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Reproductive Success of Belding's Savannah Sparrows in a Highly Fragmented Landscape

ABBY N. POWELL[1] AND CHRISTINE L. COLLIER
U. S. Geological Survey, California Science Center, and Department of Biology, San Diego State University, San Diego, California 92182, USA

Habitat fragmentation can influence the abundance and distribution of birds. Decreases in patch size increase the amount of edge habitat, which can allow greater invasion by exotic species, predators, and brood parasites (Hagan and Johnston 1992, Donovan et al. 1995). Fragmented habitats may act as population sinks and result in local extinctions unless immigration occurs from source habitats (Pulliam 1988, Howe et al. 1991, Pulliam et al. 1992, Stacey and Taper 1992).

Fragmentation is especially severe in coastal California, where about 75% of the presettlement acreage of coastal wetlands has been lost to development (Zedler 1982, Zedler and Powell 1993). This degradation has produced a highly fragmented landscape that may have a negative influence on the Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*), which is one of two wetland-dependent bird species endemic to coastal salt marshes in southern California. This nonmigratory subspecies is listed as endangered by the State of California. Statewide censuses of Belding's Savannah Sparrows reveal wide fluctuations in local population sizes, with local extinctions occurring in some years (Zembal et al. 1988). Thus, the population dynamics of Belding's Savannah Sparrow may reflect the effects of fragmentation.

Belding's Savannah Sparrows prefer to nest in the mid- to upper-littoral zones of coastal salt marshes, but the effects of habitat characteristics on reproductive success have not been explored (Massey 1979, Powell 1993). Based on geographic variation in song, Bradley (1994) suggested that populations are highly isolated and have low dispersal, but no study has examined immigration and emigration directly. The objectives of our study were to: (1) examine the effects of fragmentation on resident populations of sparrows, (2) examine the influence of habitat on reproductive success, (3) identify characteristics of breeding habitat, and (4) discuss the implications of our results for wetland conservation.

Study area and methods.—To examine the effects of fragmentation, we used sparrow population estimates from a statewide survey conducted in 1986 (Zembal et al. 1988) combined with data on the area of salt marsh vegetation for 26 coastal marshes in California (National Wetlands Inventory, U.S. Fish and Wildlife Service; www.nwi.fws.gov). The marshes ranged geographically from Carpenteria Marsh in the north to Tijuana Estuary in the south. The number of singing males was used as an index of population size for each of the 26 sites.

We also conducted a study of sparrow breeding habitat at San Diego Bay in 1995. San Diego Bay lost >92% of its salt marsh habitat (Macdonald 1990) between 1856 and 1984. The remaining 94 ha of salt marsh consist of isolated fragments surrounded by highly modified upland plant communities and urban landscapes. Remnants of the original San Diego Bay salt marshes were studied within the Sweetwater Marsh National Wildlife Refuge (32°36'N, 117°07'W), which includes F Street Marsh and a small remnant of salt marsh on the western edge of D Street Fill (Fig. 1). All three marshes were in the southern portion of San Diego Bay and were chosen because they had similar tidal flows but different degrees of disturbance and isolation.

We established four study plots in the Refuge, two within the mid-littoral zone of salt marsh habitat (SM and Vener Pond) and two within the upper-littoral zone (SH1 and SH2). Sweetwater Marsh (50.6 ha of salt marsh) was separated from Vener Pond (6.84 ha) by a levee road 10 m wide. We also established plots at two isolated marshes (F Street and D Street), both within the mid-littoral zone of salt marsh habitat (Fig. 1). F Street Marsh (2.85 ha) was separated from Sweetwater Marsh by 0.5 km, and D Street Marsh (1 ha) was separated by a distance of 0.1 km. The landscape between F Street Marsh and Sweetwater Marsh is industrial/urban, whereas D Street Marsh was separated by natural tidal channels and salt marsh (Fig. 1).

The study plots at Sweetwater Marsh, Vener Pond, and D Street Marsh measured 100 × 100 m (1 ha). Owing to impassable channels and size constraints, the plot at F Street Marsh measured only 90 × 100 m (0.9 ha). All of the plots were marked at 25-m intervals. We visited all plots once a week from 22 March until 1 September 1995. Sparrow surveys began within one-half hour of dawn and continued until about 1000, when birds typically left their territories to forage in the mid- and lower-littoral zones of the marsh. A total of 209 hours was spent on the six plots in 1995. During each visit, we mapped territory boundaries using a combination of territory-flush and spot-mapping techniques (Wiens 1969). Territory boundaries were recorded on grid maps using

[1] Present address: U.S. Geological Survey, Biological Resources Division, Northern Prairie Wildlife Research Center, Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701, USA. E-mail: abby_powell@usgs.gov

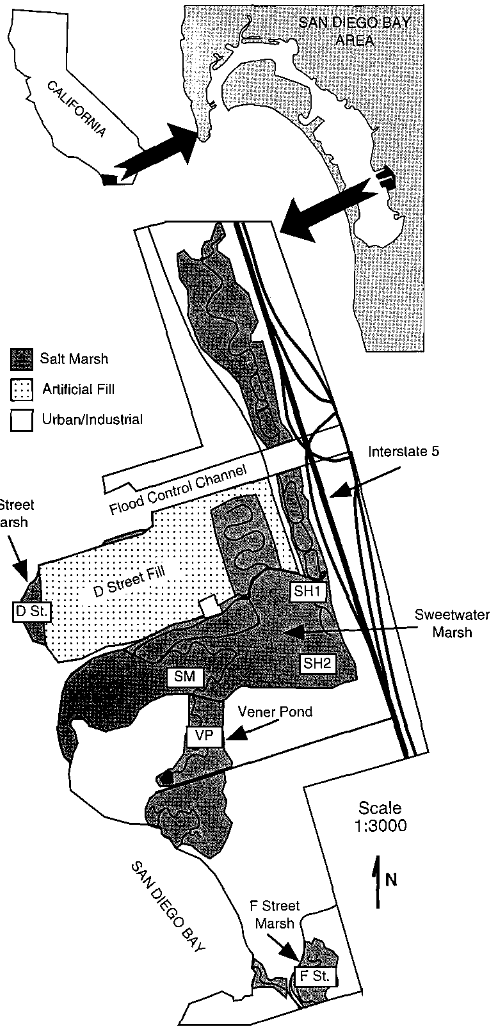

FIG. 1. Map of Sweetwater Marsh National Wildlife Refuge wetland complex, San Diego Bay, California. Study plots not shown to scale.

landscape features and plot markers as reference points. Boundary disputes, countersinging, and pair-bond associations were recorded. On average, five singing locations were mapped for each territorial male (Wiens 1969). The outermost points of each territory were taken from the grid maps and transformed into X and Y coordinates. These coordinates were entered into program CALHOME to calculate the area of each territory using the minimum convex polygon method (Kie et al. 1996).

We used mist nets to capture sparrows prior to nesting between March 1994 and April 1995. We individually color-banded 277 adult sparrows to determine dispersal among habitat patches and other marshes in the region within seasons and between years. Sex determination of adults was based on presence or absence of a brood patch or cloacal protuberance (Pyle et al. 1987).

We chose a relatively noninvasive method for determining nesting success because of the endangered status of Belding's Savannah Sparrows, and because nests were difficult to find without risking trampling and abandonment. We estimated nesting success using a reproductive index developed for rare sparrows by Vickery et al. (1992). Territories were ranked on a scale from 1 to 7 using behavioral cues to determine stages in the breeding cycle (see Vickery et al. 1992). If a bird was seen with food we considered it direct evidence that a pair had nestlings. Observations of feeding and begging behavior between adults and fledglings determined fledging success. Territories with "high success" (ranks 5 to 7) fledged at least one offspring, whereas territories with "low success" (ranks 1 to 4) fledged no offspring. Territories that produced fledglings from more than one brood within the nesting season received the highest rank of 7. If a nest was found incidentally, we banded the nestlings and recorded the type of vegetation used to build the nest, the direction of the nest opening, and the degree of nest concealment (Martin and Geupel 1992). In addition, we measured the vegetation around the nest using a 1-m^2 quadrat, with the nest placed in the center of the sampling unit.

We sampled the vegetation within each plot along 10 100-m transects (except F Street Marsh, $n = 9$ transects) that were spaced at 5-m intervals along one side of each plot. This ensured that the entire length of each plot was sampled. Five randomly placed circular quadrats, each measuring 1 m^2, were then sampled along each transect, for a total of 591 samples, or 10% of the study area. We measured the following variables within each quadrat: (1) percent cover by species; (2) average vegetation height across the quadrat; (3) maximum height of vegetation; and (4) percent cover of bare ground, channel, and litter (both organic and inorganic). We established six cover classes (<1%, 1–5%, 6–25%, 26–50%, 51–75%, 76–100%) to rank percent cover, and used the midpoints of these intervals in statistical analyses (Pacific Estuarine Research Laboratory 1990). Maximum height was the highest point of herbaceous vegetation recorded in a quadrat, and mean height was determined by measuring three random plants in each quarter of the quadrat. The coefficient of variation (CV) of plant height was calculated from mean plant heights.

Territories with ≥50% of their area outside of a study plot were excluded from statistical analyses. We used ANOVA to assess differences in reproduction among study plots and habitat types. Data for high-marsh (SH1 and SH2) and mid-marsh (SM1 and Vener Pond) plots were similar biologically and were combined for this analysis. Study plots were categorized as "large, connected" marsh (SH1, SH2, SM, Vener Pond), "small, connected" marsh (D

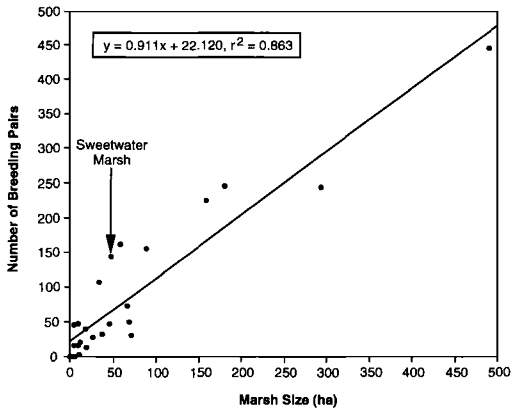

FIG. 2. Relationship between Belding's Savannah Sparrow populations and wetland size. Population data are from a 1986 statewide census (Zembal et al. 1988).

Street), or "small, isolated" marsh (F Street). Comparisons among groups were made using Sheffé's method (Sokal and Rohlf 1981). We used stepwise discriminant function analysis (DFA) to explore how well the habitat variables distinguished high- from low-success territories, and sparrow territories from non-territories (Wray and Whitmore 1979). We grouped percent cover by plant species into high-marsh (*Cordylanthus maritimus, Cressa truxillensis, Distichlis spicata, Juncus acutus, Lasthenia glabrata, Limonium californicum, Monanthochloe littoralis, Salicornia subterminalis*), mid-marsh (*Cuscuta salina, Frankenia salina, Jaumea carnosa, Salicornia virginica, Suaeda esteroa, Triglochin concinnum*), and low-marsh (*Batis maritima, Salicornia bigelovii, Spartina foliosa*) species. Edge (*Amsinckia spectabilis, Baccharis pilularis, Lycium californicum, Mesembryanthemum* spp., *Sonchus asper, Spergularia* spp.), exotic (*Bromus diandrus, Bromus mollis, Bromus rubens, Chrysanthemum* spp., *Hemizonia pungens, Parapholis incurva, Raphanus sativus*), and dune (*Camissonia cheiranthifolia, Heliotropium curvassavicum, Melilotus indica*) species also were combined. Thus, the 14 variables included total percent plant cover; cover by high-marsh, mid-marsh, low-marsh, edge, exotic, and dune species; mean, maximum, and CV of plant height; number of plant species; and percent cover by bare ground, litter, and tidal channels.

Results.—We found a positive relationship ($r^2 = 0.86$, $P < 0.01$) between indices of sparrow population size and wetland size for the 26 marshes where Belding's Savannah Sparrows have been found over the past 20 years (U.S. Fish and Wildlife Service unpublished data; Fig. 2). The relationship may have been stronger, but was influenced by the small number ($n = 4$) of wetlands larger than 100 ha in southern California. Belding's Savannah Sparrows were found in all but four of the 26 salt marshes in 1986; all of the marshes where no sparrows were found were smaller than 10 ha (Zembal et al. 1988).

By 23 March 1995, 54 males had established territories in the six plots, with the lowest densities found at F Street Marsh and the highest within the main Sweetwater Marsh complex (Table 1). Two males at D Street, one at F Street, and one at SM failed to attract a mate during the breeding season, whereas five males (SM, SH1, and SH2) were serial polygynists, attending two different females on each of their territories. In 1996, 45.5% of the banded males established territories on the same plots as in 1995. None of the three banded males at F Street, however, was seen in 1996. No birds banded as nestlings at Sweetwater Marsh were seen after fledging. Nesting densities (number of territories/study plot) were negatively correlated with mean territory size ($r^2 = 0.68$, $n = 6$, $P = 0.04$). Territory size ranged from 84.5 to 999.5 m^2; no differences were found among the six

TABLE 1. Number, size ($\bar{x} \pm$ SD), and reproductive index (based on ranking system of Vickery et al. [1992]) for Belding's Savannah Sparrow territories on 1-ha plots in three marsh types (centered in bold print) in coastal California in 1995.

Study plot	Habitat type	No. territories	Territory size (m^2)	Reproductive index: Low (<5)	Reproductive index: High (≥5)
		Large, connected			
SH1	High-marsh	8	545.2 ± 184.6	0	8
SH2	High-marsh	11	496.1 ± 166.1	1	10
SM2	Mid-marsh	15	303.7 ± 159.1	6	9
Verner Pond	Mid-marsh	8	382.3 ± 229.4	4	4
		Small, connected			
D Street	Mid-marsh	9	543.6 ± 281.7	5	4
		Small, isolated			
F Street	Mid-marsh	3	625.5 ± 186.9	3	0
All sites	—	54	447.2 ± 218.6	35%	65%

TABLE 2. Habitat variables ($\bar{x} \pm$ SD) sampled at Belding's Savannah Sparrow territories (high and low success) and "non-territories" (unoccupied areas) in coastal California in 1995.

Variable	High success (n = 172)	Low success (n = 82)	Non-territory (n = 337)	Discriminant function analysis[a]: Territory vs. non-territory	Discriminant function analysis[a]: High success vs. low success
No. plant species	5.2 ± 2.5	5.8 ± 2.2	4.8 ± 2.8	—	—
Max. height (cm)	56.8 ± 18.2	49.6 ± 17.1	45.7 ± 25.6	—	—
Mean height (cm)	27.2 ± 11.6	21.2 ± 8.8	19.8 ± 12.6	−0.17	−0.77
CV height (cm)	3.5 ± 1.7	4.0 pm 1.3	3.6 ± 2.1	−0.31	—
% Bare ground	13.4 ± 26.5	15.5 ± 25.5	25.8 ± 34.8	0.41	−0.64
% Litter	11.7 ± 23.4	16.8 ± 28.9	9.9 ± 20.3	−0.36	0.21
% Channel	3.1 ± 11.2	4.6 ± 17.8	2.6 ± 12.1	−0.19	0.17
% Total plant cover	77.9 ± 23.2	76.5 ± 22.0	66.8 ± 33.4	—	—
% High-marsh spp.	73.8 ± 49.9	52.2 ± 49.2	40.9 ± 45.4	−0.22	−0.35
% Mid-marsh spp.	31.9 ± 31.8	41.2 ± 27.9	30.7 ± 31.4	—	—
% Low-marsh spp.	8.8 ± 16.7	18.8 ± 20.5	20.9 ± 25.9	0.69	0.27
% Edge spp.	2.8 ± 8.1	0.4 ± 0.2	1.1 ± 5.6	—	−0.29
% Exotic grasses	0.4 ± 0.3	0.5 ± 0.3	1.1 ± 5.3	—	0.24
% Dune spp.	0.0 ± 0.1	0	1.3 ± 5.9	0.47	—

[a] Values are correlation coefficients for forward stepwise discriminant function analysis.

plots (Table 1). None of the birds banded at Sweetwater Marsh prior to the 1995 breeding season was subsequently seen at any other marsh within the San Diego Bay area.

Based on the reproductive index, 65% of the breeding pairs received a rank of 5 or higher (Table 1). Comparisons of reproductive indices among plots (F = 7.9, df = 3 and 48, $P < 0.01$) showed differences between higher ranks within high-marsh plots (SH1 and SH2 combined), and lower ranks at F Street ($P < 0.01$), where no fledglings were seen. Likewise, comparisons among fragment categories (F = 5.6, df = 2 and 49, $P < 0.01$) showed that large marshes had higher reproductive indices ($P < 0.05$) than small, isolated marshes (Table 1). The number of fledglings observed per nesting pair over the breeding season ranged from 0 to 4 ($\bar{x}$ = 1.2 ± SD of 1.2). This figure was an underestimation, however, because young Savannah Sparrows behave cryptically after leaving the nest (Ross 1980a), and few nestlings were banded. We found no relationship between territory size and reproductive success.

Eight of the 14 habitat variables entered into the forward stepwise DFA, with percent cover of bare ground and mean plant height being the best predictors of high-success versus low-success territories (Table 2). High-success territories were classified correctly in 88% of the cases using DFA, but low-success territories were classified correctly in only 37% of the cases. When we developed a model for territories versus non-territories, the best discriminators were percent cover of low-marsh plants, percent cover by dune species, and percent bare ground. The model correctly classified territories (64%) and non-territories (68%) based on 8 of the 14 habitat variables. Habitat characteristics of low-success territories were similar to those of high-success territories with respect to percent cover by bare ground and low-marsh plants, but overlapped with non-territories for plant height and percent cover by high-marsh species (Table 2). Few of the study plots, with the exception of F Street, had much space unoccupied by territories except for those areas with high percent cover by bare ground. Most of the vegetated areas consisting of mid- and high-marsh plant species were occupied by territories throughout the breeding season.

Six of the seven nests we located successfully hatched young. Four of the seven nests were built within vegetation dominated by *M. littoralis*, and another nest was built in both *M. littoralis* and *S. subterminalis*. The remaining two nests were built within *S. virginica* and *B. maritima*. Nests were placed close to the ground ($\bar{x}$ = 3.3 ± 5.3 cm) where the amount of plant cover surrounding the nests was high ($\bar{x}$ = 99.0 ± 1.4%).

Discussion.—Numbers of Belding's Savannah Sparrows increase with size of wetland area (see Herkert 1994 for similar results in migratory Savannah Sparrows), but only four extant wetlands in southern California are larger than 100 ha. Marshes smaller than 10 ha were less likely to support breeding sparrows.

Size and isolation of habitat of marshes in San Diego Bay appeared to be related to reproductive success, but our sample size warrants further study. Although F Street Marsh was larger than D Street Marsh, it was isolated from other marsh habitats and surrounded completely by an urban landscape. This small site supported breeding sparrows but produced no offspring during our study. In addition, no movements of banded birds were observed between

F Street and other marshes in the area, indicating that immigration may be limited. Future investigations should examine reproductive success and dispersal across a broader landscape of remnant marshes than we studied.

Other species of salt marsh-nesting sparrows, such as the Seaside Sparrow (*Ammodramus maritimus*), suffer nest loss during high tides (Marshall and Reinert 1990). Nesting habitat in drier portions of the marsh often is not limited, unlike marshes in southern California. Belding's Savannah Sparrows established territories throughout salt marsh habitats, but were associated with drier sites that had tall, dense vegetation. High tides (>1.9 m) inundated all of our study plots each month from April to August, but it was unknown whether any nests were lost during these events. The fact that Belding's Savannah Sparrows established territories even in wetter sites, however, suggested that habitat was limited.

In southern California, development surrounding coastal marshes has influenced the high-marsh habitat because it typically is dry most of the year and may not have been delineated as "wetland" prior to the establishment of recent guidelines. Thus, Belding's Savannah Sparrow habitat has been restricted not only in overall availability, but also within the high-marsh. This creates a tradeoff for the sparrows. Nests that are located away from potential tidal inundation are closer to the wetland edge, where the effects of predation and human disturbance may be higher. The edges of most salt marsh remnants in this region are "hard," abutting urban landscape features such as roads, flood-control channels, airport runways, and residential lawns.

Reproductive success has not been linked to habitat characteristics in a convincing manner in migratory Savannah Sparrows (Ross 1980a, Bédard and LaPointe 1984, LaPointe and Bédard 1985, Wheelwright and Rising 1993). Although variation in reproductive success of Savannah Sparrows in northern climates has been attributed to variation in weather (Welsh 1975, Ross 1980a, Bédard and LaPointe 1985), no severe weather occurred during the breeding season in 1995, which is typical of the Mediterranean climate in southern California. Predation on adults, eggs, and young, however, may be related to habitat features, with dense vegetation providing more escape cover than do open areas (Ross 1980b, Bédard and LaPointe 1984, LaPointe and Bédard 1986, Watts 1991). Our study showed that high-success territories were associated with tall, dense vegetation within large marsh fragments.

Conservation implications.—Preservation of wetlands is critical for many species. Avian species richness has been correlated with wetland area in freshwater marshes, although not all species are area-dependent (Brown and Dinsmore 1986, Celada and Bogliani 1995). Despite the positive relationship between wetland area and avian diversity, small wetlands are critical for poor dispersers, and modeling has shown that loss of small wetlands can increase the extinction risk for certain taxa (Gibbs 1993). Moreover, habitat fragments that serve as population sinks may be important, because they can augment the size of metapopulations and contribute to genetic diversity (Howe et al. 1991, Fleischer 1995). In addition to effects on populations, wetlands that are isolated from natural upland habitats may have lower biodiversity (Burke and Gibbons 1995).

Although coastal salt marshes may not support a high diversity of breeding birds compared with freshwater wetlands (Burger et al. 1982), they are critical to wetland-dependant species such as Belding's Savannah Sparrows. Our results underscore the need for restoration plans (Zedler 1996) that include the preservation and enhancement of both large and small salt marsh ecosystems (Bildstein et al. 1991, Erwin et al. 1995).

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