

## FLOODING AND PREDATION: TRADE-OFFS IN THE NESTING ECOLOGY OF TIDAL-MARSH SPARROWS

RUSSELL GREENBERG, CHRISTOPHER ELPHICK, J. CULLY NORDBY, CARINA GJERDRUM, HILDIE SPAUTZ, GREGORY SHRIVER, BARBARA SCHMELING, BRIAN OLSEN, PETER MARRA, NADAV NUR, AND MAIKEN WINTER

*Abstract.* Tidal-marsh vertebrates experience two distinct challenges to successful reproduction: inundation of the soil with water, which is variable and often unpredictable, and the simple vegetative structure, which offers few safe havens from predation. We review both published and unpublished studies of tidal-marsh birds and their relatives to determine if overall nest success is lower and if predation and flooding are higher than in non-tidal-marsh relatives. In addition, we examine information on clutch size, breeding season, and nest location for differences between tidal and non-tidal taxa. Overall, we find little support for the idea that the additive effects of flood- and predation-loss leave tidal-marsh sparrows with a net high nest loss rate compared to ecologically comparable sparrows. In part, the two sources of mortality are negatively correlated and hence, at least partly compensatory. Flooding is an important cause of mortality in some populations, notably those along the north Atlantic Coast and south San Francisco Bay. However, in general, predation is the most important source of mortality in tidal-marsh populations. The importance of predation may be masked in populations that also suffer high rates of flood-related nest loss. Within tidal-marsh sparrows, clutch size is lower at sites with higher predation rates. The effect of other sources of mortality and latitude disappear when the variables are entered in a step-wise regression. If predation does effect variation in clutch size in tidal-marsh species, it probably is a result of the effect lower brood size has on nest conspicuousness rather than a bet-hedging strategy against high nest loss. Overall, clutch size is relatively low in tidal-marsh forms, although these comparisons are often confounded by other variables, such as latitude, altitude, or continentality of climate. Nesting seasons tend to be longer in tidal-marsh birds. However, few studies have quantified annual nest success and, hence, partitioned the role of clutch size versus season length in determining between population variation in overall reproductive success.

*Key Words:* *Ammodramus*, avian life history, *Melospiza*, nest predation, nest success, saltmarsh.

## INUNDACIÓN Y DEPREDACIÓN: INTERCAMBIOS EN LA ECOLOGÍA DE ANIDACIÓN DE GORRIONES DE MARISMA DE MAREA

*Resumen.* Los vertebrados de marisma de marea experimentan dos retos distintos para reproducirse exitosamente: inundación del suelo con agua, el cual es variable y a menudo impredecible, y la estructura vegetativa simple, la cual ofrece pocos refugios seguros para la depredación. Revisamos estudios tanto publicados como no publicados de aves de marisma de marea y sus parientes, con el fin de determinar si la totalidad del éxito de nidos es menor si la depredación y la inundación son mas altas que en los parientes que no son de marisma de marea. Además, examinamos información del tamaño de la nidada, época de apareamiento, y localización de nidos para las diferencias entre taxa de marea y de no marea. Sobre todo, encontramos poco respaldo para la idea de que efectos aditivos de pérdida de inundación- y depredación- dejan a los gorriones de marisma de marea con un grado de pérdida de nido neto alto, comparado a gorriones ecológicamente comparables. En parte, las dos fuentes de mortandad están negativamente correlacionadas y por ello, al menos parcialmente compensatoria. Las inundaciones son una causa de mortandad importante en algunas poblaciones, notablemente en aquellas a lo largo de la costa noratlántica y en al sur la Bahía de San Francisco. Sin embargo, en general, la depredación es la fuente más importante de mortandad en poblaciones de marisma de marea. La importancia de la depredación quizás se encuentre enmascarada en poblaciones que también sufren altos grados de pérdida de los nidos relacionada a inundaciones. Dentro de los gorriones de marisma de marea, el tamaño de la nidada es mas baja en sitios con mayores grados de depredación. El efecto de otras fuentes de mortandad y latitud desaparecen cuando las variables son ingresadas en regresión de paso acertado. Si es que la depredación afecta la variación en el tamaño de la nidada en especies de marisma de marea, probablemente sea el resultado del efecto que el tamaño menor de cría tiene sobre lo evidente que es el nido, en vez de una estrategia de apuesta-protectiva en contraste a una alta pérdida de nido. Sobre todo, el tamaño de la nidada es relativamente baja en formas de marisma de marea, a pesar que estas comparaciones son confundidas a menudo por otras variables, tales como latitud, altitud, o continentalidad del clima. Las épocas de anidación tienden a ser mas largas en aves de marisma de marea. Sin embargo, pocos estudios han cuantificado éxitos anuales de nidos, y por ello, han dividido el rol del tamaño de la nidada contra la longitud de la época por determinar entre la variación de la población en el éxito reproductivo total.

Tidal marshes are characterized by simple vegetative structure and both regular and irregular inundation with surface water, which can at least occasionally cover most or all vegetation. In this habitat, any vertebrate that relies upon nests for successful reproduction is faced with two sources of nest failure, thereby forcing adaptive compromises in nest structure, placement, and the timing of reproduction. First, placing the nest on or close to the substrate will increase the probability of flooding. Second, placing the nest higher in the vegetation will reduce the cover to hide the nest from potential predators. Flooding is also a problem for birds nesting in non-tidal wetlands. However, with the exception of storm-caused flooding, in most cases water levels remain relatively stable over the time scales required for completing a successful nest attempt. Tidal-marsh species face a generally more variable and often less predictable maximum water level (Reinert, *this volume*). This lack of predictability may force birds to place nests higher than would be optimal in the short-term to minimize the chance of episodic catastrophic flooding.

The clearest indication that adjustments are made in nesting behavior in response to tidal-marsh conditions is the nearly universal tendency for the nests to be higher in the vegetation than those of their non-tidal-marsh relatives, which are either facultative or obligatory ground nesters. According to Johnston (1956a), all tidal-marsh Song Sparrow (*Melospiza melodia*) nests are elevated off the ground and attached to marsh vegetation. Arcese et al. (2002), on the other hand, reports that most Song Sparrow nests are on the ground. Nice (1937) found a tendency in Ohio for early season Song Sparrow nests to be placed on the ground, in fact, over two-thirds of first and second attempts were ground nests. Coastal Plain Swamp Sparrow (*Melospiza georgiana nigrescens*) nests average 30 cm above the ground ( $SD = 6$  cm; Nest height measurements were from ground to top of nest cup in all studies listed.) and no ground nests have been reported in >400 nests located (B. Olsen, unpubl. data). In contrast, non-tidal-marsh Swamp Sparrow (*M. g. georgiana*) nests are frequently placed on the ground; 30% of nests were so located in Rhode Island (Ellis 1980) and western Maryland (B. Olsen, unpubl. data). The third *Melospiza* species, Lincoln's Sparrow (*M. lincolnii*), characteristically nests on the ground in boggy vegetation (Ammon 1995).

The tendency to place nests at a more elevated site also characterizes tidal-marsh *Ammodramus* and related genera. Seaside Sparrow (*Ammodramus maritima*) nests are elevated, on the average, between 14–28 cm

above the substrate (varying between population studied; Post and Greenlaw 1994); Salt-marsh Sharp-tailed Sparrow (*Ammodramus caudicatus*) nests are also elevated, ranging from 1–25 cm above the substrate (Greenlaw and Rising 1994; C. Elphick, unpubl. data) with a mean of 12 cm estimated from a population in Connecticut (C. Elphick, unpubl. data). In contrast to the Seaside and Saltmarsh Sharp-tailed sparrows, both of which are found only in tidal marshes, grassland breeding *Ammodramus*, (including the LeConte's Sparrow [*A. lecontei*], probable sister taxa to the tidal-marsh species) nest almost entirely on the ground (M. Winter, unpubl. data; Vickery 1996, Lowther 1996, Green et al. 2002). Furthermore, Savannah Sparrows (*Passerculus sandwichensis*) characteristically nest on the ground (Wheelwright and Rising 1993), but Belding's Savannah Sparrow (*P. s. beldingi*), a subspecies restricted to saltmarshes, usually builds nests that are elevated a few centimeters (Davis et al. 1984; A. Powell, pers. comm.).

The consistent elevation of the nest to avoid flooding compared to non-tidal-marsh relatives probably increases vulnerability of nests to predation if tidal marshes follow the general pattern of relatively high success for nests located on the ground compared with other strata (Martin 1993). The potential impact of two major sources of nest mortality with the seemingly mutually exclusive counter strategies of raising and lowering nest heights would seem a good area to examine the role of adaptive compromise in tidal-marsh sparrow life history. Furthermore, understanding how these forces shape nesting strategies is essential to predicting the effects of changes in predation pressure, hydrology, and sea level on the population of endemic birds. However, although the effects of flooding and predation on reproductive success and have been addressed in studies of individual species, no overview of the nesting biology of tidal-marsh birds has been published. In this paper we provide such an overview of information from published and unpublished studies to examine the following hypotheses: (1) nest success is generally lower in tidal-marsh taxa than in comparable upland or freshwater marsh taxa, (2) predation, particularly from aerial predators is high because the potential of flooding, forces birds to build nests in higher strata where the nests are more vulnerable to predation (Martin 1993), and (3) the frequency of flooding events causing nest mortality will be higher than for sparrow populations in grassland, or even freshwater marsh. In addition, we will examine differences in reproductive parameters, such as breeding season and clutch size that also might be shaped by the tidal-marsh environment.

## METHODS

## STUDIES USED

This paper is based on analyses of data from 16 studies of individual populations of salt-marsh sparrows. The sample sizes of nests for nest-success calculations range from 18–1,616 per study and total 5,154 nests. Sample sizes for clutch-size estimates range from 18–1,086 and total 3,713 clutches. All studies were multi-year, averaging 3 yr in duration. Some of the studies are summarized in published articles or unpublished dissertations, but we also incorporated data from several unpublished studies by authors of this paper. Published studies include Johnston (1956b) on Song Sparrows; Greenberg and Droege (1990) on Coastal Plain Swamp Sparrow; Post and Greenlaw (1982), DeRagon (1988), and Shriver (2002) on Saltmarsh Sharp-tailed Sparrows; and Post et al. (1983) and Post and Greenlaw (1982) on Seaside Sparrow. DiQuinzio et al. (2001) presented multi-year data on nest success in Saltmarsh Sharp-tailed Sparrows, but because this project was explicitly focused on the effects of a change in marsh management (opening the marsh to a more natural tidal regime), we did not use those data. Comparative studies of non-tidal-marsh relatives include Reinert (1979) and Ellis (1980) on Swamp Sparrows in Rhode Island peat bogs. Data were also obtained from less comprehensive studies cited in *Birds of North America* (Poole 2006).

Unpublished data (six–eight seasons) for Song Sparrows were provided by Point Reyes Bird Observatory (PRBO) from three sites in San Pablo and two in Suisun Bay, and an additional three sites for south San Francisco Bay by J. C. Nordby and A. N. Cohen (two seasons). In addition, R. F. Johnston provided his original data sheets for three seasons of his Song Sparrow study (Johnston 1956b) which allowed us to calculate and use Mayfield exposure estimates (Mayfield 1961, 1975) instead of relying upon originally published crude nest-survival values. For non-tidal-marsh Song Sparrow populations, unpublished data on nest success and clutch size for a 23-yr study at Palomarin Ranch, Marin County, California, were made available by PRBO, as were 2 yr of data on clutch size and nest success from the Consumnes River in the Central Valley south of Sacramento, California. Information about nesting Belding's Savannah Sparrows was provided by J. Williams and A. Powell. Data on Swamp Sparrows in Woodland Beach, Delaware and vicinity, and (for an interior population) Garrett County in extreme western Maryland by B. Olsen. Unpublished

data on Seaside and Saltmarsh Sharp-tailed sparrows were provided by B. Schmeling and P. Marra for the Blackwater Wildlife Refuge in Maryland, and by C. Gjerdrum and C. Elphick for Coastal Connecticut. Unpublished data on the LeConte's Sparrow, the putative sister taxa to Seaside and Sharp-tailed sparrows, were provided by M. Winter.

## PARAMETERS

We assembled 16 population studies of tidal-marsh sparrows that present data on several key attributes of reproduction: percentage total nest failure, percentage of failure due to predation, flooding, abandonment and other causes, brood parasitism, and length of the nesting season. We then used linear regression and ANCOVA (Statsoft, Inc. 2003) to explore the relationship between clutch size, nest success, failure cause, and location variables (tidal amplitude and latitude). In almost all cases, overall nest success is determined by a modified Mayfield method to correct for differences in the period of nest exposure after detection by researchers. For one study (B. Schmeling and P. Marra, unpubl. data) program MARK (White and Burnham 1999) was used, which provides daily nest-survival estimate similar to the Mayfield method. For the two studies for which only uncorrected nest success was available (DeRagon 1988, Marshall and Reinert 1990), we used the predicted value of corrected nest success based on the overall regression between Mayfield values and uncorrected values for the remaining 14 studies (by the formula:  $\text{Mayfield loss} = 28.5 + 0.69 \times \text{uncorrected loss}$ ;  $r^2 = 0.60$ ,  $P = 0.0006$ ). Overall nest failure due to flooding, predation, and abandonment was determined by calculating the proportions of total losses for each of these causes and multiplying these by the total Mayfield loss. Clutch size and standard error of clutch size were either previously reported or calculated for each study population. Breeding-season length is measured as the number of days between initiation of the first and last clutch in a population without any attempt to weight by seasonal distribution of efforts (Ricklefs and Bloom 1977). Nest parasitism rates are presented as the proportion of nests with at least one Brown-headed Cowbird (*Molothrus ater*) egg or nestling. For each site, we determined its latitude and, based on 2003 tide tables (National Oceanic and Atmospheric Administration 2004a, b), the mean and maximum tidal range. The latter two parameters were highly correlated, so we conducted all analyses using mean tidal range.

## RESULTS

## MELOSPIZA SPARROWS

## Nest success

Tidal-marsh populations of Song Sparrows had higher nest failure rates than interior population (see Table 1 for values for individual studies). The mean nest failure rates were 90, 81, and 85% for the Suisun, San Pablo, and south San Francisco Bay subspecies, respectively, compared to 73% at Palomarin and 75% at Consumnes River. However, we estimated a failure rate of only 48% for the population of the San Pablo Song Sparrow (*Melospiza melodia samuelis*) studied by Johnston (1956b) in the San Pablo Marsh in Richmond, California 1952–1955. His study site is not one sampled in the more recent studies, but the considerably higher success (mostly due to much lower predation rates) provides the tantalizing possibility that nest success has declined in the 50 yr between the studies.

Coastal Plain Swamp Sparrows also had a relatively high nest failures rate compared to non-tidal populations of Swamp Sparrows. The coastal populations averaged 81% over 3 yr and five sites (R. Greenberg and B. Olsen, unpubl. data) compared to 63% for the Rhode Island (Ellis 1980) and 53% in western Maryland (B. Olsen, unpubl. data) for the interior populations.

## Causes of failure

Nest predation was almost the exclusive reason for nest failure in Song Sparrows at Palomarin accounting for 97% of nest failures. This translates to an absolute predation rate of 71%, which is comparable to the predation rates for the tidal-marsh populations, averaging 75.6, 56.6, and 35.7% for the Suisun, San Pablo, and south San Francisco Bay sites, respectively. Failure due to flooding effected 1.7, 9.2, and 29.4% of the nests in the three embayments. Johnston (1956b) found a comparable rate of nest flooding (10.5%) for San Pablo Bay, but much lower predation rates (19.5%) than any of the recently monitored populations.

Between-year variation in predation rates was relatively much lower than that for flood loss. The mean coefficient of variation (CV) for six populations with four or more years of data was 0.21 for predation (0.19–0.36) and 1.27 for flooding (0.53–3.0) and the CVs for predation and flooding are significantly different (Wilcoxon signed rank test;  $Z = 2.2$ ,  $P = 0.03$ ). Analyzing each population and season as a separate observation, failure rates were strongly

negatively related to predation rates ( $r^2 = 0.71$ ) and unrelated to flood loss ( $r^2 = 0.05$ ). In this analysis, failure due to predation and flooding are negatively related ( $r^2 = 0.30$ ; Fig. 1a).

Nest loss in both the inland and tidal-marsh Swamp Sparrow populations studied was mostly due to predation (100 and 83%, respectively) with 13% of the Coastal Plain Swamp Sparrow nests lost to flooding. Flood losses were a result of heavy rains and winds rather than tidal inundations acting alone (B. Olsen, pers. obs.). Western Maryland populations lost no nests to flooding during our study. However, other published reports indicate flooding can be an important, episodic source of nest loss in Swamp Sparrows (Mowbray 1997), particularly early in the breeding season. Ellis (1980), for example, reported an

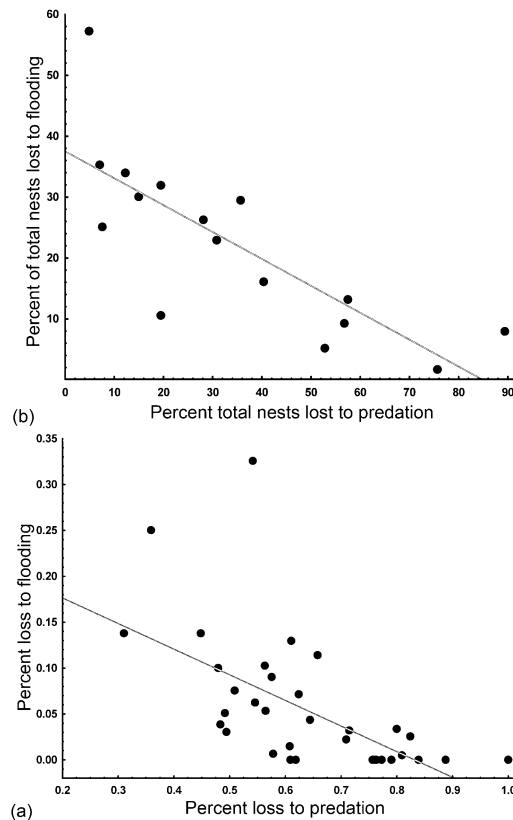


FIGURE 1. (a) Percentage of nests lost to flooding versus predation in San Francisco Bay Song Sparrows. Each point represents a different year within a particular study site. (b) Percentage of nests lost to flooding versus predation across all 16 studies of tidal-marsh sparrows. Each point represents the average value for a study. In the case of San Francisco Bay, for Figs. 3–6, single sites have been pooled for each of the embayments (San Pablo, San Francisco, and Suisun bays).

TABLE 1. NESTING PARAMETERS FOR STUDIES OF TIDAL-MARSH SPARROWS.

State	Species <sup>a</sup>	Site	Reference	Years of study	N of nests	N of for clutch	Latitude of study	Tidal range (meters)	Total percent loss	Percent predation	Percent flood loss	Mean clutch size	SD clutch size	Cowbird percent nests	Breeding season length (days)
CA	SOSP	Suisun	PRBO	6	1,027	667	38.2	1.1	90	76	2	2.95	0.6	1.9	99
CA	SOSP	San Pablo	PRBO	7	1,626	1,086	38.2	1.4	81	57	9	3.07	0.6	1.3	97
CA	SOSP	San Pablo	Johnston (1956b)	4	157	157	37.8	1.3	49	20	11	3.18	0.5	1	114
CA	SOSP	South Bay	C. Nordby (unpubl. data)	2	364	149	37.5	1.8	85	36	29	3.14	0.59	13.1	140
FL	SESP	Gulf	Post and Greenlaw (1982)	2	108	108	28.2	0.8	95	89	8	3.02	0.31	0	158
NY	SESP	Oak Beach	Post and Greenlaw (1982)	2	298	298	41.5	0.2	65	15	30	3.7	0.58	0	77
CT	SESP	Various	C. Gjerdrum and C. Elphick (unpubl. data)	2	19	19	41.3	1.1	36	8	25	4	0.8	0	70
MD	SESP	Blackwater	P. Marra and B. Shmeling (unpubl. data)	2	245	151	38.3	0.8	63	58	5	3.35	0.85	0	73
MA	SESP	Buzzards Bay	Marshall and Reimert (1990)	2	60	55	41.5	1.2	71	5	57	3.9		0	52
ME	SMSTS	Scarborough Marsh	Shriver (2002)	3	69	69	43.1	2.5	54	12	34	3.58	0.95	0	58
MD	SMSTS	Blackwater	P. Marra and B. Shmeling (unpubl. data)	2	18	18	38.3	0.8	64	40	16	3.34	0.77	0	71
RI	SMSTS	Various	DeRagon 1988	2	172			1.2	56	7	35			0	72
CT	SMSTS	Various	Gjerdrum and Elphick (unpubl. data)	2	122	122	41.3	1.1	77	31	23	3.7	0.7	0	65
NY	SMSTS	Oak Beach	Post and Greenlaw (1982)	4	240	176	37.5	0.2	73	28	26	3.87	0.63	0	80
ME	NESTS	Scarborough Marsh	Shriver (2002)	3	53	53	43.1	2.5	73	19	32	3.49	0.93	0	55
CA	BeSS	Pt. Magu	J. Williams (unpubl. data)	4	255	356	33					3.2	0.1		
DE	CPSS	Woodland Beach	B. Olsen and R. Greenberg (unpubl. data)	4	400	400	39.3	1.4	71	58	13	3.2	0.6	0.03	110

<sup>a</sup>Species abbreviations are SOSp (Song Sparrow), SESP (Seaside Sparrow), SMSTS (Saltmarsh Sharp tailed Sparrow), NESTS (Nelson's Sharp tailed Sparrow), BeSS (Belding's Savannah Sparrow), CPSS (Coastal Plain Swamp Sparrow).

average of 8.5% of nests loss due to flooding in a Rhode Island peat bog.

Brood parasitism appears to be rare and patchy in tidal-marsh *Melospiza* sparrows and lower than found in non-tidal-marsh populations. Song Sparrow populations had an average parasitism rates of approximately 1.6% (this is the average of the yearly average for the five San Pablo and Suisun Bay populations), with the exception of the southern San Francisco Bay populations of *M. m. pusillula*, where 13.5% of the nests were parasitized. This latter value is by far the highest rate reported for any tidal-marsh sparrow population (Table 1). The parasitism rates for the other subspecies of saltmarsh Song Sparrows may have been underestimated because in the PRBO studies only nestling cowbirds (and not eggs) were identified. However, the *pusillula* populations were on very small marsh patches, which may have created a much larger edge effect than that found in other studies. Arcese *et al.* (2002) reported that Song Sparrows are a preferred host of cowbirds and parasitism rates in the Pacific region ranged from 5.5–9.9%. In contrast, the average for the Palomarin site was only 2.4%, demonstrating that variation can be substantial even among upland populations.

Only 0.4% (two of 436) of all Coastal Plain Swamp Sparrow nests located were parasitized (R. Greenberg, unpubl. data). Brood parasitism is often episodic and local—the two instances of brood parasitism in the Coastal Plain Swamp Sparrow were for two nests within 50 m of each other in one, 2-wk period. Mowbray (1997) reported that for four studies of interior Swamp Sparrows in eastern North America (883 nests) that parasitism rates averaged 14.9% ( $SD = 12.3$ ).

#### Clutch size

Johnston (1954) was the first to note that Song Sparrows nesting in tidal marshes had small clutches compared to their upland counterparts in a paper on latitudinal variation in clutch size in West Coast populations of the species. His analysis was based on data from 545 completed clutches taken from *ö*ological collections and the field notes of various field biologists. He found that clutch size generally increased with latitude from 3.05 in Baja California to 4.17 in Alaska. He compared sample of 143 clutches from non-tidal-marsh birds in north-central California (37.5–39° N) with 86 clutches from *Melospiza melodia pusillula* (south San Francisco Bay) and 48 from *M. m. samuelis* (San Pablo Bay). Although only mean values are presented, the clutches from the saltmarsh populations averaged 3.31 and 3.28, respectively which is

considerably smaller than 3.53 for the non-salt-marsh birds of northern California and 3.71 for non-saltmarsh birds of south-central California. The difference in clutch size persisted even when only first clutches were compared (to eliminate an effect of seasonal change in clutch size). He later published mean clutch size of 3.2 ( $SD = 0.6$ ) based on 147 nests from the population of *M. m. samuelis* he studied for 4 yr

Recent studies provide access to much larger sample size for expanding this analysis. Studies in Suisun and San Pablo bays demonstrate that these populations have a slightly, but significantly smaller clutch size than a population monitored in coastal scrub habitat in the Palomarin population. The latter population had an average clutch size of 3.20 ( $SD = 0.61$ ,  $N = 597$ ) over an 8-yr study, whereas populations in Suisun Bay averaged 3.07 and San Pablo Bay 2.95. Three populations monitored for 2 yr in south San Francisco Bay had a clutch size of 3.14 ( $SD = 3.59$ ,  $N = 149$ ) which was not significantly different than the Palomarin site. However, an interior population in central California (Consumnes River) had a clutch size of 3.65, which was significantly higher than all of the tidal-marsh and coastal-upland populations.

Greenberg and Droege (1990) compared clutch size in Coastal Plain Swamp Sparrows breeding in Black Marsh, Baltimore County, Maryland, to data from nest cards for the nominate subspecies in Pennsylvania and New York. They found the tidal-marsh clutch size was significantly smaller (3.25 versus 4.1). Other field studies have found clutch sizes for the interior subspecies averaging 3.9 (Mowbray 1997). Further work in Delaware showed also showed a mean clutch size of 3.28 ( $SD = 0.6$ , 255 nests) for tidal-marsh nesting Swamp Sparrows compared 3.59 ( $SD = 0.6$ , 65 nests) for the closest inland population in western Maryland (Garrett County).

#### Breeding season

Johnston (1954) found that nesting began and ended progressively later in Song Sparrows as one moved north or higher in elevation. Set against this was a much earlier breeding peak in the saltmarsh populations than in comparable non-saltmarsh populations. For example, both *M. m. pusillula* and *M. m. samuelis* initiated 50–60% of their clutches by early March, whereas this value was <10% for other California populations (including those in southern California). As a result, the saltmarsh forms have a long breeding season, lasting 95 and 120 d for *M. m. pusillula* and *M. m. samuelis*, respectively. Non-saltmarsh populations in north-central California, in contrast, had a breeding season of

approximately 91 d. These estimates are based on pooled data from many different years, which may provide a high estimate of nesting season, where the duration of the season is relatively constant, but the initiation date is highly variable. Johnston's study on the San Pablo Bay population showed an average breeding season length of 114 d, which is comparable to his earlier pooled estimates.

More recently collected data support the idea of both an earlier and longer breeding season in the saltmarsh populations. PRBO data showed first clutches occurring during the second or third week of March for the Suisun Bay and San Pablo Song sparrows compared to the first week in April at Palomarin. The estimated breeding season was 99 and 97 d for the Suisun and San Pablo Bay populations, respectively and only 88 d for Palomarin. Data from *M. m. pusillula* (J. C. Nordby and A. N. Cohen, unpubl. data) indicate a nesting season beginning in late February and averaging 140 d. It is unclear what accounts for variation between studies. Coastal Plain Swamp Sparrows also have a substantially longer breeding season than nearby interior populations (110 versus 85 d). The longer breeding season is mainly a result of an extension of nesting activity at the end of the season (well into August), where the interior populations cease reproductive activities in mid-July.

#### AMMODRAMUS SPARROWS

##### *Nest success*

Average nest loss for the 11 study populations of tidal-marsh *Ammodramus* was 66% (SE = 8.3%). Nest loss was similar between Seaside ( $\bar{x}$  = 66, SE = 9.4), Saltmarsh Sharp-tailed ( $\bar{x}$  = 65, SE = 4.5), and Nelson's Sharp-tailed sparrow ( $\bar{x}$  = 73, N = 1). LeConte's Sparrows, the closest non-tidal-marsh relative of the Seaside and Sharp-tailed sparrows, had a nest loss rate of 47% (N = 50 nests) over a set of northern prairie study sites (M. Winter, unpubl. data). Other studies of grassland *Ammodramus* report nest loss values between 50–80% (Vickery 1996, Green et al. 2002, Herkert et al. 2002).

##### *Causes of nest failure*

The mean loss to predation for all 11 tidal-marsh *Ammodramus* populations was 27.9% (SE = 7.6) which is similar to the loss due to flooding 26.5% (SE = 14.3). Sharp-tailed and Seaside sparrows showed no significant interspecific difference in the amount of loss to either factor and both factors comprised over 75% of all nest loss. In contrast, predation comprised 94% known

causes for nest loss in LeConte's Sparrows and overall nest loss to predation was 59.0%. This latter value is unlikely to have come from the same distribution as for the tidal-marsh *Ammodramus* which has a 99% confidence limit of 52.1.

##### *Clutch size*

Mean clutch size for Saltmarsh Sharp-tailed Sparrow and Seaside sparrows are similar (3.62 and 3.59, respectively) as is the single value for coastally breeding Nelson's Sharp-tailed Sparrow (3.49). Clutch size in tidal-marsh *Ammodramus* declines with increasing nest loss to predation ( $r^2$  = 0.69, P = 0.003, N = 11; Fig. 3). Clutch size in these species also increases with latitude ( $r^2$  = 0.42, P = 0.01; Fig. 4). Because, predation rate decreases with latitude ( $r^2$  = 0.89), it is impossible to tease apart the relative importance of latitude and predation in explaining variation in clutch size.

Clutch size in grassland *Ammodramus* is larger than tidal-marsh congeners even at equivalent latitudes. For example, clutch size in LeConte's Sparrows from the northern prairie region has been reported to be 4.51 (SE = 0.10; M. Winters, unpubl. data) and 4.53 (Lowther 1996). Although the northern prairie study area is farther north than the northernmost sites for which clutch size has been determined for tidal-marsh *Ammodramus*, these values are similar to those found for other grassland *Ammodramus* species found at in more southerly areas. McNair (1987) found an average of 4.4 eggs per clutch for Grasshopper Sparrows (*Ammodramus saviannarum*) based on egg-slip data from a large portion of the species' range. A study site in West Virginia (which would be at the latitude of the Maryland coastal studies) reported an annual mean varying from 4.1–4.5 eggs/clutch (Wray et al. 1982). Finally, mean clutch sizes from three studies of the Henslow's Sparrow (*Ammodramus henslowii*) ranged from 3.8–4.2 eggs.

##### *Season length*

Nest season length varies from 52–97 d and averages 67 (SD = 9.5) d across all tidal-marsh *Ammodramus* populations. Season length is strongly and negatively correlated with latitude ( $r^2$  = 0.79, P = 0.0006, N = 11). The nesting season of LeConte's Sparrows in wet prairies was 54 d – comparable to the northernmost populations of Sharp-tailed Sparrows in coastal marshes (52 d).

##### *Brood parasitism*

None of the 11 studies of the tidal-marsh *Ammodramus* reported cowbird parasitism

(N = 1,404 nests); apparently, no substantiated reports exist for either Seaside Sparrow or saltmarsh populations of sharp-tailed sparrow (Post and Greenlaw 1994, Greenlaw and Rising 1994). These zero values can be compared to other *Ammodramus* and grassland sparrows in general based on a recent review of parasitism values in grassland birds (Shaffer et al. 2003). The average parasitism rate for 28 studies of four *Ammodramus* species (LeConte's Sparrow, Henslow Sparrow, Grasshopper Sparrow, and Baird's Sparrow [*A. bairdii*]) was 16.5 (SD = 15.2%, N = 1,162 nests) with 93% of the studies reporting values >0. The mean value for 59 studies of four additional grassland sparrow species (Lark Sparrow [*Chondestes grammacus*], Vesper Sparrow [*Poocetes gramineus*], Savannah Sparrow, and Chesnut-collared Longspur [*Calcarius ornatus*]) was 14.3% (SD = 14.6%, with 85% of the values >0). A nested ANOVA (*Ammodramus* vs. non-*Ammodramus*, irrespective of habitat with species nested within the two taxonomic groupings) showed no significant difference between the two groups or between species within a group ( $F_{1,80} = 0.085$ ;  $F_{5,80} = 1.1$ ). However, a nested ANOVA with tidal-marsh *Ammodramus* included as a third group showed a significant difference among groups ( $F_{2,89} = 4.11$ ,  $P = 0.02$ ) with parasitism rates for tidal-marsh *Ammodramus* significantly lower for grassland *Ammodramus* ( $P = 0.003$ ) and other grassland sparrows ( $P = 0.006$ ) based on Bonferroni's post hoc test. We conclude that tidal-marsh *Ammodramus* have much lower nest parasitism rates than is typical for grassland sparrows and the grassland *Ammodramus* have rates consistent with grassland sparrows as a whole.

#### OVERALL PATTERNS

##### Nest success

The mean overall nest failure for 16 tidal-marsh sparrow populations was 66% (SD = 19%), with approximately 80% of failure caused by predation (36.4% of total nests) and flooding (22%). As we saw with Song Sparrow populations, predation rates are negatively related to flood loss rates ( $r^2 = -0.42$ ,  $P = 0.009$ ; Fig. 2). Nest failure tended to be higher in populations of *Melospiza* than *Ammodramus*, but not significantly so (75.5 versus 66.2%;  $t = 0.8$ ,  $df = 14$ ,  $P = 0.29$ ). Nest success was weakly and positively related to latitude ( $r^2 = 0.26$ ,  $P < 0.05$ ) and unrelated to mean tidal range ( $r^2 = 0.03$ ). Almost half of the between population variance in nest loss can be explained by predation (Fig. 2;  $r^2 = 0.45$ ,  $P = 0.008$ ), whereas none is related to flood loss ( $r^2 = 0.06$ ).

##### Losses due to flooding

Loss to flooding is highly variable between populations of tidal-marsh sparrows, averaging 22.3 (SD = 14.4%) and ranging from 1.7–57.3% of all nests. Overall, nest loss to flooding is unrelated to mean tidal range ( $r^2 = 0.09$ ) and is weakly related to latitude ( $r^2 = 0.29$ ,  $P = 0.04$ ). Loss due to flooding is not well documented for interior *Ammodramus*, but may occur in early season nests of LeConte's Sparrow (M. Winters, unpubl.data; Lowther 1996).

##### Losses due to predation

Average loss to predation averages almost twice as high as loss to flooding ( $\chi^2 = 34.5$ ,  $SD = 5.5\%$ ) with considerable between population variation (values range from 4.8–89.3%). Predation rate is significantly related to latitude ( $r^2 = 0.56$ ,  $P = 0.001$ ). Flood loss and predation are strongly, negatively related ( $r^2 = 0.63$ ; Fig. 1b).

##### Clutch size

Average clutch size for all tidal-marsh sparrow populations considered was 3.38 eggs—Song and Swamp sparrows both averaged 3.25, Saltmarsh Sharp-tailed Sparrows averaged 3.64 eggs, Seaside Sparrows averaged 3.58 eggs, and Belding's Savannah Sparrows averaged 3.20 eggs. Although the sample size is limited, the three *Ammodramus* have considerably higher clutch sizes (3.6) than the two *Melospiza* (3.2). Because of this taxonomically related variation, subsequent analysis will use genus as a categorical variable in ANCOVA.

Clutch size shows a striking relationship to the amount of predation (Fig. 3;  $r^2 = 0.63$ ,  $P < 0.0004$ ). An ANCOVA for heterogeneity in slopes based on clutch size as the dependent, predation rate as the independent, and genera as the grouping variables showed a significant genera vs. latitude and predation rate interaction ( $F_{2,13} = 14.2$ ,  $P = 0.0009$ ). Within *Ammodramus*, the relationship between clutch size and predation rate is strong and significant ( $r^2 = 0.73$ ,  $P = 0.0004$ ), with clutch size declining as predation rate increases. In contrast, clutch size is not significantly correlated with predation rate in the five *Melospiza* populations ( $r^2 = 0.51$ ,  $P = 0.17$ ). In contrast to predation, clutch size shows no relationship to loss due to flooding ( $r^2 = 0.07$ ) for tidal-marsh sparrows as a whole.

Clutch size also varies with latitude, in this case positively, within saltmarsh sparrows, but the relationship is much weaker (Fig. 4;  $r^2 = 0.33$ ,  $P < 0.02$ ). Once again, heterogeneity in this relationship can be found between populations



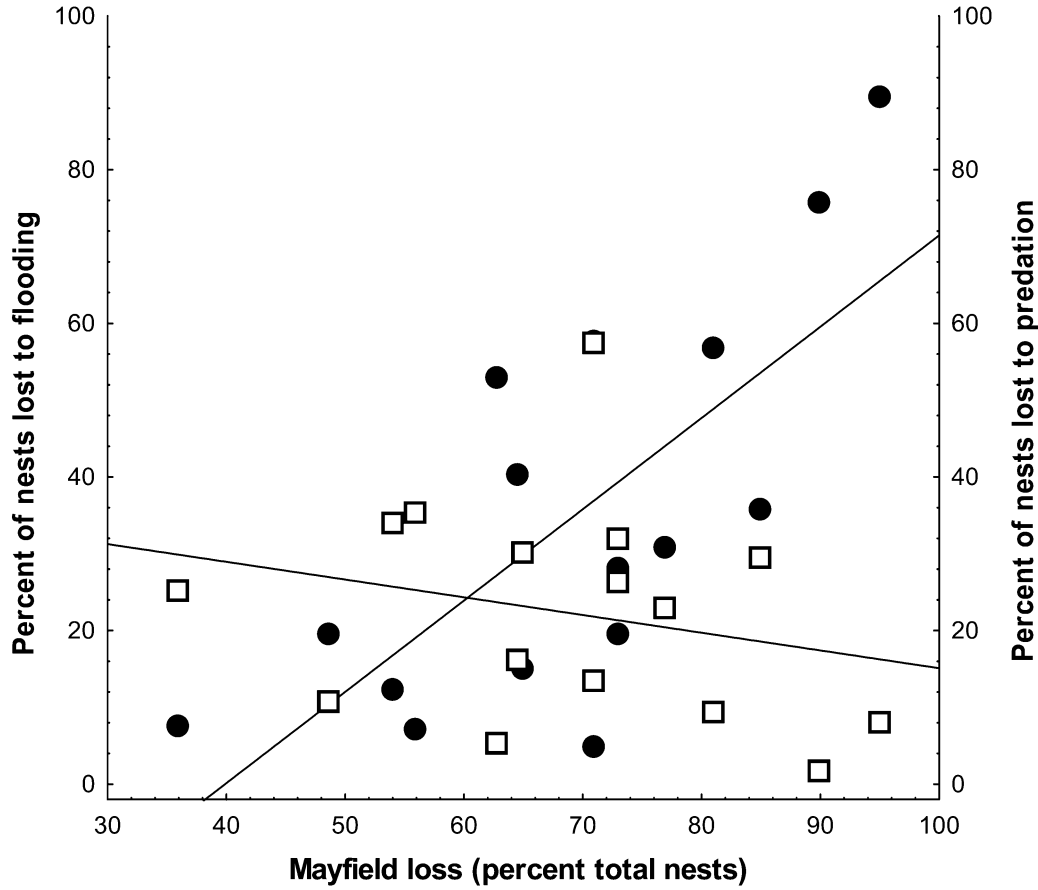


FIGURE 2. Proportion of total nests lost to predation and flooding plotted against crude success rate for tidal-marsh sparrow populations. Each point represents the average for a population (Table 1). Crude nest success is highly correlated with predation rates ( $r^2 = 0.44$ ) but not flood loss ( $r^2 = 0.0$ ).

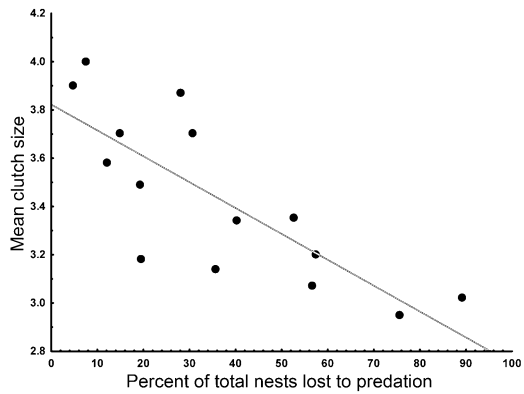


FIGURE 3. Mean clutch size plotted against percentage loss to predation across populations of tidal-marsh sparrows.

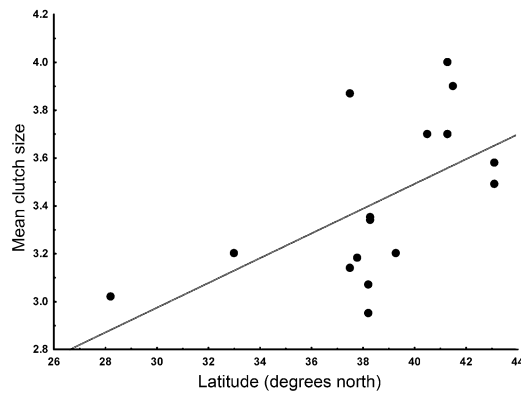


FIGURE 4. Mean clutch size plotted against latitude across populations of tidal-marsh sparrows.

of *Ammodramus* and others (*Melospiza* and *Passerculus*); the ANCOVA for heterogeneity in slopes shows a significant interaction exists between genus and latitude ( $F_{3,11} = 3.8$ ,  $P = 0.05$ ). When predation rate, flooding rate, and latitude are entered into a multiple regression (Statsoft 2004) with clutch size as the dependent variable, only predation rate is included as a significant variable ( $r^2 = 0.75$ ,  $P < 0.001$ ). The variables show some intercorrelation; however, collinearity is not a problem because the correlation coefficients are moderate (0.48–0.79) and the tolerances are between 0.3 and 0.62 (Belsley 1980). These results suggest that although clutch size varies with latitude, that predation pressure is a more important factor in explaining differences in clutch size among populations.

#### Brood parasitism

Brood parasitism is generally low, averaging 1.1% of nests across the 16 populations. In fact, brood parasitism by cowbirds has not been found for any tidal-marsh nesting *Ammodramus* and is reported to average 1.6% or less for all populations of *Melospiza* except those in south San Francisco Bay.

#### Nesting season

The period between the first and last nest initiations is a relatively crude index of the nesting season length, being very sensitive to the extreme tails of the seasonal distribution of nesting efforts. Despite the short-comings of this indicator, the general patterns associated with nesting season are quite clear. Nesting season is, expectedly, related to latitude. With all data included, the relationship is significant, but weak ( $r^2 = 0.26$ ,  $P = 0.04$ ). The Florida population of Seaside Sparrow is a clear outlier to the pattern found in more northerly populations. With this population removed from the analysis, the relationship is much stronger (Fig. 5;  $r^2 = 0.53$ ,  $P = 0.003$ ). As stated in the analysis of the individual genera, the relationship between breeding season and latitude is particularly striking within the *Ammodramus* and is not significant in *Melospiza*. However, the latter genus lacks widely distributed populations along a single coastline.

## DISCUSSION

### OVERALL NEST SUCCESS

Overall nest success is generally low in tidal-marsh birds, averaging about 31% but ranging from 5–64% between populations. But this average is similar to that found for grassland or

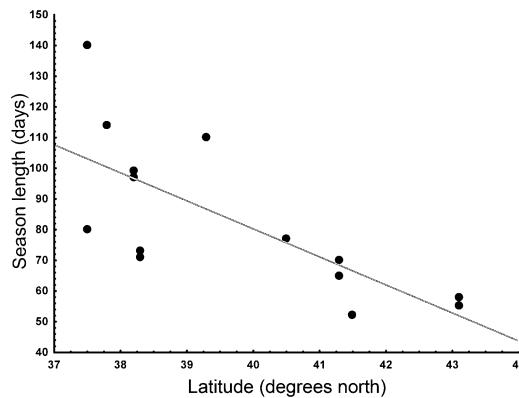


FIGURE 5. Mean annual breeding season (initiation of first and last clutch) plotted against latitude across populations of tidal-marsh sparrows.

shrub-nesting sparrows, which generally range from 20–50%. Therefore, the hypothesis that tidal-marsh sparrows facing the dual threat of predation and flooding suffer an inordinately high level of nest loss is not supported.

Few data are available to compare inland and tidal-marsh *Melospiza*, but they support the hypothesis that overall nest loss is higher in the tidal-marsh populations. The values for recent studies of *Melospiza*, particularly Song Sparrows in San Francisco Bay are quite high (82–95%) for a temperate-zone, open-nesting passerine (Martin 1993). This is intriguing because the *Melospiza* are recent colonists of saltmarshes (Chan et al, *this volume*) and, at least in the case of the Song Sparrow, may have made a more profound ecological shift to occupy saltmarshes from upland scrub and riparian habitats than did the *Ammodramus*. Hence one might predict that they would be less well adapted to marsh environments. Also, the relatively sparse cover provided by *Salicornia* marshes, where Pacific Coast Song Sparrows live, may make hiding nests more difficult than is the case for *Ammodramus* sparrows nesting in *Spartina*.

However, the data showing low nest success in Song Sparrows have all been collected in the last decade. The older data set from Johnston (1956b) suggests that nest success may have been much higher in the past. These data also suggest that predation, in particular, has increased dramatically, which is consistent with the invasion of new potential predators and the general increase in population of feral animals in and around bayside marshes, as well as the increasing fragmentation of the marshes themselves (Takekawa et al., *chapter 11, this volume*). Whether the low nest success of tidal-marsh Song Sparrows, or even that of other tidal-marsh

species, is a result of very recent environmental changes or is a more long-term characteristic of these taxa is a fundamental question to answer. If low nest success due to predation is a recent phenomenon related to recent human activity, then it will be less appropriate to invoke this as a factor that has shaped tidal-marsh sparrow life history.

As noted by Reinert (*this volume*) for tidal-marsh Red-winged Blackbirds, cowbird parasitism rates are low for tidal-marsh sparrows, particularly for East Coast populations of *Ammodramus*. The low parasitism rates could result from the lack of perches (Post and Greenlaw 1994), the isolation from habitats where cowbirds can feed, or, perhaps more interestingly, from the lack of tolerance to saline conditions in nestling or fledgling cowbirds and, hence, selection pressure adults against searching in tidal-marshes for nests. With regard to the first hypothesis, grasslands are often reported to have relatively low parasitism rates. As we reported above, the studies of grassland *Ammodramus* suggest that while often low, parasitism rates are quite variable—which is distinctly different from the invariably low values for tidal-marsh sparrows. Many tidal-marshes are adjacent to agricultural or suburban areas and have edge vegetation with trees and other elevated posts. The idea that selection has shaped an aversion of cowbirds from entering tidal marshes to search for nests is an attractive and testable hypothesis.

#### THE IMPORTANCE OF PREDATION AND FLOODING

Despite the challenge of locating a nest safe from tidal and storm-driven inundation, predation accounts for more nest loss than does flooding in most tidal-marsh sparrows. Furthermore, both within- and across-species analyses show that variation in nest success between localities is correlated with nest predation rates, but not loss of nests to flooding or other factors. Flooding, however, can be a critical factor within certain populations, especially Saltmarsh Sharp-tailed Sparrows. With the exception of tidal marshes along the northeastern coast of North America (Shriver 2002; Reinert, *this volume*), loss to flooding is a less predictable and more variable cause of nest loss than predation for tidal-marsh sparrows, even within sites (as exemplified by the San Francisco Bay Song Sparrow data). High predation rates coupled with a substantial and variable source of density-independent mortality (flooding) may make the life history of tidal-marsh sparrows unusual for a temperate song bird.

Further investigation into the how these qualitatively different sources of mortality shape the life history of tidal-marsh birds could make a profound contribution to avian life history studies. Based on a cross-population regression, we found a negative relationship between predation loss and flood loss both between populations of Song Sparrows and across all tidal-marsh populations. Along these lines, DiQuinzio et al. (2002) studied a single population of Saltmarsh Sharp-tailed Sparrows in a Rhode Island marsh where natural tidal flow was reinstated. They found a shift in the major source of nest failure from predation to flooding over the subsequent 5-yr period. In this case, overall nest failure increased dramatically with a rise in the number of flooding events.

Two possible explanations for the negative relationship between nest loss to predation and flooding are: (1) a trade-off exists between nest placement that reduces predation versus one that lowers the probability of flood loss, or (2) the sources of mortality are compensatory so that nests that are flooded have reduced exposure to possible predation. Thus, the true potential impact of predation is underestimated in populations that experience flooding and the difference in predation between tidal and the non-tidal population is underestimated in these data.

#### CLUTCH SIZE IN TIDAL-MARSH POPULATIONS

Clutch size showed a very strong relationship to nest predation loss. Within a regression analysis, predation loss was a much stronger predictor of clutch size than was latitude or other sources of nest loss. This provides evidence to suggest that predation selects for smaller clutch size among tidal-marsh sparrow populations. The strong role of predation would be consistent with the hypothesis of some workers that food is not an important limiting factor shaping reproductive strategies in tidal-marsh sparrows (Post and Greenlaw 1982). However, we need more direct evidence on the possible role of food in shaping such life-history parameters as clutch size in tidal-marsh sparrows. Although latitude, which might correlate with both increasing day length (Lack 1947) and a greater seasonal peak in food resources (Ricklefs 1980) does not show as strong a relationship with clutch size as does predation loss, it is possible that a more direct index of food availability might be a better predictor.

Accepting the importance of predation in selecting for smaller clutch sizes within tidal-marsh birds, we can evaluate two hypotheses originally proposed for small clutch size in

tropical birds for why this might be the case. First, smaller clutches (and particularly, smaller resulting broods) attract less attention from visual predators, such as mammals and birds (Skutch 1949). Second, in the face of a high probability of nest loss and a long breeding season, the best strategy might be to reduce the investment in individual clutches and save reserves to maximize a female's ability to lay and care for multiple clutches and broods, in the chance that one will survive (Foster 1974). The fact that predation loss alone shows a much stronger relationship with clutch size than does overall nest loss, and that flood loss is actually positively related to clutch size, would suggest that the predation-reduction hypothesis would be the most likely to explain the relationship between predation levels and clutch size in tidal-marsh sparrows.

As a group, tidal-marsh sparrows have relatively small clutches, averaging 3.5 across all populations, compared to inland populations of closely related taxa. This result accords with previously published suggestions that tidal-marsh sparrows have unusually small clutches (Johnston 1954, Greenberg and Droege 1990). Such a difference in clutch size is also found between the freshwater-marsh King Rail (*Rallus elegans*) and the saltmarsh-breeding Clapper Rail (*R. longirostris*; Meanly 1992, Eddleman and Conway 1998). Unfortunately few comparative data are available from related and ecologically similar species, where latitude, elevation, and other environmental differences not associated with habitat differences are not confounding the comparison. For example, the Belding's Savannah Sparrow has the smallest clutch size of North American Savannah Sparrows, but it is also located at the lowest latitude (Wheelwright and Rising 1993). We have too few data to make perhaps the most appropriate comparisons between the subspecies of Nelson's Sharp-tailed Sparrow, Saltmarsh Sharp-tailed, and Seaside sparrows have clutches between 3.5–4 eggs even toward the northern end of their breeding distribution, which is considerably smaller than the 4.6 clutch size reported for the related LeConte's Sparrow. However, the latter data come from 5° further north than the coastal *Ammodramus* and from a regional with otherwise highly continental climate. The higher clutch size is also found in populations of less closely related *Ammodramus* at latitudes of 38–39° N, which is comparable to the study sites for saltmarsh species. These populations are still at more interior sites with more continental climates. It has been hypothesized that populations facing environments with a smaller difference between summer maximum and

winter minimum resources will have smaller clutch sizes. For example, Cody (1968) suggested that birds in areas with more equable climates have smaller clutch size because with large non-breeding carrying capacity and high adult survivorship, fewer high-quality young will be better able to fight for vacancies in the population structure.

The strongest test of the difference in clutch size between tidal-marsh and grassland sparrows comes from the classic analysis of clutch-size trends in San Francisco Bay Song Sparrows completed by Johnston (1954). His discovery that the tidal-marsh populations have smaller clutches than comparable (same latitude) populations from west-central California is largely supported by our analyses of larger samples observed in marshes in the last decade. The birds in San Pablo Bay, for example, show a significantly smaller (0.2 eggs) clutch size than populations 20 km west in coastal scrub of Marin County. Clutch sizes from interior central California are larger by 0.6 eggs. Only the data from the south San Francisco Bay population (3.18 eggs) are similar to the west Marin County data and they are still lower than the interior population. Another appropriate comparison comes from the inland and tidal-marsh populations of Coastal Plains Swamp Sparrows in Maryland, where clutches average 0.3 eggs greater in the interior populations. Seaside Sparrows in Florida provide yet another possible comparison where latitude is controlled. Unfortunately the data are contradictory. Post and Greenlaw (1994) report a substantially higher clutch size in the non-tidal-marsh populations of *A. m. nigrescens* and *A. m. mirabilis* (3.5 vs. 3.1). However the much larger data set for *A. m. mirabilis* published by Lockwood et al. (1997) includes a mean clutch size of 3.1—which is identical to the tidal-marsh populations.

#### OTHER ASPECTS OF TIDAL-MARSH SPARROW LIFE HISTORY

Sparrow demography will only be complete when we have studies of life history focusing less on a single parameter, such as clutch size and nest survivorship, and more on integrating these into a broader understanding of life history as a whole (Young 1996, Martin et al. 2000). The length of the breeding season, changes in survival probability within a breeding season, probability of surviving to another breeding season, dispersal strategies, and opportunities for successfully fledged young to enter the breeding population are all factors that shape life history over and above what we have discussed here. In the long run, our understanding

of saltmarsh sparrow life history will require long-term data on annual productivity, survivorship, and juvenile dispersal success for multiple populations. However, to date, few studies have measured or estimated these components of tidal-marsh sparrow fitness for entire breeding seasons.

Annual reproductive success (as measured by the number of young fledged/pair/season) has been found to vary from the extremely low value of 0.6 for a Florida population of Seaside Sparrows (Post and Greenlaw 1994), to the moderately low values of 2.1 young/pair in the Belding's Savannah Sparrows, to 2.3 in the Coastal Plain Swamp Sparrow, and finally to higher values of 4.7 for the San Pablo Song Sparrow (Johnston 1956b) and 4.3 and 4.7 for Saltmarsh Sharp-tailed and Seaside sparrows, respectively, in New York (Post and Greenlaw 1982). Modal values of two-five young per pair appear to be typical of temperate zone songbirds (Wray et al. 1982) and we will need more data to see how components of reproductive strategy contribute to between population variation in productivity (Ricklefs and Bloom 1977).

It could also be argued that the less seasonal climate and productivity of tidal marshes might allow for higher adult survival in their endemic sparrows than is found in upland relatives. As has been argued for tropical birds (Young 1996, Martin et al. 2000), this might select for lower reproductive effort within a breeding season and hence smaller clutch sizes. However, too few data exist to even begin to estimate survivorship patterns in saltmarsh passerines. Those estimates that are available are equivocal on this point. Average (2 yr) return rate of adult Saltmarsh Sharp-tailed Sparrows was approximately 57% (Post and Greenlaw 1982). This value is similar to those estimated for Seaside Sparrows (6 yr of data) from the same area, which ranged from 40-60% (Post and Greenlaw 1994). De Quinzio et al. (2001) found an annual adult survivorship of 60% the first year of a 4-yr study of Saltmarsh Sharp-tailed Sparrows in Rhode Island. The survivorship dropped to approximately 35% for the following seasons, but this was probably affected by large changes in marsh hydrology. Johnston reported annual return rates averaging 53% for the San Pablo Song Sparrows. Two studies report survivorship for saltmarsh sparrows that are substantially higher than is typical for temperate songbirds: Post et al. (1982) reported 85.7% for a resident population along the Gulf Coast of Florida and Grenier (pers. comm.) found an overall annual survival of 80.2% for a population of San Pablo Song Sparrows. The latter study and that of DiQuinzio et al. (2001) were

the only ones to use mark-recapture models in their estimation procedures.

Two studies have suggested that natal dispersal may be more localized in saltmarsh sparrows. DiQuinzio et al. (2001) estimated that approximately 35% of the Saltmarsh Sharp-tailed Sparrows settled locally in their natal marsh. Johnston (1956a) plotted the settlement pattern of young San Pablo Song Sparrows and found that young appeared to disperse a shorter distance than was found for a Song Sparrow population in Ohio (Nice 1937). Both studies emphasized that the patchy distribution of marshes and their stability (in the short run) may favor local dispersal. This in turn may reduce selection on producing many fledglings, but increase selection on producing fewer high-quality young.

#### SMALL MAMMALS: THE NEST ECOLOGY FRONTIER

It should be noted that the challenges of avoiding flooding and predation in tidal marshes face other saltmarsh birds (Reinert, *this volume*) and other terrestrial vertebrates. For example, small mammals in tidal marshes are largely terrestrial and depend upon nests for breeding and resting. The natural-history literature, however, strongly suggests that nest structure and placement differ in tidal-marsh populations and species when compared to upland relatives. Fisler (1965) noted that the subspecies of saltmarsh harvest mouse (*Reithrodontomys raviventris halicoetes*) that lived in less tidal, brackish marshes made nests similar to the upland species (*R. megalotis*). However, the subspecies associated with highly tidal saltmarshes (*R. r. raviventris*) probably did not make nests, but used abandoned bird nests (which would be much smaller and elevated off the substrate). Similarly, that in the marsh rice rat (*Oryzomys palustris*) of eastern marshes, which normally constructs a nest of woven grass and sedges on the ground at the base of shrubs, nests may attach to marsh vegetation in areas that are flooded at high tide and use the elevated nests of Marsh Wrens (*Cistothorus palustris*; Wolfe 1982). Johnston and Rudd (1957) described the breeding nests as being fairly substantial (8-24 cm × 6-12 cm × 4-6 cm) and placed under or in a cavity of an object on the substrate. Resting nests were found to be invariably elevated in the *Salicornia*. Interestingly, the authors note that a substantial portion of the young monitored in their study were lost due to tidal flooding. However, the sample size was small. Other small mammals that occupy tidal marshes that regularly build nests include voles (*Microtus*) and cotton rats (*Sigmodon*), but we are unable to ascertain any

special properties of tidal-marsh nests in these genera. Adaptation for reproduction in tidal-marsh mammals certainly is an area that could use further research.

#### CONCLUSIONS AND FUTURE STUDY

1. Tidal-marsh sparrows suffer from relatively low nest success, particularly populations in the genus *Melospiza*.
2. Overall, predation is the greatest source of nest loss, but flooding can be locally important. The two sources of mortality show a negative relationship in frequency of occurrence. This may simply be a result of flooding removing nests from the pool of potentially depredated nests, or it could indicate a trade-off between strategies to reduce one cause of failure or another. Predation rates are the best predictor of between population variation in nest-success rates. Nest loss due to flooding is variable and often unpredictable within and between seasons.
3. Clutch size is strongly related to predation rate, with smaller clutches occurring where nest predation rates are high. Overall nest success is much more weakly correlated with clutch size, which increases with flood loss. This suggests that the effect of predation on clutch size is specific to reducing predation and that clutch reduction as a bet-hedging strategy against frequent nest loss is a less likely explanation.
4. Clutch size is also related to latitude, but much more weakly than it is to predation. In a multiple regression analysis, only predation is included as a significant independent variable.
5. Brood parasitism is very low. It is unknown from *Ammodramus* species and generally around 1% for tidal-marsh *Melospiza*. Traditional explanations focus on the isolation of marsh from cowbird habitat and the lack of elevated perches. However, these explanations are not completely convincing and the possibility that saltmarsh searching in cowbirds has been selected against because cowbird young would survive poorly needs further experimental research.
6. Evolutionary explanations for patterns in clutch size and nest success need to be treated with some caution given the much higher nest survival and lower nest predation rates found in a saltmarsh Song Sparrow population in San Francisco Bay 50 yr prior to other studies cited here.
7. Data on other aspects of tidal-marsh sparrow demography, such as total fledging success/pair/season, survivorship, dispersal, and life-time reproductive success are absent or spotty. Studies suggesting shorter dispersal are tantalizing. More local dispersal may be part of a reproductive strategy where young compete to enter already dense local populations. The tidal-marsh sparrows would be an excellent system for long-term, comparative demographic studies focusing on how life-history parameters vary with biotic (predation) and abiotic (flooding) sources of mortality and how these relationships might change with sea-level rise.
8. The constraints of flood avoidance and predation need more detailed analysis through correlational studies with seasonal changes in nest placement. This topic would be particularly amenable to experimental manipulations. Sparrows would provide ideal study species for such research, but it must be remembered that other bird species and small mammals must solve the problem of when and where to place nest structures in tidal marshes to minimize mortality.

#### ACKNOWLEDGMENTS

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