sex ratios, a pattern more prevalent in globally threatened species and small, isolated populations (Dale 2001, Donald 2007). Highly skewed adult sex ratios increases a species' risk of extinction, a process observed during the extinction of the dusky seaside sparrow (*Ammodramus maritimus nigrescens*; Delany et al. 1981). Nonbreeding male sparrows occur in larger populations during the breeding season but not in large numbers (Dean and Morrison 1998); however, recent evidence suggests lower female survival may have greater impacts in smaller sparrow populations, because we frequently observe a large proportion of unmated males (R. L. Boulton, Rutgers University, personal communication). High recapture rates, for both male and female sparrows, reflect high site fidelity and nonmigratory behavior of Cape Sable seaside sparrows (Dean and Morrison 1998, Lockwood et al. 2001). Males during the breeding season sing from sawgrass tops, making males easier to resight than females, which are more elusive. The sparrows' cryptic behavior during the nonbreeding season makes them impossible to detect, restricting our resight period to a few months during breeding.

Juvenile survival is typically hard to measure in the field, and the Cape Sable seaside sparrow is no exception. We banded young sparrows while they were still in the nest and we rarely observed them during their fledgling period or

even as independent juveniles within their banding year. We provided our best estimate for survival of young sparrows but acknowledge that this survival rate is likely to be an underestimate of true juvenile survival. Moderate levels of natal dispersal will lower apparent juvenile survival if young birds permanently emigrate from the study area. We have limited data on sparrow dispersal but radiotagged juveniles moved on average 577 m from natal territories (Dean and Morrison 1998). In addition, examination of the resighting data set reveals 8 between-population movements of which only 3 involved juvenile birds. Our apparent juvenile survival was variable (range = 0.09–0.47) but overlapped with the estimate of 11.4% recorded for the closely related saltmarsh sharp-tailed sparrow (*Ammodramus caudacutus*, hatching to second yr; DiQuinzio et al. 2001), and Ricklefs (1973) estimated that average juvenile survival for resident temperate passerines is approximately 25% of adult survival. Our analysis is the first to attempt survival estimates for juvenile Cape Sable seaside sparrows and provides managers with a more appropriate estimate instead of using surrogate studies or arbitrary estimates when constructing management decisions.

Water levels can quickly rise in the Everglades, particularly in the wet season when one thunderstorm can produce 10–30 cm of rain in a 24-hour period. Water flows and levels throughout the Everglades are somewhat mediated by management actions that divert water through the extensive canal systems, but we still observed >20-cm increases in water levels within 24-hour periods across all of our study plots. Extremely variable water levels and the complexity of the Everglades water flow make it difficult to assign water-level parameters to annual sparrow survival and potentially limited our inability to detect strong influences on survival. In addition, we monitored most sparrows in our study in populations that are somewhat protected from extreme water fluctuations. Unfortunately, low sparrow densities in all small peripheral populations, which all experience more extreme ends of Everglades water fluctuations relative to the larger populations we monitored (A, C, D, and F; Fig. 1), means we cannot conduct rigorous survival analysis for these populations. Although we provide an overall survival estimate for population A, we were unable to examine water-level covariates with so few individuals detected each year. However, there is no clear evidence that sparrow survival in the wetter population A was any lower than sparrow survival in drier populations B and E.

Long-term sparrow surveys show the species' decline between 1981 and 1996, after 1996 sparrow numbers and occupancy remained relatively constant (Casey et al. 2007). During the last 11 years, while occupancy remained constant, we observed highly variable survival, which possibly helps explain the lack of recovery during this period. Post et al. (1983) regarded Cape Sable seaside sparrow population declines as paradoxical in light of their high reproductive potential and high survival rate. Our results help resolve this paradox, demonstrating why the sparrows' variable survival and short lifespan make it



susceptible to population declines but not quick to recover. For example, high breeding-season water levels like those experienced in population A from 1993 to 1996 would have allowed little annual recruitment (Nott et al. 1998). Water levels recorded in this habitat were high enough to have likely drowned most active nests or prohibited sparrows from nesting altogether. Our estimates of low juvenile and female survival and an average life span of only 2–3 years provide support that extreme environmental factors (natural or otherwise; e.g., high water levels, fire, or severe hurricanes) that cause sharp declines in sparrow numbers will be slow to reverse.

## MANAGEMENT IMPLICATIONS

High variability in annual survival of both adult and juvenile Cape Sable seaside sparrows we observed suggests that this vital rate may respond positively (or negatively) to management activities. With the expected construction of Comprehensive Everglades Restoration Projects (1999) set to commence within the next 5 years there is an enormous opportunity to closely monitor the sparrow's survival response to these adaptive management actions. Although we did not reveal strong relationships between water levels and survival we recommend that water managers attempt to mediate unnaturally high water levels in sparrow habitat due to the species' susceptibility to extended unsuitable conditions. We suggest that future research focus on identifying probable causes of high juvenile and female mortality and attempt to better identify sources of variation in survival to help guide management recommendations.

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