

## MULTIPLE-SCALE HABITAT RELATIONSHIPS OF TIDAL-MARSH BREEDING BIRDS IN THE SAN FRANCISCO BAY ESTUARY

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*Abstract.* We modeled the abundance or probability of occurrence of several tidal-marsh-dependent birds found in the San Francisco Bay estuary—the San Pablo Song Sparrow (*Melospiza melodia samuelis*), Alameda Song Sparrow (*M. m. pusillula*), Suisun Song Sparrow (*M. m. maxillaris*), Salt Marsh Common Yellowthroat (*Geothlypis trichas sinuosa*), California Black Rail (*Laterallus jamaicensis coturniculus*), and Marsh Wren (*Cistothorus palustris*)—based on marsh characteristics at several scales. Local habitat variables included vegetation type, structure, and height, and tidal-channel characteristics. Landscape variables included marsh size and configuration, distance to edge, and type of surrounding land use. For each species considered, both landscape and local habitat factors were significant predictors in multi-variable, multi-scale, linear or logistic regression models. While the best models contained both local and landscape variables, all four bird species were also well predicted by local habitat or landscape variables alone. Predictor variables differed by species, but each species responded strongly to vegetation composition (specific plant species) as well as the overall structure (height or complexity) of the vegetation. Scale effects also differed by species. For Song Sparrows, land-use variables were most important at a relatively small spatial scale (500 m) while for Marsh Wrens and Common Yellowthroats they were important at the largest scale examined (2,000 m). Certain elements of vegetation type and structure, as well as marsh size and configuration (perimeter to area ratio) and surrounding land use, were important across several species, suggesting a suite of habitat and landscape characteristics that may be useful in identifying sites important to multiple bird species.

*Key Words:* *Cistothorus palustris*, *Geothlypis trichas sinuosa*, habitat selection, *Laterallus jamaicensis coturniculus*, *Melospiza melodia*, San Francisco Bay, tidal marsh.

## RELACIONES DE HABITAT A ESCALAS MULTIPLES DE AVES REPRODUCTORAS DE MARISMA DE MAREA EN EL ESTUARIO DE LA BAHÍA DE SAN FRANCISCO

*Resumen.* Modelamos la abundancia de la probabilidad de ocurrencia de varias especies de aves dependientes de marisma de marea, encontradas en el estuario de la Bahía de San Francisco—el Gorrión Cantor de San Pablo (*Melospiza melodia samuelis*), el Gorrión Cantor de Alameda (*M. m. pusillula*), el Gorrión Cantor Suisun (*M. m. maxillaris*), la Mascarita Común de Marisma Salado (*Geothlypis trichas sinuosa*), la Polluela Negra de California (*Laterallus jamaicensis coturniculus*), y el Chivirín Pantanero (*Cistothorus palustris*)—basados en las características de la marisma a diferentes escalas. Las variables locales incluyeron el tipo de vegetación, estructura y altura, y las características del canal de la marea. Variables del paisaje incluyeron el tamaño de la marisma y su configuración, la distancia a la orilla, y tipo de uso del suelo de los alrededores. Para cada especie considerada, tanto el paisaje como los factores locales del hábitat fueron vaticinadores significativos en los modelos de multi-variable, multi-escala, lineal o de regresión logística. Mientras que los mejores modelos contenían tanto variables locales como de paisaje, las cuatro especies fueron también bien pronosticadas por el hábitat local o las variables de paisaje solas. Las variables de predicción se diferenciaron por especies, pero cada especie respondió fuertemente a la composición de la vegetación (especies de planta específicas) como también a la estructura total (altura o complejidad) de la vegetación. Efectos de escala también difirieron por las especies. Para los Gorriónes Cantores, las variables del uso del suelo fueron más importantes a una escala espacial relativamente pequeña (500 m), mientras para los Chivirines Pantaneros y las Mascaritas Comunes de Marisma Salada fueron más importantes a la escala mayor examinada (2,000 m). Ciertos elementos del tipo y de la estructura de la vegetación, como también el tamaño y la configuración de la marisma (perímetro al radio del área) y el uso del suelo de los alrededores, fueron importantes a través de algunas especies, sugiriendo un juego de características del hábitat y el paisaje que quizás sea utilizado para identificar sitios importantes para múltiples especies de aves.

Tidal marsh, formerly the dominant habitat type in the San Francisco Bay estuary (hereafter the estuary), has been reduced to <20% of its original extent as a result of human activities, such as diking, dredging, and urban development (Goals Project 1999). In addition, many remaining tidal marshes have been hydrologically altered and subdivided by levees, mosquito-control ditches, boardwalks, and power lines. Many have also been

degraded by contaminants, invasive species, and recreational use (Takekawa et al., chapter 11, *this volume*). This habitat loss and degradation has adversely affected a unique assemblage of marsh-dependent plants, animals, and invertebrates, many of which are specifically adapted to the range of salinity and tidal regimes in the estuary's marshes.

Tidal-marsh passerine birds, including three endemic subspecies of Song Sparrow (San Pablo Song Sparrow [*Melospiza melodia samuelis*], Alameda Song Sparrow [*M. m. pusillula*], and Suisun Song Sparrow [*M. m. maxillaries*] hereafter referred to as Song Sparrows or tidal-marsh Song Sparrows), the endemic Salt Marsh Common Yellowthroat (*Geothlypis trichas sinuosa*), and the Marsh Wren (*Cistothorus palustris*), have experienced a severe habitat loss, and have been restricted in many areas to isolated and degraded marsh fragments with extensive urban upland edges. All but the Marsh Wren are considered species of special concern by the state of California. The California Black Rail (*Laterallus jamaicensis coturniculus*), a state of California threatened species and a federal species of management concern, is a tidal-marsh-dependent species that is now absent from many estuary marshes, and its small population size raises concerns about its long-term persistence in the estuary (Evens et al. 1991, Nur et al. 1997). All of these species merit special attention due to their limited distributions and relatively small population sizes, but they may also serve as habitat indicators for other tidal-marsh-dependent plant and animal species, several of which have state and/or federal threatened or endangered status.

Important earlier studies of the three focal songbird species in the San Francisco Bay estuary, primarily concerning the Song Sparrow (Johnson 1956a, b; Collins and Resh 1985, Marshall and Dedrick 1994), were based on field data limited in scale and extent. Until recently, data sufficient for analyzing regional and landscape-level habitat associations have not been available. Studies that published data on estuary-wide songbird distributions (Hobson et al. 1986, Nur et al. 1997) did not generally contain corresponding information on critical habitat and landscape characteristics. Black Rail distribution patterns in the estuary have been more systematically identified due to their special conservation status (Evens et al. 1991, Evens and Nur 2002), but landscape-level habitat associations of this species other than relationship with marsh size have not been previously analyzed.

In 1996, we began conducting annual surveys of breeding songbirds and Black Rails in

21 San Francisco Bay estuary tidal marshes, adding new sites each year to result in a total of 79 marshes surveyed at least once between 1996 and 2003. This comprehensive dataset provides a unique opportunity to examine regional distribution and abundance patterns and, most importantly, to assess the effects of local habitat characteristics, landscape composition, and habitat fragmentation on these distribution and abundance patterns. Knowledge of specific habitat requirements of these tidal-marsh birds will improve the ability of land managers and wildlife agencies to plan restoration, management, and acquisition activities.

All bird species display some degree of specificity in terms of the habitat types in which they choose to set up territories, forage, seek shelter, and breed; habitat relationship models seek to quantify and clarify these apparent preferences (Cody 1985). Birds tend to respond to particular characteristics of vegetation structure and patchiness, often at several scales (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Saab 1999). Habitat characteristics found to be important for wetland birds include various aspects of vegetation structure and density (Collins and Resh 1985, Leonard and Picman 1987, Weller 1994, Benoit and Askins 1999, Whitt et al. 1999, Poulin et al. 2002), water depth and cover (Leonard and Picman 1987, Craig and Beal 1992), and tidal-channel characteristics (Collins and Resh 1985). However, many bird species may also respond to the landscape context of a habitat patch, as well as its size and shape. Numerous studies over a range of habitat types have demonstrated a significant effect of surrounding landscape at various scales on species richness, relative abundance, and nest success of breeding passerines (Flather and Sauer 1996, Bolger et al. 1997, Bergin et al. 2000, Fairbairn and Dinsmore 2001, Naugle et al. 2001, Tewksbury et al. 2002), as well as scale-dependent responses to habitat characteristics (Pribil and Picman 1997, Naugle et al. 1999).

Bird relationships to patch size and shape have been studied in other habitats, especially with regard to the process of habitat fragmentation. Many researchers have evaluated island biogeography (MacArthur and Wilson 1967) principles for habitats ranging from eastern deciduous forest (Ambuel and Temple 1983, Robbins et al. 1989) to southern California chaparral (Soulé et al. 1988, Bolger et al. 1991) to wetlands (Brown and Dinsmore 1986, Naugle et al. 2001). Others have focused on fragmentation as a process occurring along a gradient, recognizing the intermediate stages between

contiguous habitat and isolated fragments (Wiens 1994) and the potential for differential effects on wildlife along that fragmentation gradient (Andrén 1994). More recent reviews and meta-analyses have suggested that, for most species, habitat fragmentation may actually have little demonstrable effect beyond the direct effects of habitat loss and degradation (Bender *et al.* 1998, Harrison and Bruna 1999). In addition, fragmentation effects on breeding birds appear to be scale-dependent (Chalfoun *et al.* 2002, Stephens *et al.* 2004). However, few studies have evaluated the effects of tidal-marsh fragmentation on breeding songbirds or rails (but see Benoit and Askins 2002).

The Baylands Ecosystem Habitat Goals Report (Goals Project 1999) recommended the creation and maintenance of large, interconnected blocks of tidal marsh with a minimum of upland intrusions and urban edge interface. But these recommendations were based largely on expert opinion, rather than empirical evidence. The Goals Report also summarized the best available information at the time regarding the habitat preferences of the Song Sparrow (Cogswell 2000), Salt Marsh Common Yellowthroat (Terrill 2000), and Black Rail (Trulio and Evens 2000), including qualitative analyses of habitat requirements; but at the time, no one had attempted to develop quantitative, predictive multiple scale models for the habitat requirements of these taxa.

For this study we developed models predicting breeding songbird responses to differences in landscape patterns and local habitat characteristics, in order to provide information about an ecosystem that has been increasingly fragmented and degraded by human activities.

The specific objectives of this study were: (1) to identify elements of marsh-vegetation composition and structure that affect Song Sparrow, Salt Marsh Common Yellowthroat, Marsh Wren, and Black Rail abundance or probability of occurrence during the breeding season; (2) to identify the importance of surrounding land use, marsh size, and landscape-scale habitat configuration on abundance or probability of occurrence; (3) to identify the spatial scale at which landscape influences on marsh-bird distribution and abundance are most strongly expressed; (4) to compare the relative influence of local habitat- and landscape-level factors on each species evaluated; (5) to contrast the patterns observed among the four species; (6) to evaluate the variation in relative abundance across the San Francisco Bay estuary; and (7) to consider implications of these results for monitoring programs, restoration projects, and land and wildlife managers.

## METHODS

### STUDY AREA

Study sites were located in tidal marshes throughout the San Francisco Bay estuary in San Francisco, San Pablo, and Suisun bays (Fig. 1). Although access limited marshes available for bird surveys, efforts were made to select sites that encompassed a range of habitat conditions over a broad geographic area. A special effort was made to identify and survey marshes in a range of sizes from the smallest fragments to larger areas of contiguous marsh (Table 1).

The data used in these analyses were obtained from bird surveys conducted during the spring and summer of 2000 and 2001. Point count surveys (Ralph *et al.* 1993) were conducted twice per year and Black Rail surveys were conducted only in 2001.

### POINT-COUNT SURVEY METHODS

We conducted point-count surveys at 421 locations in 54 fully tidal and muted tidal marshes—marshes that receive less than full tidal flow due to physical impediments (Goals Project 1999)—distributed fairly evenly across the estuary (Table 1). Surveys were conducted within 4 hr of sunrise, one or two times between 20 March and 31 May in 2000 and twice between 20 March and 29 May in 2001. Successive survey rounds were conducted at least 3 wk apart.

We placed survey points 150–200 m apart along transects, with a randomly chosen start location and one to 20 points per site, depending on marsh size. In the smallest marsh fragments there was only enough room for one survey point ( $N = 5$ ). Points were often placed along levees or boardwalks to decrease impact to marsh habitat, but where possible they were placed within the marsh vegetation to reduce the bias of sampling from habitat edges. At each point, a trained observer recorded all birds detected by sight and sound for 5 min. For detections within 100 m from the observer, distance was estimated within 10-m bands; detection type (visual or auditory) was also recorded for each bird.

We calculated an abundance index (number of birds detected per hectare) for each passerine species at each survey point within a 50-m radius of the observer to correspond with the area in which we collected vegetation measurements (see below). Because some surveys were conducted from habitat edges, we adjusted this index for area surveyed by dividing by the actual area of marsh habitat surveyed, calculated from geographic information system (GIS)

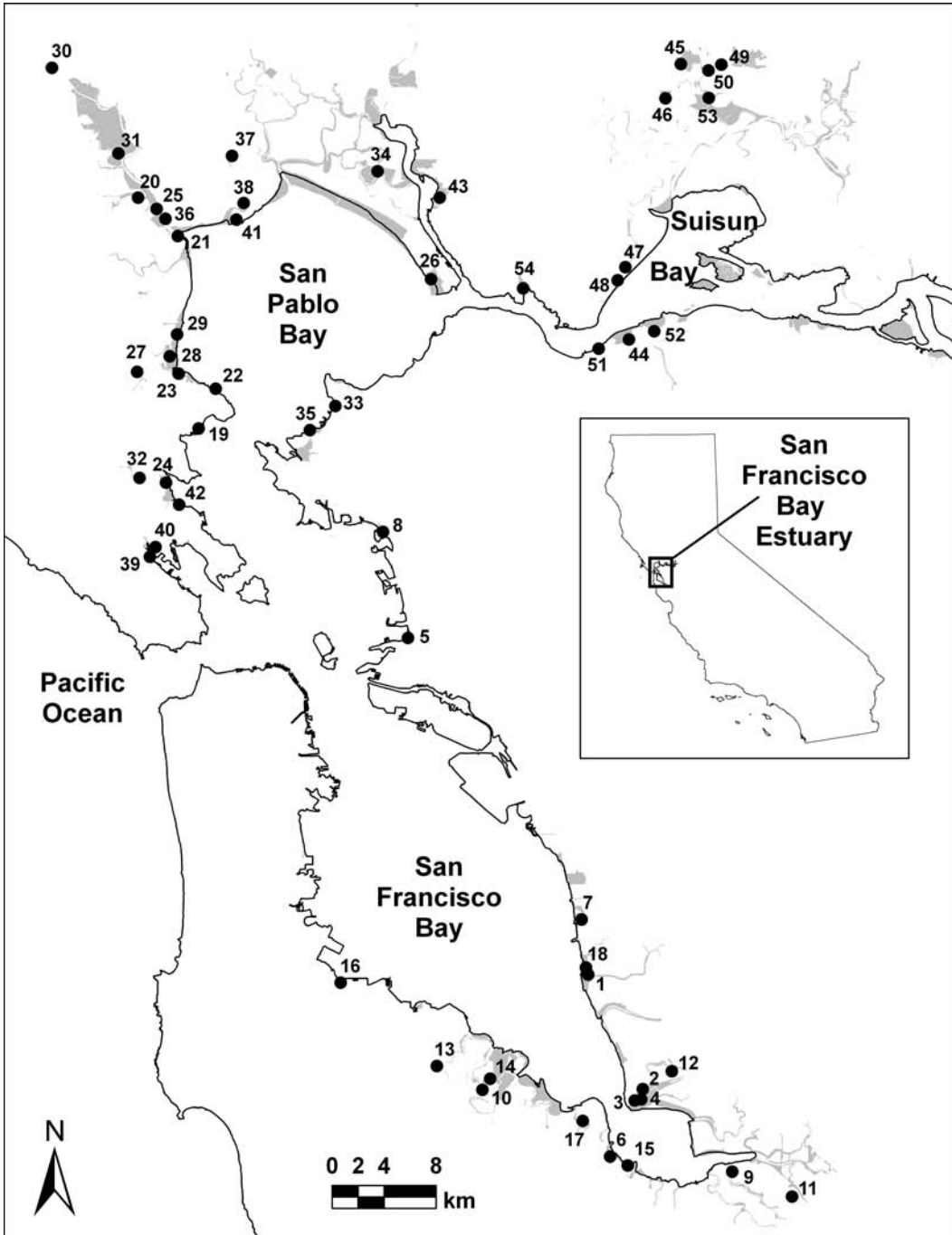


FIGURE 1. San Francisco Bay estuary tidal marsh study sites used in analyses. See Table 1 for corresponding study site names. Tidal-marsh habitat is shown with gray shading.

TABLE 1. TIDAL-MARSH BIRD SURVEY SITES IN THE SAN FRANCISCO BAY ESTUARY SURVEYED BETWEEN MARCH 2000 AND MAY 2001.

Site Name	Number of survey points	Perimeter/area ratio (meters/hectares)	Patch size (hectares)
San Francisco Bay			
1. Old Alameda Creek	6	133.4	234.5
2. Hetch-Hetchy east	5	64.3	446.2
3. Hetch-Hetchy west	7	64.3	446.2
4. Dumbarton Marsh	14	64.3	446.2
5. Emeryville Crescent	5	223.6	20.1
6. Faber-Laumeister Tract, east Palo Alto	7	68.3	124.5
7. Hayward regional shoreline	11	116.3	100.8
8. Hoffman Marsh, El Cerrito	5	209.6	14.8
9. Mouth of Alviso Slough	6	292.4	10.0
10. Middle Bair Island west	5	20.1	1,283.8
11. New Chicago Marsh	6	96.7	1,768.9
12. Newark Slough	7	64.3	446.2
13. Oral B fragment	1	468.9	6.5
14. Outer Bair Island west	3	20.1	1,283.8
15. Palo Alto baylands	9	68.3	124.5
16. Park Plaza fragment	1	396.9	2.0
17. Ravenswood Slough	8	233.2	35.7
18. Whalestail marsh	12	133.4	234.5
Total number of survey points	118		
San Pablo Bay			
19. Beach fragment	1	387.9	1.3
20. Black John Slough	20	34.2	1,806.5
21. Day Island	8	70.6	1,132.8
22. China Camp fragments	2	929.4	0.4
23. China Camp State Park	16	70.6	1,132.8
24. Corte Madera Ecological Reserve	10	96.9	104.6
25. Green Point Centennial Marsh	7	34.2	1,806.5
26. Mare Island	20	37.5	1,428.7
27. Mitchell fragment	3	155.0	11.8
28. McInnis Marsh	10	70.6	1,132.8
29. Hamilton south / McInnis north	10	70.6	1,132.8
30. Petaluma Dog Park	4	98.78	36.7
31. Petaluma Ancient Marsh	9	34.2	1,806.5
32. Piper Park	5	221.4	58.8
33. Point Pinole south	3	256.5	9.3
34. Pond 2A restoration	10	12.1	5,767.8
35. San Pablo Creek	9	97.1	60.6
36. Petaluma River Mouth (Carl's Marsh)	10	67.1	393.0
37. Sears Point	10	164.7	123.2
38. Tolay Creek	11	67.1	393.0
39. Tam High School (Richardson Bay)	5	156.0	38.5
40. Travelodge fragment	1	344.2	2.4
41. Lower Tubbs Island (muted marsh)	8	67.1	393.0
42. Triangle/MCDS fragment	1	204.7	5.0
43. White Slough Marsh	5	71.6	265.2
Total number of survey points	198		
Suisun Bay			
44. Bullhead Marsh	10	65.2	205.8
45. Cordelia fragment	3	13.1	6,658.5
46. Grey Goose	6	13.1	6,658.5
47. Goodyear Slough north	10	13.1	6,658.5
48. Goodyear Slough south	10	13.1	6,658.5
49. Hill Slough east	6	133.5	28.3
50. Hill Slough west	5	171.6	12.8
51. Martinez Regional Shoreline	10	137.5	40.8
52. Point Edith	10	23.1	1,034.5
53. Rush Ranch	10	42.7	557.9
54. Southampton Bay/ Benicia State Park	10	112.7	71.3
Total number of survey points	90		

Note: Numbered site locations are shown in Fig. 1.

data (San Francisco Estuary Institute 2000) and verified in the field. For analysis, the area-adjusted abundance index was averaged over all surveys for that point (see below).

#### BLACK RAIL SURVEY METHODS

Black Rail surveys were conducted at 216 points in 28 San Pablo and Suisun bay marshes (Table 1) between 18 April and 29 May during the breeding season of 2001. We did not survey San Francisco Bay sites because Black Rails are not usually found there during the breeding season. We established one to 20 survey points in each marsh, depending on marsh size. In several marshes we surveyed from rail survey points previously established by Evens et al. (1991), but most marshes were surveyed from points that we established for point-count surveys. Survey points were placed at least 100 m apart but at most sites they were 200 m apart, as was the case for point counts.

Surveys were conducted following a standardized taped-call-response protocol (Evens et al. 1991, Nur et al. 1997). The observer listened passively for 1 min after arriving at the survey point, and then broadcasted tape-recorded black rail vocalizations consisting of 1 min of "grr" calls followed by 0.5 min of "ki-ki-kr" calls. The observer then listened for another 3.5 min for a total of 6 min per point. At each point, rails heard calling  $<30^\circ$  apart were considered the same bird (unless the calls were simultaneous), and those  $>30^\circ$  apart were considered different birds. We summarized the data by counting the number of rails detected within 50 m of the observer to correspond with the point count and vegetation data; this is also the maximum distance at which Black Rails can be reliably counted (Spear et al. 1999).

We determined whether rails were present during any rail survey or breeding season point count survey in either year (i.e., a point was coded absent for Black Rails if none was detected at any survey in 2000 or 2001) and included in our analysis only the points where rail taped-call-response surveys were conducted in 2001.

#### VEGETATION SURVEY METHODS

At each survey point, vegetation and other local habitat data were collected in the field in 2000 or 2001 by trained observers (Table 2). These data were limited to the habitat within 50 m of each point. By walking through the habitat along perpendicular, randomly selected transects we estimated visually the percent of marsh habitat, percent cover of tidal channels,

shrub and non-woody vegetation (and of each individual plant species), and pans or ponds. We scored cover for each habitat variable as proportion of total cover, measured on a 0–1 scale and scored cover of each plant species as proportion of total vegetation cover, also measured on a 0–1 scale. We measured vegetation density by counting the number of times vegetation hit a 6 mm-diameter pole at 10 cm intervals from the ground at five sample points on the transects. We summed all hits, and also summed those under and over 30 cm, a height previously determined to be important for marsh birds and grassland birds (Rotenberry and Wiens 1980, Collins and Resh 1985). For analysis we calculated mean hits for each density-height category. We also measured the distance from the center of the survey point to the nearest tidal channel and that channel's width; and developed a channel index by counting the number of channels of several width categories ( $<1$  m and  $<2$  m) crossed by the transects.

#### GIS METHODS

For each survey-point location, we used ArcView GIS 3.2a (Environmental Systems Research Institute 2000) and extensions to derive a set of landscape parameters characterizing that point and the surrounding marsh. GIS data for bayland habitats were obtained from the EcoAtlas modern baylands GIS layer (San Francisco Estuary Institute 2000). To characterize upland habitats, we derived a composite land-use layer for the San Francisco Bay region consisting of the most recent 1:24,000 land-use GIS layers from the California State Department of Water Resources (Department of Water Resources 1993–1999) where available, and 1:24,000 land-use GIS layers from the U.S. Geological Survey (USGS) Midcontinent Ecological Science Center (1985). We generated three general classes of landscape metrics (Table 3): edge proximity metrics, habitat configuration metrics, and landscape composition metrics.

Edge proximity metrics were calculated for each point-count location using the Alaska Pak extension for ArcView 3.x (National Park Service 2002). Habitat configuration (marsh size and shape) metrics were calculated for the marsh patch underlying each point count using the Patch Analyst extension for ArcView 3.x (Elkie et al. 1999). Marsh patches were defined as contiguous areas of tidal marsh, muted marsh, tidal channels  $<60$  m across, diked baylands, ruderal baylands, managed marsh, and inactive salt ponds (San Francisco Estuary Institute 2000). Landscape composition metrics were calculated for each point-count location

TABLE 2. LOCAL-HABITAT VARIABLES EXAMINED.

Variable	Description
Proportion of cover of dominant native and non-native plant species:	Relative proportion of vegetated area (if >0.01).
Salt grass ( <i>Distichlis spicata</i> )	Short dense grass found in saline soils of upper marsh.
Gumplant ( <i>Grindelia stricta</i> )	Leafy, composite woody shrub with many stems; found on channel banks in more saline marshes.
Rushes ( <i>Juncus</i> spp)	Short rush found in brackish to fresh water areas; most typically Baltic rush ( <i>J. balticus</i> ).
Pepperweed ( <i>Lepidium latifolium</i> )	Tall perennial non-native herb (>1 m tall) found in brackish to fresh areas, along channel banks and in the upper marsh; forms dense tangled canopy mid-season; falls to near-horizontal when foliage is densest.
Common reed ( <i>Phragmites australis</i> )	Tall grass up to 2 m high; forms dense stands; found in brackish to fresh areas; may be non-native.
Pickleweed ( <i>Salicornia virginica</i> syn. <i>Sarcocornia pacifica</i> )	Short often dense perennial, found in upper marsh, saline soils; dominant in San Pablo Bay and San Francisco Bay; typically 30–40 cm tall but can grow taller.
All sedge species and alkali bulrush ( <i>Schoenoplectus</i> spp. and <i>Bolboschoenus maritimus</i> )	
Common tule and California bulrush ( <i>Schoenoplectus acutus</i> - <i>S. californicus</i> )	Tall, rounded perennial sedge (>2 m tall) found in brackish to fresh areas; often on channel banks, often submerged.
Olney's bulrush ( <i>Schoenoplectus americanus</i> )	Short- to medium-height perennial sedge found in saltier areas than common tule and California bulrush; old stems form dense structure used for nesting.
Alkali bulrush ( <i>Bolboschoenus maritimus</i> )	Medium height triangular perennial sedge found in saltier areas than Olney's bulrush; old stems form dense structure used for nesting.
Smooth cordgrass ( <i>Spartina alterniflora</i> ; non-native invasive)	Perennial cordgrass forms taller (>1 m), denser stands in lower and higher elevations than native California cordgrass; interbreeds with and outcompetes native; focus of invasion in the estuary is San Francisco Bay.
California cordgrass ( <i>Spartina foliosa</i> )	Native perennial cordgrass (~1 m) found in narrow band in low marsh and in channels.
All <i>Spartina</i> spp.	
Cattails ( <i>Typha</i> spp.)	Tall (>1 m) perennial in fresh water areas.
Vegetation species richness	Total number of plant species counted within 50 m.
Vegetation species diversity	Shannon diversity index <sup>a</sup> .
Ground cover proportion	Estimated ground cover proportion within 50 m of survey point.
Marsh habitat proportion	Estimated proportion of marsh habitat, including internal levees, within 50 m of survey point.
Shrub cover proportion	Shrubs including gumplant and coyote brush ( <i>Baccharis pilularis</i> ).
Vegetation cover proportion	All herbaceous and woody marsh vegetation
Pond/pan cover proportion	Estimated proportion of tidal or non-tidal open water or dry pans within 50 m of survey point.
Channel cover proportion	Estimated proportion of tidal channels or sloughs within 50 m of survey point.
Distance to closest channel (meters)	Distance to closest channel >0.2 m in width.
Width of closest channel (meters)	Width of the closest channel >0.2 m in width.
Channel density; channels <1 m in width	Number of channels of less than 1-m width crossed on two 100-m transects centered on survey point and set at right angles; divided by total length of transects.
Channel density; channels <2 m in width	As above but using channels of <2-m width.
Number of stems at height:	Mean count of stems touching a 6-mm dowel placed at five sample points (predetermined distances but randomly selected directions from center survey point).
<10 cm	
10–20 cm	
20–30 cm	
<30 cm	
>30 cm	
Total number of stems	Sum of all stems counted.

<sup>a</sup> (Krebs 1989).

Note: All variables were measured within a 50-m radius circle of survey points. Only variables that were significantly correlated with bird abundance or probability of occurrence ( $P < 0.05$  for passerine species;  $P < 0.20$  for Black Rail [*Laterallus jamaicensis*]; see text) were considered in the model selection procedure.

TABLE 3. LANDSCAPE METRICS CALCULATED FROM GIS DATA LAYERS.

Landscape metric	Type	Data source <sup>a</sup>
Edge proximity		
Distance to nearest water edge (meters)	Point	EcoAtlas.
Distance to nearest non-marsh edge (meters)	Point	EcoAtlas.
Distance to nearest upland edge (meters)	Point	EcoAtlas.
Distance to nearest urban edge (meters)	Point	EcoAtlas, DWR, USGS.
Habitat configuration <sup>b</sup>		
Marsh patch size (hectares), Log [marsh patch size, hectares]	Patch	EcoAtlas.
Distance to nearest marsh patch (meters)	Patch	EcoAtlas.
Marsh patch perimeter/area ratio (meters/hectare)	Patch	EcoAtlas.
Fractal dimension: $[2 \times \log [\text{patch perimeter (meters)}]] / [\text{patch area (meters}^2\text{)}]$	Patch	EcoAtlas.
Landscape composition		
Tidal and muted marsh proportion within circles of radius 500 m/1,000 m/2,000 m	Point	EcoAtlas.
Non-tidal wetland proportion within circles of radius 500 m/1,000 m/2,000 m	Point	EcoAtlas, DWR, USGS.
Urbanization proportion within circles of radius 500 m/1,000 m/2,000 m	Point	EcoAtlas, DWR, USGS.
Agriculture proportion within circles of radius 500 m/1,000 m/2,000 m	Point	EcoAtlas, DWR, USGS.
Salt pond proportion within circles of radius 500 m/1,000 m/2,000 m	Point	EcoAtlas, DWR, USGS.
Agriculture proportion within circles of radius 500 m/1,000 m/2,000 m	Point	EcoAtlas, DWR, USGS.

<sup>a</sup>DWR = California Department of Water Resources (1993–1999), USGS = U.S. Geological Survey (1996), EcoAtlas (SFEI 2000).

<sup>b</sup> Marsh patches were defined as contiguous areas of tidal marsh, muted marsh, tidal channels <60 m across, diked baylands, ruderal baylands, managed marsh, and inactive salt ponds (San Francisco Estuary Institute 1998).

Note: Point-level metrics were calculated from the center of the point count station. Patch-level metrics were calculated for the entire marsh patch, which generally included several point-count locations.

by creating circular buffers of different widths (500, 1000, and 2000 m) and using ArcView's Spatial Analyst extension (Environmental Systems Research Institute 1999) to calculate the area of each land use category within each buffer area.

#### STATISTICAL METHODS

For analysis of Song Sparrow abundance, we used a square-root transformation to improve the normality of regression model residuals. Relationships between this variable and the habitat variables were analyzed using linear models (Neter et al. 1990) in Stata 8 (StataCorp. 2003). For the less abundant Common Yellowthroat, Marsh Wren, and Black Rail, we evaluated presence/absence per survey point with logistic regression analysis (Hosmer and Lemeshow 1989) using the logit command in Stata 8 (StataCorp. 2003).

For each species, we constructed linear or logistic regression models (Neter et al. 1990) to assess the separate and combined effects of local habitat and landscape-level variables, and to develop models with maximum explanatory power and predictive ability. We were not testing specific hypotheses about the determinants of bird abundance or presence, but rather attempting to characterize the suite of variables that were important for each species and identify specific habitat and landscape variables of predictive value.

To select local-habitat variables for analysis (from a potential list of 32 variables, Table 2) we first looked at the Pearson correlation coefficient ( $r$ ) between the bird abundance or presence variable and each of the habitat variables. For Song Sparrows, Marsh Wrens, and Common Yellowthroats, we selected the variables for which the pairwise Pearson correlation coefficient was statistically significant ( $P < 0.05$ ); this produced a set of 14–19 candidate local habitat variables for each passerine species. For Black Rails, we used a less stringent significance criterion ( $P < 0.20$ ) because of the reduced sample size (less than half the number of survey stations), but corresponding to a comparable strength of association criterion ( $|r| \geq 0.1$  for all four species).

For each bird species and each surrounding landscape-composition variable (Table 3), we first chose the most appropriate scale of measurement (500-, 1000-, or 2000-m radius), selecting the scale that resulted in the highest  $r^2$  value in a separate multiple variable regression analysis, thus reducing the total number of landscape variables to 15. We also compared the predictive ability of log-transformed marsh area to marsh area untransformed (while controlling for a bay main effect), and selected the best variable for each species.

We used two variable-selection approaches in order to identify two sets of variables: first, a more concise core set of variables (ideally, 5–10 variables) that were the most predictive with



respect to abundance or presence of each species, and second, a more complete set of variables that included the concise set of variables as a subset, but also included variables of lesser importance, which nonetheless could improve the predictive ability to characterize abundance or presence/absence. To compare predictive abilities of the concise models and the inclusive models we used  $r^2$  or, for logistic regression, its analogue, pseudo  $r^2$ .

After reducing the number of candidate variables to be considered, as described above, we constructed local-habitat models using stepwise regression or logistic regression analysis (backward elimination,  $P < 0.05$ ) on our local-habitat variables of interest (Table 2), thus producing a single local-habitat model for each species. Then we repeated this process with landscape variables (Table 3) to generate a landscape model for each species, using the same elimination procedure. We included all landscape variables (for a given spatial scale) in the starting model for each species. In this approach, a habitat or landscape variable was retained only if its retention reduced the deviance of that model by 3.84 units, i.e., reduced AIC by 1.84 units (Lebreton et al. 1992), compared to the comparable model without the specified variable; note that  $AIC = deviance + 2 \times k$ , where  $k$  = number of parameters in the model (Burnham and Anderson 2002).

We compared these models, which we termed concise models, to models obtained through an AIC-minimizing backward stepwise process (Catchpole et al. 2004), which we termed inclusive models. Beginning with the full model, variables resulting in the greatest reduction (and thus improvement) in AIC were removed sequentially until the AIC value could no longer be reduced further and removing the remaining variables would result in an increase in AIC. Thus, the AIC-minimization approach was more inclusive; a variable was retained if so doing reduced the deviance by at least 2.00 units, i.e., reduced AIC by any amount at all. The AIC-minimization criterion is asymptotically equivalent to using a P-value of  $P < 0.157$  to retain a variable when using a likelihood ratio test with 1 df (Lebreton et al. 1992).

To carry out the stepwise AIC-minimization procedure, we used the swaic command for Stata 8.0 (Z. Wang, unpubl. Stata extension). For linear regression models (i.e., for Song Sparrows only), we carried out the stepwise procedure using the comparable P-value to decide whether to retain the specified variable (i.e.,  $P < 0.157$ ).

To evaluate the relative contribution of local-habitat and landscape variables as predictors

of bird abundance/presence, we entered the variables from each final inclusive model (local habitat and landscape) into a single backwards elimination stepwise regression analysis to obtain a combined scale model. We used both selection criteria ( $P < 0.05$  and aic minimization) to arrive at competing final multi-scale models. Finally, we examined each of the remaining significant variables for differences in their effects across bays by testing each variable individually for significant ( $P < 0.05$ ) variable  $\times$  bay interactions, while adjusting for the remaining variables in the model. Where it was possible to test for interactions across all bays (three bays for the passerine species, two bays for the Black Rail), we report any variable whose effect differed significantly across bay regions.

## RESULTS

### SONG SPARROW

Song Sparrow relative abundance (hereafter abundance) was significantly higher in San Pablo Bay than in Suisun or San Francisco bays ( $F_{2,419} = 8.99$ ,  $P < 0.001$ ; Table 4). Controlling for differences among bays, Song Sparrow abundance was positively associated with the cover of the shrubs gumplant (*Grindelia stricta*) and coyote brush (*Baccharis pilularis*) within a 50-m radius of each survey point (Table 5a; Fig. 2). A negative association was found between the cover of rushes (*Juncus* spp.) and ponds and

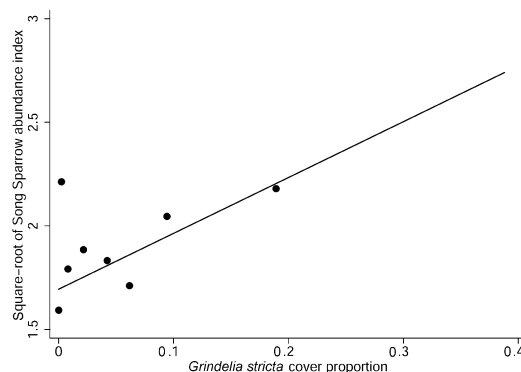


FIGURE 2. Tidal-marsh Song Sparrow (*Melospiza melodia*) abundance versus gumplant (*Grindelia stricta*) cover within 50 m. The linear regression line represents the effect of gumplant cover on Song Sparrow abundance after controlling for all other variables in the final multi-scale model (Table 8a). Points represent the mean abundance for each decile of gumplant cover values (i.e., 10% of the observations contained in each category, with 36% equal to zero). These mean values are shown for illustration purposes only and were not used to calculate regression line.

TABLE 4. MEAN VALUES BY BAY OF DEPENDENT VARIABLES AND SELECTED INDEPENDENT VARIABLES.

Variable	San Francisco Bay	sd (N)	San Pablo Bay	sd (N)	Suisun Bay	sd (N)
<b>Dependent variables</b>						
Song Sparrow ( <i>Melospiza melodia</i> ) abundance index (birds/hectare)	3.39	2.37 (122)	4.15	2.37 (199)	3.01	1.66 (100)
Common Yellowthroat ( <i>Geothlypis trichas</i> ) presence proportion	0.123	0.330 (122)	0.171	0.377 (199)	0.760	0.429 (100)
Marsh Wren ( <i>Cistothorus palustris</i> ) presence proportion	0.451	0.500 (122)	0.482	0.501 (199)	0.940	0.239 (100)
Black Rail ( <i>Laterallus jamaicensis</i> ) presence proportion	-	-	0.438	0.498 (146)	0.381	0.490 (63)
<b>Independent variables</b>						
Salt grass ( <i>Distichlis spicata</i> ) cover	0.027	0.061 (120)	0.056	0.116 (199)	0.075	0.094 (91)
Gumplant ( <i>Grindelia stricta</i> ) cover	0.041	0.065 (120)	0.049	0.063 (199)	0.021	0.034 (91)
Pickleweed ( <i>Salicornia virginica</i> ) cover	0.675	0.212 (120)	0.660	0.266 (199)	0.141	0.228 (91)
All sedge species cover	0.017	0.079 (120)	0.118	0.217 (199)	0.203	0.163 (91)
Alkali bulrush ( <i>Bolboschoenus maritimus</i> ) cover	0.016	0.079 (120)	0.112	0.204 (199)	0.036	0.088 (91)
Vegetation cover	0.810	0.327 (120)	0.888	0.117 (198)	0.883	0.110 (91)
Channel cover	0.140	0.165 (120)	0.057	0.058 (198)	0.055	0.068 (91)
Distance to closest channel (meters)	16.8	17.1 (96)	19.6	32.6 (181)	24.3	29.3 (90)
Number of stems <30 cm	7.40	3.84 (79)	6.86	3.06 (199)	7.90	4.09 (90)
Number of stems >30 cm	0.80	1.760 (84)	1.57	1.47 (199)	5.24	3.44 (90)
Total number of stems	7.40	3.84 (79)	6.86	3.06 (199)	7.90	4.09 (90)
Marsh patch size (hectares)	451	504 (116)	1,159	1214 (214)	2,263	2,966 (94)
Marsh patch perimeter/area ratio (meters/hectare)	110	82 (116)	86.5	103.9 (214)	66	54 (94)
Marsh patch fractal dimension [ $2 \times \log$ [patch perimeter (meter)]]/[patch area (meters <sup>2</sup> )]	1.15	0.567 (115)	1.61	0.478 (214)	1.11	0.028 (94)
Tidal and muted marsh proportion within 2,000 m	0.176	0.116 (120)	0.176	0.114 (210)	0.165	0.123 (95)
Non-tidal-marsh proportion within 2,000 m	0.048	0.051 (120)	0.033	0.043 (210)	0.214	0.188 (95)
Agriculture proportion within 2,000 m	0.005	0.017 (120)	0.150	0.161 (210)	0.011	0.029 (95)
Natural upland proportion within 2,000 m	0.009	0.023 (120)	0.130	0.142 (210)	0.167	0.119 (95)
Urbanization proportion within 2,000 m	0.164	0.195 (120)	0.158	0.193 (210)	0.166	0.159 (95)
Salt Pond proportion within 2,000 m	0.284	0.216 (120)	0.038	0.133 (210)	0	0 (95)
Distance to nearest non-marsh edge (meters)	82	115 (120)	148	125.5 (210)	84	80.4 (95)
Distance to nearest water edge (meters)	351	328 (120)	401	494 (210)	405	317 (95)
Distance to nearest urban edge (meters)	998	905 (120)	737	674 (210)	637	515 (95)
Distance to nearest upland edge (meters)	819	938 (120)	401	557 (210)	256	233 (95)

Note: The bird abundance index represents the number of birds detected per hectare of tidal-marsh habitat surveyed (within a 50-m radius). Presence proportion is the proportion of survey stations with one or more detections of a species over all surveys at that station.

TABLE 5. REGRESSION COEFFICIENTS AND MODEL STATISTICS FOR LOCAL HABITAT REGRESSION MODELS.

(a). SONG SPARROW ( <i>Melospiza melodia</i> )			
$r^2 = 0.176^a$	B + SE	P	Partial $r^2$
Coyote brush ( <i>Baccharis pilularis</i> ) cover	3.46 + 1.05	0.001	0.033
Gumplant ( <i>Grindelia stricta</i> ) cover	2.57 + 0.490	<0.001	0.069
Rushes ( <i>Juncus</i> spp.) cover	-2.49 + 0.653	<0.001	0.041
All sedge species cover		NS	
Olney's bulrush ( <i>Schoenoplectus americanus</i> ) cover		NS	
Alkali bulrush ( <i>Bolboschoenus maritimus</i> ) cover		NS	
Smooth cordgrass ( <i>Spartina alterniflora</i> ) cover	(-)	NS	
Shrub cover		NS	
Vegetation cover		NS	
Pond/pan cover	-0.0145 + 3.87e-2	<0.001	0.044
Distance to closest channel (meters)		NS	
Width of closest channel (meters)		NS	
Channel density <1 m		NS	
Channel density <2 m		NS	
Bay main effect		0.030	0.023
N	401		

(b). COMMON YELLOWTHROAT ( <i>Geothlypis trichas</i> )			
Pseudo $r^2 = 0.427^a$	B + SE	P	Partial $r^2$
Coyote brush ( <i>Baccharis pilularis</i> ) cover		NS	
Rushes ( <i>Juncus</i> spp.) cover	(+)	NS	
Pepperweed ( <i>Lepidium latifolium</i> ) cover	8.84 + 2.79	<0.001	0.028
Common reed ( <i>Phragmites australis</i> ) cover		NS	
Pickleweed ( <i>Salicornia virginica</i> ) cover	(+)	NS	
Common tule and California bulrush ( <i>Schoenoplectus acutus</i> - <i>S. californicus</i> ) cover	(+)	NS	
Olney's bulrush ( <i>Schoenoplectus americanus</i> ) cover	(+)	NS	
Alkali bulrush ( <i>Bolboschoenus maritimus</i> ) cover	3.03 + 0.889	<0.001	0.027
California cordgrass ( <i>Spartina foliosa</i> ) cover		NS	
All <i>Spartina</i> spp. cover		NS	
Cattails ( <i>Typha</i> spp.) cover	(+)	NS	
Vegetation species richness	(-)	NS	
Vegetation species diversity	(+)	NS	
Marsh habitat proportion		NS	
Shrub cover	0.126 + 0.0308	<0.001	0.045
Vegetation cover		NS	
Channel cover	-0.0531 + 0.0267	0.029	0.011
Distance to closest channel (meters)	-0.0222 + 8.88e-3	<0.001	0.049
Width of closest channel (meters)		NS	
Number of stems between 20–30 cm		NS	
Number of stems >30 cm	0.211 + 0.0747	0.004	0.019
Total number of stems		NS	
Bay main effect		<0.001	0.138
N	330		

<sup>a</sup> AIC minimization model  $r^2 = 0.183$ .

<sup>a</sup> AIC minimization model pseudo  $r^2 = 0.489$ ,  $N = 329$ .

Note: NS = not significant and dropped during backwards stepwise process. Signs in parentheses indicate direction of relationship for additional variables retained in an alternative inclusive final model developed using Akaike information criteria (AIC) minimization. For (b), (c), and (d), P values refer to likelihood ratio tests.

pans within 50 m. Using AIC minimization criteria, Song Sparrow abundance was also negatively associated with smooth cordgrass (*Spartina alterniflora*) cover (Table 5a). The local-habitat model (including bay) explained 17.6% of the variance in Song Sparrow abundance (Table 5a).

Landscape-level characteristics were also significant predictors of Song Sparrow abundance.

Song Sparrows responded to land use most strongly at the smallest scale examined, 500 m (Table 6). The final landscape model (including bay) explained 18.8% of Song Sparrow abundance (Table 7a). Abundance was positively associated with log-transformed marsh-patch size (Fig. 3), with the proportion of natural uplands within 500 m, and with the distance of a survey point from the nearest water edge.

TABLE 5. CONTINUED.

(c). MARSH WREN ( <i>Cistothorus palustris</i> )			
Pseudo $r^2 = 0.405^a$	B + SE	P	Partial $r^2$
Coyote brush ( <i>Baccharis pilularis</i> ) cover	60.6 + 23.8	0.002	0.028
Salt grass ( <i>Distichlis spicata</i> ) cover	-6.36 + 1.83	<0.001	0.030
Gumplant ( <i>Grindelia stricta</i> ) cover		NS	
Rushes ( <i>Juncus</i> spp.) cover		NS	
Pepperweed ( <i>Lepidium latifolium</i> ) cover		NS	
Common reed ( <i>Phragmites australis</i> ) cover		NS	
Pickleweed ( <i>Salicornia virginica</i> ) cover		NS	
Common tule and California bulrush ( <i>Schoenoplectus acutus</i> - <i>S. californicus</i> ) cover	(+)	NS	
Olney's bulrush ( <i>Schoenoplectus americanus</i> ) cover	(+)	NS	
Alkali bulrush ( <i>Bolboschoenus maritimus</i> ) cover	17.4 + 3.38	<0.001	0.142
Cattails ( <i>Typha</i> spp.) cover		NS	
Vegetation species richness		NS	
Vegetation species diversity		NS	
Marsh habitat proportion	0.0191 + 8.92e-3	0.027	0.010
Vegetation cover	(+)	NS	
Distance to closest channel (m)	-0.0191 + 6.51e-3	0.002	0.030
Width of closest channel		NS	
Number of stems below 10 cm		NS	
Number of stems between 10-20 cm		NS	
Number of stems <30 cm		NS	
Number of stems above >cm		NS	
Bay main effect		<0.001	0.223
N	361		

<sup>a</sup>AIC minimization model pseudo  $r^2 = 0.428$ , N = 361.

(d). CALIFORNIA BLACK RAIL ( <i>Laterallus jamaicensis</i> )			
Pseudo $r^2 = 0.102^a$	B + SE	P	Partial $r^2$
Salt grass ( <i>Distichlis spicata</i> ) cover	-4.53 + 1.79	0.006	0.032
Gumplant ( <i>Grindelia stricta</i> ) cover	(+)	NS	
Common reed ( <i>Phragmites australis</i> ) cover		NS	
Pickleweed ( <i>Salicornia virginica</i> ) cover	(-)	NS	
Common tule and California bulrush ( <i>Schoenoplectus acutus</i> - <i>S. californicus</i> ) cover	-16.0 + 5.07	<0.001	0.066
Alkali bulrush ( <i>Bolboschoenus maritimus</i> ) cover		NS	
California cordgrass ( <i>Spartina foliosa</i> ) cover	(-)	NS	
All <i>Spartina</i> spp. cover		NS	
Vegetation species richness		NS	
Vegetation cover	(+)	NS	
Distance to closest channel (meters)	(-)	NS	
Channel density <1 m	36.9 + 17.4	0.030	0.020
Channel density <2 m		NS	
Bay main effect		0.023	0.023
N	176		

<sup>a</sup>AIC minimization model  $r^2 = 0.168$ , N = 168.

Note: NS = not significant and dropped during backwards stepwise process. Signs in parentheses indicate direction of relationship for additional variables retained in an alternative inclusive final model developed using Akaike information criteria (AIC) minimization. For (b), (c), and (d), P values refer to likelihood ratio tests.

Negative associations occurred with the proportion of agriculture as well as tidal and non-tidal marsh within 500 m (Table 7). No additional landscape variables were retained using the AIC minimization procedure.

When local habitat and landscape variables were combined in one model, all vegetation and landscape variables remained highly significant

except tidal-marsh proportion (Table 8a). The combined model's explanatory power was 32.2%—close to the summed combined power of the individual local and landscape level models (36.4%). Smooth cordgrass cover was the only additional significant variable retained using the AIC minimization procedure. Controlling for all variables in the final model

TABLE 6. COMPARISON OF RELATIVE SIGNIFICANCE OF THREE DIFFERENT SCALES OF SURROUNDING LAND USE.

Scale	Tidal Marsh Song Sparrow ( <i>Melospiza melodia</i> ) $r^2$	Salt Marsh Common Yellowthroat ( <i>Geothlypis trichas</i> ) pseudo $r^2$	Marsh Wren ( <i>Cistothorus</i> <i>palustris</i> ) pseudo $r^2$	California Black Rail ( <i>Laterallus jamaicensis</i> ) pseudo $r^2$
500 m	<b>0.12</b>	0.33	0.23	0.07
1,000 m	0.11	0.35	0.24	<b>0.09</b>
2,000 m	0.09	<b>0.39</b>	<b>0.26</b>	0.07

Note: For each species, all surrounding land-use variables of a particular scale were put into a model along with bay. The scale of the model with the highest  $r^2$  or pseudo  $r^2$  (values in **bold**) were used for the multi-variable landscape model.

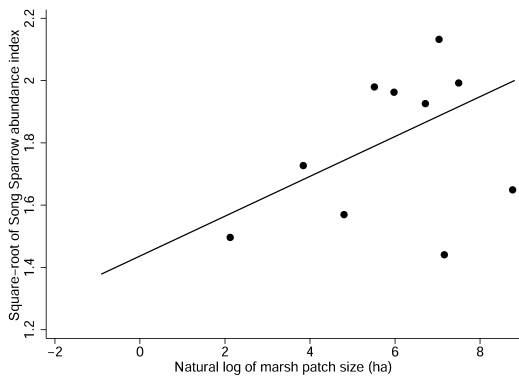


FIGURE 3. Tidal-marsh Song Sparrow (*Melospiza melodia*) abundance index versus log-transformed marsh patch size (hectare). The linear regression line represents the effect of marsh patch size on Song Sparrow abundance after controlling for all other variables in the final multi-scale model (Table 8a). Points represent the mean abundance for each decile of log-transformed patch size (hectare) values (i.e., 10% of the observations contained in each category). These mean values are shown for illustration purposes only and were not used to calculate regression line.

left a significant interaction between bay and the proportion of non-tidal marsh (significantly negative in San Francisco and Suisun bays only) and patch size (significant only in San Francisco and San Pablo bays; Table 9).

#### SALT MARSH COMMON YELLOWTHROAT

The proportion of points with Common Yellowthroats was significantly higher in Suisun Bay than in San Pablo and San Francisco bays; it was lowest in San Francisco Bay ( $F_{2,419} = 99.26$ ,  $P < 0.001$ ; Table 4). For the Common Yellowthroat, local habitat variables (while controlling for variation among bays) predicted 42.7% of the variation in probability of occurrence (Table 5b). Common Yellowthroats were more likely to be found at sites with more stems above 30 cm in height and with higher shrub cover (primarily gumplant and coyote brush), pepperweed (*Lepidium latifolium*) cover and alkali bulrush (*Bolboschoenus maritimus*) cover (Table 5b). A

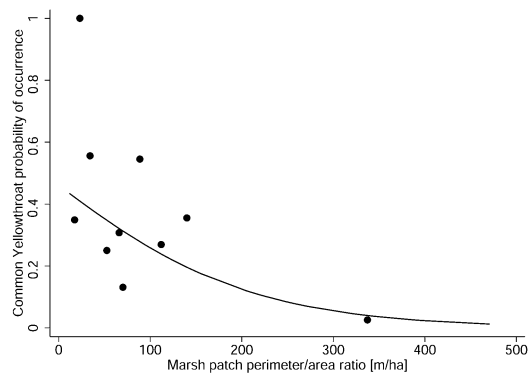


FIGURE 4. Common Yellowthroat (*Geothlypis trichas*) probability of occurrence versus marsh patch perimeter/area ratio (meters/hectare). The logistic regression line represents the effect of marsh patch perimeter/area ratio on Common Yellowthroat probability of occurrence without controlling for any other variables in the final multi-scale model. Points represent the mean probability of occurrence for each decile of perimeter/area ratio values (i.e., 10% of the observations contained in each category). These mean values are shown for illustration purposes only and were not used to calculate regression line.

negative relationship existed with distance to channel and channel cover proportion within 50 m (Table 5b). Using AIC minimization methods, additional positive relationships occurred with cover of rushes, pickleweed (*Salicornia virginica*), common tule (*Schoenoplectus acutus*), Olney's bulrush (*Schoenoplectus americanus*), cattails (*Typha* spp.), and vegetation diversity, and a negative relationship with vegetation species richness (Table 5b).

At the landscape level, Common Yellowthroats were most sensitive to variation in surrounding land use at the 2,000-m scale (Table 6). Common Yellowthroats had a higher probability of occurrence in areas with a higher proportion of agriculture within 2,000 m (Table 7b). A negative relationship occurred with patch perimeter/area ratio (Fig. 4). These variables predicted 38.5% of the variation in presence/absence. Using AIC minimization methods, several additional landscape variables were significantly associated

TABLE 7. REGRESSION COEFFICIENTS AND MODEL STATISTICS FOR LANDSCAPE REGRESSION MODELS.

(a). SONG SPARROW ( <i>Melospiza melodia</i> )			
$r^2 = 0.188^a$	B + SE	P	Partial $r^2$
Distance to nearest water edge (meters)	3.04e-4 + 9.12e-5	0.001	0.024
Distance to nearest non-marsh edge (meters)		NS	
Distance to nearest upland edge (meters)		NS	
Distance to nearest urban edge (meters)		NS	
Marsh patch size (hectares)		NS	
Log (marsh patch size, hectares)	0.128 + 0.0236	< 0.001	0.076
Distance to nearest marsh patch (meters)		NS	
Marsh patch perimeter/area ratio (meters /hectares)		NS	
Marsh patch fractal dimension		NS	
Tidal-marsh proportion within 500 m	-0.326 + 0.164	0.048	0.008
Non-tidal-marsh proportion within 500 m	-1.30 + 0.247	<0.001	0.058
Urban proportion within 500 m		NS	
Agriculture proportion within 500 m	-2.06 + 0.439	<0.001	0.046
Natural upland proportion within 500 m	0.755 + 0.322	0.019	0.012
Salt pond proportion within 500 m		NS	
Bay main effect		0.040	0.014
N	392		

<sup>a</sup> AIC minimization model contained no additional variables.

(b). COMMON YELLOWTHROAT ( <i>Geothlypis trichas</i> )			
Pseudo $r^2 = 0.385^a$	B + SE	P	Partial $r^2$
Distance to nearest water edge (meters)	(-)	NS	
Distance to nearest non-marsh edge (meters)		NS	
Distance to nearest upland edge (meters)	(+)	NS	
Distance to nearest urban edge (meters)		NS	
Marsh patch size (hectares)		NS	
Log (marsh patch size, hectares)	(-)	NS	
Distance to nearest marsh patch (meters)		NS	
Marsh patch perimeter/area ratio (meters /hectares)	-6.93e-3 + 0.307e-3	0.015	0.012
Marsh patch fractal dimension		NS	
Tidal-marsh proportion within 2000 m		NS	
Non-tidal-marsh proportion within 2,000 m		NS	
Urbanization proportion within 2,000 m		NS	
Agriculture proportion within 2,000 m	8.13 + 1.64	<0.001	0.073
Natural upland proportion within 2,000 m	(+)	NS	
Salt pond proportion within 2,000 m		NS	
Bay main effect		<0.001	0.333
N	392		

<sup>a</sup> AIC minimization model pseudo  $r^2 = 0.401$ , N = 392.

Note: NS = not significant. Signs in parentheses indicate direction of relationship for additional variables retained in an alternative inclusive final model developed using Akaike information criteria (AIC) minimization. For (b), (c), and (d), P values refer to likelihood ratio tests.

with Common Yellowthroat presence: distance to nearest upland edge and proportion of natural upland within 2,000 m (positive), distance to the nearest water edge and log marsh size (negative; Table 7b).

Combining the local habitat and landscape variables resulted in a model explaining 51.9% of the variation in probability of occurrence (Table 8). All variables remained significant in this final model, including two that were retained in the AIC minimization procedure for the local or landscape models: common tule and distance to nearest water edge. Additional variables retained here using AIC minimization were cover of rushes, pickleweed, Olney's bulrush, cattails, vegetation species richness,

and vegetation species diversity. A significant interaction was found between bay and patch perimeter/area ratio; the association with perimeter/area ratio was negative in San Francisco and San Pablo bays, but positive in Suisun Bay (Table 9). A significant interaction occurred between bay and pepperweed cover, although it was not possible to test the slopes of all three bays, probably due to small sample size in San Francisco Bay (Table 9).

#### MARSH WREN

Comparing across bays, Marsh Wrens were detected at more points in Suisun Bay, followed by San Pablo and San Francisco bays; this

TABLE 7. CONTINUED.

(c). MARSH WREN ( <i>Cistothorus palustris</i> )			
Pseudo $r^2 = 0.319^a$	B + SE	P	Partial $r^2$
Distance to nearest water edge (meters)	(-)	NS	
Distance to nearest non-marsh edge (meters)	(+)	NS	
Distance to nearest upland edge (meters)	1.61 e-3 + 2.96e-4	<0.001	0.068
Distance to nearest urban edge (meters)	(+)	NS	
Marsh patch size (hectares)		NS	
Log (marsh patch size, hectares)	(-)	NS	
Distance to nearest marsh patch (meters)		NS	
Marsh patch perimeter/area ratio (meters /hectare)	-8.71e-3 + 2.35e-3	<0.001	0.030
Fractal dimension		NS	
Percent tidal-marsh within 2,000 m		NS	
Percent non-tidal-marsh within 2,000 m	(+)	NS	
Percent urban within 2,000 m		NS	
Percent agriculture within 2,000 m	5.79 + 1.12	<0.001	0.057
Percent natural uplands within 2,000 m	(+)	NS	
Percent salt ponds within 2,000 m	-3.20 + 1.19	0.005	0.015
Bay main effect		<0.001	0.202
N	392		

<sup>a</sup> AIC minimization model pseudo  $r^2 = 0.349$ , N = 392.

(d). BLACK RAIL (*Laterallus jamaicensis*)

Pseudo $r^2 = 0.126^a$	B + SE	P	Partial $r^2$
Distance to nearest water edge (meters)	-1.50 e-3 + 7.21 e-4	0.033	0.016
Distance to nearest non-marsh edge (meters)	(-)	NS	
Distance to nearest upland edge (meters)		NS	
Distance to nearest urban edge (meters)		NS	
Marsh patch size (hectares)		NS	
Log (marsh patch size, hectares)		NS	
Distance to nearest marsh patch (meters)	0.017 + 6.96 e-3	0.003	0.032
Marsh patch perimeter/area ratio (meters /hectare)		NS	
Marsh patch fractal dimension		NS	
Tidal-marsh proportion within 1,000 m	2.39 + 0.866	0.005	0.029
Non-tidal-marsh proportion within 1,000 m		NS	
Urbanization proportion within 1,000 m		NS	
Agriculture proportion within 1,000 m	10.8 + 3.54	<0.001	0.044
Natural upland proportion within 1,000 m	2.60 + 1.13	0.021	0.019
Salt pond proportion within 1,000 m		NS	
Bay main effect		NS	
N	204		

<sup>a</sup> AIC minimization model pseudo  $r^2 = 0.134$ .

Note: NS = not significant. Signs in parentheses indicate direction of relationship for additional variables retained in an alternative inclusive final model developed using Akaike information criteria (AIC) minimization. For (b), (c), and (d), P values refer to likelihood ratio tests.

difference was statistically significant ( $F_{2,419} = 42.27$ ,  $P < 0.001$ ; Table 4). The local-habitat model (including bay) explained 40.5% of the variation in Marsh Wren probability of occurrence (42.8% using AIC minimization; Table 5c). Marsh Wren presence was positively associated with the percent marsh habitat within 50 m, as well as with coyote brush and alkali bulrush cover (Fig. 5); and negatively associated with saltgrass (*Distichlis spicata*) cover and distance to closest channel (Table 5c). Using AIC minimization methods, Marsh Wren abundance was also positively associated with total vegetation cover and cover of common tulle, California bulrush, and Olney's bulrush (Table 5c).

Land-use composition variables within a 2,000-m radius were the best explanation of variation in Marsh Wren probability of occurrence (Table 6). Landscape variables (including bay) explained 31.9% of the variation in Marsh Wren presence (34.9% using AIC minimization; Table 7c). Probability of occurrence was negatively associated with the proportion of salt ponds within 2,000 m and with marsh perimeter/area ratio; and positively associated with the proportion of agriculture in the surrounding landscape and with the distance to the nearest upland edge (Table 7c). Using AIC minimization methods, Marsh Wren probability of occurrence was also positively associated

TABLE 8. REGRESSION COEFFICIENTS AND MODEL STATISTICS FOR FINAL COMBINED LOCAL AND LANDSCAPE REGRESSION MODELS.

(a). SONG SPARROW ( <i>Melospiza melodia</i> )			
Model statistics: $r^2 = 0.322$ , $F_{(11,371)} = 16.03$ , $P < 0.001^a$			
Independent variables	B + SE	P	Partial $r^2$
Coyote brush ( <i>Baccharis pilularis</i> ) cover	2.98 + 0.985	0.003	0.019
Gumplant ( <i>Grindelia stricta</i> ) cover	2.73 + 0.468	<0.001	0.066
Rushes ( <i>Juncus</i> spp.) cover	-2.58 + 0.611	<0.001	0.035
Smooth cordgrass ( <i>Spartina alterniflora</i> ) cover	(-)		
Pond/pan cover	-0.0151 + 3.53e-3	<0.001	0.040
Distance to nearest water edge (meters)	2.64e-4 + 8.44e-5	0.002	0.020
Log (marsh patch size, hectares)	0.102 + 0.0171	<0.001	0.080
Non-tidal-marsh proportion within 500 m	-0.963 + 0.176	<0.001	0.058
Agriculture proportion within 500 m	-1.96 + 0.396	<0.001	0.048
Natural upland proportion within 500 m	0.717 + 0.315	0.023	0.012
Bay main effect		0.036	0.013

<sup>a</sup> AIC minimization model  $r^2 = 0.328$ .

(b). COMMON YELLOWTHROAT ( <i>Geothlypis trichas</i> )			
Model statistics: pseudo $r^2 = 0.519$ , likelihood ratio $\chi^2 = 229.9$ , $P < 0.001$ , $N = 342^a$			
Independent variables	B + SE	P	Partial $r^2$
Rushes ( <i>Juncus</i> spp.) cover	(+)		
Pepperweed ( <i>Lepidium latifolium</i> ) cover	16.1 + 4.69	<0.001	0.039
Pickleweed ( <i>Salicornia virginica</i> ) cover	(+)		
Common tule and California bulrush ( <i>Schoenoplectus acutus</i> - <i>S. californicus</i> ) cover	8.32 + 3.89	<0.001	0.026
Olney's bulrush ( <i>Schoenoplectus americanus</i> ) cover	(+)		
Alkali bulrush ( <i>Bolboschoenus maritimus</i> ) cover	4.44 + 1.19	<0.001	0.033
Cattail ( <i>Typha</i> spp.) cover	(+)		
Vegetation species richness	(-)		
Vegetation species diversity	(+)		
Shrub cover	0.0935 + 0.0320	0.003	0.020
Distance to closest channel (meters)	-0.0192 + 9.00e-3	0.016	0.013
Distance to water (meters)	-1.81e-3 + 5.44e-4	<0.001	0.029
Marsh patch perimeter/area ratio (meters /hectare)	-7.85e-3 + 3.58e-3	0.019	0.012
Agriculture proportion within 2,000 m	10.4 + 2.42	<0.001	0.063
Bay main effect		<0.001	0.191

<sup>a</sup> AIC minimization model pseudo  $r^2 = 0.548$ ,  $N = 341$ .

Note: Signs in parentheses indicate direction of relationship for additional variables retained in an alternative inclusive final model developed using AIC minimization. For (b), (c), and (d), P values refer to likelihood ratio tests.

with distance to nearest non-marsh edge and nearest urban edge, and the proportion of non-tidal marsh and natural uplands within 2,000 m; and negatively associated with distance to water, marsh-patch size, and distance to nearest marsh (Table 7c).

Combining local-habitat and landscape variables, the resulting model explained 50.2% of the variation in Marsh Wren probability of occurrence (Table 8). The proportion of marsh within the 50-m point-count radius and the proportion of agriculture in the surrounding 2,000 m were not significant in this final combined model. Using AIC minimization methods, cover of common tule, California bulrush, and Olney's bulrush, distance to water edge, and proportion salt ponds and non-tidal marsh in the surrounding 2,000 m were significant. In the final model a significant interaction was found between bay and coyote

brush cover—the relationship was positive in San Pablo Bay and not significant in the other two bays (Table 9).

#### BLACK RAIL

Black Rails were detected at more points in San Pablo Bay than in Suisun Bay, although this difference was not statistically significant ( $F_{1,180} = 0.89$ ;  $P = 0.35$ ; Table 4). At the local scale, Black Rail presence was negatively associated with common tule, California bulrush, and saltgrass cover; and positively with the number of tidal channels <1-m wide (Table 5d). The local model (including bay) accounted for only 10.2% of the variance in probability of occurrence. Using AIC minimization methods, additional significant variables included a positive relationship with gumplant and total vegetation cover, and a negative relationship with pickleweed and



TABLE 8. CONTINUED.

(c). MARSH WREN ( <i>Cistothorus palustris</i> )			
Model statistics: pseudo $r^2 = 0.502$ , likelihood ratio $\chi^2 = 230.72$ , $P < 0.001$ , $N = 343^a$			
Independent Variables	B + SE	P	Partial $r^2$
Coyote Brush ( <i>Baccharis pilularis</i> ) cover	49.5 + 21.6	0.002	0.020
Saltgrass ( <i>Distichlis spicata</i> ) cover	-5.28 + 2.16	0.009	0.015
Common tule and California bulrush ( <i>Schoenoplectus acutus</i> - <i>S. californicus</i> ) cover	(+)		
Olney's bulrush ( <i>Schoenoplectus americanus</i> ) cover	(+)		
Alkali bulrush ( <i>Bolboschoenus maritimus</i> ) cover	25.4 + 4.87	<0.001	0.147
Distance to nearest channel (meters)	-0.0225 + 7.27e-3	<0.001	0.026
Distance to nearest water edge (meters)	(-)		
Distance to nearest upland edge (meters)	6.23e-4 + 2.63e-4	0.014	0.013
Distance to nearest non-marsh edge (meters)	3.70e-3 + 1.81e-3	0.034	0.010
Marsh patch perimeter/area ratio (meters/hectare)	-0.0121 + 3.18e-3	<0.001	0.040
Non-tidal-marsh proportion within 2,000 m	(+)		
Salt pond proportion within 2,000 m	(-)		
Bay main effect		<0.001	0.230

<sup>a</sup> AIC minimization model pseudo  $r^2 = 0.542$ ,  $N = 343$ .

(d). BLACK RAIL (*Laterallus jamaicensis*)

Model statistics: pseudo $r^2 = 0.180$ , likelihood ratio $\chi^2 = 44.34$ , $P < 0.001$ , $N = 180^a$			
Independent variables	B + SE	P	Partial $r^2$
Total vegetation cover	0.0379 + 0.0188	0.034	0.018
Distance to nearest channel (meters)	(-)		
Distance to nearest marsh patch (kilometers)	-0.0176 + 6.96e-3	0.002	0.038
Tidal-marsh proportion within 1,000 m	2.63 + 0.956	0.005	0.032
Agriculture proportion within 1,000 m	11.7 + 3.66	<0.001	0.055
Natural upland proportion within 1,000 m	5.08 + 1.48	<0.001	0.055
Bay main effect		0.579	0.001

<sup>a</sup> AIC minimization model pseudo  $r^2 = 0.234$ ,  $N = 163$ .

Note: Signs in parentheses indicate direction of relationship for additional variables retained in an alternative inclusive final model developed using AIC minimization. For (b), (c), and (d), P values refer to likelihood ratio tests.

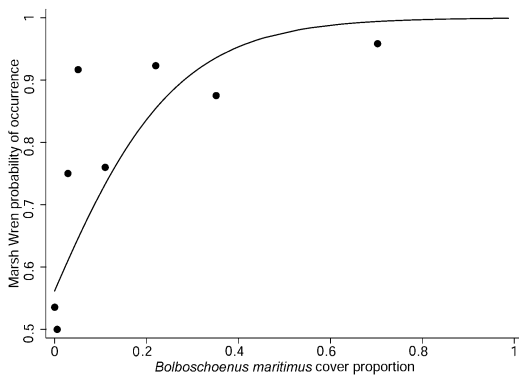


FIGURE 5. Marsh Wren (*Cistothorus palustris*) probability of occurrence versus alkali bulrush (*Bolboschoenus maritimus*) cover within 50 m. The logistic regression line represents the effect of alkali bulrush cover on Marsh Wren probability of occurrence without controlling for all other variables in the final multi-scale model. Points represent the mean probability of occurrence for each fifth percentile of alkali bulrush cover values (i.e., 5% of the observations contained in each category, with 64% equal to zero). These mean values are shown for illustration purposes only and were not used to calculate regression line.

California cordgrass (*Spartina foliosa*) and with distance to closest tidal channel; this model accounted for 16.8% of variance in probability of occurrence (Table 5d).

Land-use composition variables within a 1,000-m radius were the best explanation of variation in Black Rail probability of occurrence (Table 6). At the landscape level, Black Rail presence was positively associated with the proportion of tidal-marsh, agriculture and natural uplands within a 1,000-m radius; and negatively with the distance to the nearest marsh patch and distance to nearest water edge. The landscape model (including bay) predicted 12.6% of the variance in probability of occurrence among points (Table 7d). Using AIC minimization, distance to nearest non-marsh edge was also significantly negatively associated with Black Rail presence, and partial  $r^2$  was slightly higher at 13.4% (Table 7d).

When considering local and landscape variables together, the only local-habitat variable that remained significant was total vegetation cover (which had a positive relationship to Black Rail presence; Table 8d). The landscape variables that remained significant were: distance to nearest

TABLE 9. VARIABLES WHOSE EFFECTS VARIED AMONG BAYS.

Species	Interaction terms	Bay-specific slopes			
		San Francisco	San Pablo	Suisun	
Tidal-marsh Song Sparrow ( <i>Melospiza melodia</i> )	Overall interaction P value				
	Bay × (Non-tidal-marsh proportion within 500 m)	$\beta = -1.46$ +0.390	$\beta = -0.196$ +0.412	$\beta = -1.08$ +0.200	
	P = 0.006	P < 0.001	P = 0.634	P < 0.001	
Marsh Wren ( <i>Cistothorus palustris</i> )	Bay × (patch size)	$\beta = 0.184$ +0.031	$\beta = 0.0866$ +0.0228	$\beta = 0.0423$ +0.0308	
	P = 0.002	P < 0.001	P < 0.001	P = 0.170	
	Bay × (coyote brush [ <i>Baccharis pilularis</i> ] cover)	NS	$\beta = 61.8$ +25.5	NS	
	P < 0.001	P > 0.9	P = 0.015	P > 0.9	
Salt Marsh Common Yellowthroat ( <i>Geothlypis trichas</i> )	Bay × (perimeter / area ratio)	$\beta = -0.0142$ +0.0071	$\beta = -0.0351$ +0.0145	$\beta = 0.0221$ +0.0108	
	P = 0.015	P = 0.038	P = 0.016	P = 0.041	
	Bay × (pepperweed cover) <sup>a</sup>				
	P = 0.011				
California Black Rail ( <i>Laterallus jamaicensis</i> )	Bay × (vegetation cover)	<sup>b</sup>	NS	$\beta = -0.139$ +0.0641	
	P = 0.013		P > 0.9	P = 0.030	

<sup>a</sup> We were not able to estimate the slopes separately for each bay.<sup>b</sup> Black Rails were not surveyed in San Francisco Bay.

Note: We examined for interaction all variables in the final combined models shown in Table 8.

marsh patch (negative); and the three variables related to surrounding land use in the surrounding 1,000 m: tidal marsh, agriculture, and natural uplands, all of which were positively related to rail presence (Table 8d). The variables in the final combined model accounted for 18.0% of the variance in probability of occurrence among points. One additional variable, distance to closest channel, was retained using AIC minimization methods. A significant interaction occurred between bay and vegetation cover—the relationship between Black Rail presence and vegetation cover proportion was positive in Suisun Bay and not significant in San Pablo Bay (Table 9).

## DISCUSSION

Our results demonstrated that each of the four tidal-marsh species we examined responded to both local-habitat features and to broader-scale characteristics of the habitat patch and the surrounding landscape. For each species, we were able to develop separate predictive models that accounted for substantial variation in the distribution or abundance of that species based solely on local habitat features or solely on patch and landscape characteristics. And in each case, the final combined model included both local-habitat and landscape variables. This suggests that the distribution and abundance of tidal-marsh birds is influenced by a range of ecological processes, operating at both small (local) and large (landscape) spatial scales. Clearly, these species are responding to local-habitat (mainly vegetation) characteristics, but vegetation alone may not indicate quality habitat.

Interestingly, landscape models were comparable in terms of predictive ability to local-habitat models in accounting for the local distribution of these species. This suggests that information based on remote sensing data (i.e., aerial photos or satellite imagery) can be used to develop useful broad-scale guidelines for conservation and management of the tidal-marsh bird community. Nevertheless, better predictive models can be developed by incorporating multi-scale data. These results are consistent with other studies in shrub (Bolger et al. 1997) and wetland (Naugle et al. 2001) habitats that have demonstrated the importance of multi-scale habitat-landscape models for predicting variation in bird distribution and abundance. In contrast, others have found that landscape models are either better than local-habitat models (Saab 1999) or worse than local-habitat models (Scott et al. 2003).

This study also demonstrated important differences among species, including the degree to which variation in abundance or probability

of occurrence can be explained by the suite of local habitat and landscape variables that we examined. For Marsh Wrens and Common Yellowthroats, the explanatory power of our models was relatively high; for Black Rails, the explanatory power was fairly low; and for Song Sparrows, our results were intermediate. Marsh Wren and Common Yellowthroat presence were better predicted by local-habitat characteristics while for Song Sparrows and Black Rails landscape-level characteristics were better. Several potential explanations may account for these differences, including variations in species detectability, and the degree of habitat specialization. Black Rail presence has previously been shown to be related to variation in marsh area (Evens and Nur 2001), but here we have evidence of a weak relationship between Black Rail presence at individual points and a large suite of variables at several scales. It is likely that Black Rails may respond more strongly to vegetation or habitat characteristics that we did not quantify, or that their presence is primarily controlled by other ecosystem processes such as predation.

In contrast, the moderately low predictive ability of models for the Song Sparrow—the most abundant tidal-marsh bird species in the estuary being present at 97% of the points surveyed—may reflect the relative generalist nature of this species which is found in a wide range of wet and/or scrubby habitats across North America (Nice 1937, Marshall 1948a, Aldrich 1984, Hochachka et al. 1989, Arcese et al. 2002). The tidal-marsh subspecies, in particular, have the highest reported densities for the species (Johnston 1956b) and are well distributed throughout different parts of tidal marshes, including levees and other upland edges (Cogswell 2000). The San Francisco Bay subspecies (*M. m. pusillula*), has even been found to nest—with low success—in areas invaded by non-native smooth cordgrass (Guntenspergen and Nordby, *this volume*).

Common Yellowthroats and Marsh Wrens responded most strongly to vegetation characteristics, having somewhat more specialized habitat preferences within the marsh primarily related to vegetation structure and height for nesting (Foster 1977a, b; Leonard and Picman 1987, Rosenberg et al. 1991, Marshall and Dedrick 1994).

## INTER-BAY DIFFERENCES

The highest relative abundance of Song Sparrow and presence of Black Rail was in San Pablo Bay, while the Marsh Wren and Salt Marsh Common Yellowthroat were present at more points in Suisun Bay. For each of the

species, inter-bay differences in presence and abundance are likely due primarily to differences in local-habitat characteristics (determined ultimately by salinity, elevation, tidal influence, local seed sources, and disturbance regime), and surrounding land use. In general, San Pablo Bay and San Francisco Bay are higher in salinity than Suisun Bay, and consequently, the vegetation communities are different with more pickleweed-dominated saltmarsh in the former two bays. In the Suisun Bay and in the upper reaches of rivers draining into San Pablo Bay, more tall plant species adapted to brackish or fresh conditions occur; these areas also have a higher plant-species diversity (Josselyn 1983). Many of the brackish plant species more commonly found in Suisun Bay (e.g., bulrush and cattail species) are taller than the high-salinity species (e.g., pickleweed and saltgrass), provide more structure at greater heights, and provide preferred nesting habitat and cover for the Marsh Wren and Common Yellowthroat; whereas the more saline marshes of San Pablo Bay are apparently preferred by the Song Sparrow and Black Rail, both which nest regularly in pickleweed. Black Rails do not regularly nest in San Francisco Bay, likely due to the scarcity of high-marsh habitat (Trulio and Evens 2000).

Controlling for local-habitat and landscape conditions, however, Song Sparrows and Black Rails still had significantly different probabilities of occurrence across bays, suggesting that vegetation influences the abundance of these species but does not completely determine their regional distribution patterns. For both of these species landscape level characteristics were the strongest predictors of abundance or presence.

#### LOCAL HABITAT ASSOCIATIONS

Our local-habitat models provided more specific information on the regional-habitat associations of each species than has been previously reported. Even after controlling for bay and landscape setting, the tidal-marsh bird species examined in this study appeared to respond to species-specific vegetation composition as well as to general vegetation structure and habitat features. One implication of this result is that monitoring and research studies should collect both types of data at the local scale. A long-standing tradition in avian ecology is the obtaining of information on general vegetation structure, but researchers do not always collect information on species-specific vegetation composition, which can be just as important as structure to particular bird species (Wiens and Rotenberry 1981).

The results of our local-habitat models highlight the different habitat associations of each tidal-marsh species evaluated, and accordingly, different management needs. While the Song Sparrow and Marsh Wren both exhibited positive associations with coyote brush, an upland shrub often found in higher elevations on levees and at marsh edges, their similarities ended there. Song Sparrows were more abundant in areas with higher relative cover of the halophytic wetland shrub, gumplant (Fig. 3), which is known to be one of their preferred nesting substrates (Johnston 1956a, b; Nur et al. 1997; PRBO, unpubl. data), and less abundant in rushes which are short, brackish-marsh plants not typically used for nesting, as well as in smooth cordgrass, a non-native cordgrass that is sometimes used for nesting except where it occurs in monotypic stands (Guntenspergen and Nordby, *this volume*). Neither do they typically nest in coyote brush which is found primarily on levees and upland edges, but their positive association with this species was probably due to its value for song perches and cover. Collins and Resh (1985) also found a positive relationship between Song Sparrow density and coyote brush in Petaluma Marsh, an old high-elevation marsh, where coyote brush is common along the high banks of tidal channels. Although the relationships were not significant when controlling for variability in other local-habitat variables (primarily vegetation), Song Sparrows appeared to be most abundant near channels (where vegetation tends to be thickest and highest, especially in saline marshes) and in areas with more medium-width to narrow channels. Others have already demonstrated that Song Sparrow territories tend to be established along channels, sloughs, and mosquito ditches (Johnston 1956a, b; Collins and Resh 1985). Our results suggest, however, that this channel affinity is likely due to the higher availability of shrubs or other dense vegetation along channels, which is preferred for nesting.

Common Yellowthroats were also more likely to be present at points nearer to tidal channels with a greater cover of tall plants, including alkali bulrush, Olney's bulrush, rush and cattail species, and high overall shrub cover. Common Yellowthroats were also strongly associated with the non-native invasive pepperweed, a tall and dense plant found in brackish marshes, particularly in higher elevation areas and along channels. Pepperweed appears to be expanding throughout the region and is difficult to control. While its expansion may be positive for Common Yellowthroat distribution, more information on other effects of pepperweed on Common Yellowthroats and other bird species

is needed. For example, the impact of pepperweed on the food web (particularly on invertebrate populations), and its relative utility as cover for nesting and refuge from predators are unknown.

Marsh Wrens also appeared to be highly associated with channels and with several sedge species, tall plants that are often used for nesting—alkali bulrush (*Bolboschoenus maritimus*; saline, primarily in San Pablo Bay; Fig. 5), common tule and California bulrush (*Schoenoplectus acutus* and *S. maritimus*; fresh-brackish, primarily in Suisun Bay), and Olney's bulrush (*S. americanus*; brackish, primarily in Suisun Bay). The Marsh Wren demonstrated a negative relationship with saltgrass, a short grass found in saltier high-marsh areas that are not likely to be used by the species for nesting or cover. These results are not surprising in that Marsh Wren nests are usually found at approximately 1 m above the ground in tidal marshes (PRBO, unpubl. data); thus they require tall vegetation for nesting.

Black Rails were not positively associated with any particular plant species (other than a weak relationship with gumplant only in the inclusive model), but they did exhibit negative associations with saltgrass, common tule and California bulrush. Saltgrass is used occasionally as a nesting substrate, particularly when mixed with pickleweed and/or alkali bulrush, but areas with large contiguous areas of saltgrass do not apparently make preferred Black Rail habitat. Common tule and California bulrush, unlike the other sedge species in local marshes, are found along and within channels; these species grow most commonly in low-elevation areas subject to regular tidal flooding and generally have little or no vegetation cover beneath them in which Black Rails can nest. The stems are thick, smooth, and rigid and are commonly used as nest substrate only by Marsh Wrens and Red-winged Blackbirds (*Agelaius phoeniceus*). Black Rails were also most likely to be present closer to channels, and in areas with more channels <1 m in width, which are likely to be third- and fourth-order channels found in upper-marsh areas. However, when controlling for landscape variables, the only local-habitat variables that remained significantly associated with Black Rail presence were overall vegetation cover (significant in San Pablo Bay only) and distance to channel; no individual plant species cover variables were significant.

#### LANDSCAPE ASSOCIATIONS

Significant landscape-level predictors of abundance also varied among species, although some relationships were common across several

species. With respect to edge-proximity relationships, we observed some differentiation among species. Song Sparrows had higher abundances away from the water edge (usually open bay), while Marsh Wrens and Common Yellowthroats were more likely to be present away from the upland edge and closer to the water edge, even while controlling for vegetation variables. This may be due in part to the demonstrated vegetation preference of these species, with Song Sparrows preferring to nest in high marsh, in shrubs along marsh edges and channels, and Marsh Wrens and Common Yellowthroats preferring sedge species which are more tolerant of conditions along the bay edge, particularly in San Pablo Bay. However, the relationships between upland water-edge proximity and abundance/presence were similar to the relationships of these variables with various measures of Song Sparrow nest survivorship (PRBO, unpubl. data), suggesting that edge aversion may be related to species-specific predation pressures. For the Black Rail, there was an affinity for marsh edge and water edge, but these variables were not significant when controlling for vegetation cover.

With respect to patch configuration (size and shape), all species except the Black Rail exhibited a strong association with either log-transformed patch size (positive) or patch perimeter/area ratio (negative). The lack of a Black Rail response may be due to the fact that marsh patches as we defined them included non-tidal wetlands that may not be used by this species. This species was not detected in marshes of <8 ha, suggesting that there may at least be a threshold size below which Black Rails do not occur; but our sample size was too small to detect a significant difference at that level (only four marshes smaller than 8 ha were surveyed).

For all three passerine species, the relationship of abundance or presence with size and perimeter/area ratio were correlated (i.e., opposite relationships of similar magnitude), indicating that the negative associations with perimeter/area ratio may have been driven more by patch size than by patch shape. This was also borne out by the lack of importance of the fractal-dimension index, a scale-independent measure of fragmentation or patch shape (McGarigal and Marks 1995). A weak response to landscape pattern (i.e., patch shape), above and beyond landscape composition (marsh size) is consistent with the findings of other recent studies (Fahrig 1997, Harrison and Bruna 1999). Some researchers believe that landscape pattern becomes important only in landscapes with low proportions of suitable habitat (Andr en 1994)

or for species with certain life-history traits (Hansen and Urban 1992).

Nonetheless, the relative importance of patch size and shape differed by species. For the Song Sparrow, only the effect of log-transformed patch size was significant (Fig. 2), and only in Suisun and San Francisco bays. This was the most significant of all variables examined for the Song Sparrow. While we found few marshes that did not contain Song Sparrows, their relative per-point abundance (a measure of relative density, rather than the total number of individuals within a given patch) was higher in large versus small patches, suggesting lower habitat quality in smaller patches, or reduced survivorship due to predation or other factors (Takekawa et al., chapter 11, *this volume*). If survival or reproductive success is reduced in small patches, and recolonization rare, then extirpation could occur over time. The relationship of Song Sparrow density to area was somewhat non-linear—the largest patches did not have the highest densities of Song Sparrows.

For the Common Yellowthroat and Marsh Wren, which did not occur in patches of <8 ha, probability of occurrence (at the survey-point level) increased with patch size but perimeter/area ratio was a stronger predictor of occurrence, suggesting that marsh fragmentation (resulting in a higher perimeter/area ratio) may have some detrimental effects on these species, perhaps by increasing their exposure to edge-associated predators or other negative upland-associated factors. Alternatively, vegetation composition and structure may differ between marsh edges and marsh interiors, due to differences in elevation and hydrology, which may in turn affect these species' distributions. For the Common Yellowthroat, the negative relationship with perimeter/area ratio was evident in San Francisco and San Pablo bays while in Suisun Bay the relationship was actually positive, indicating a probable difference in edge quality among bays.

We also observed an effect of marsh isolation (i.e., reduced probability of occurrence with increase in distance to nearest marsh patch) for all but the Song Sparrow. This is potentially due to the high affinity of these three species for wetland areas, especially the Black Rail, which, in the San Francisco Bay region, is found exclusively in tidal-marsh habitats (Evens et al. 1991). The Common Yellowthroat and Song Sparrow are more likely to use adjacent upland habitats such as ruderal scrub (Song Sparrow) and riparian woodland (Common Yellowthroat and Song Sparrow) during the non-breeding season and therefore are likely to have different barriers to movement and dispersal than the other species

(Cogswell 2000, Terrill 2000); the barriers for Black Rails are probably more extensive than for Song Sparrows.

While all four species responded to surrounding land use, their strongest responses were at different spatial scales ranging from 500–2,000 m. The tidal-marsh Song Sparrow, a year-round tidal-marsh resident with a small territory size (Marshall 1948; Johnston 1956a, b), was most strongly influenced by more immediate landscape conditions (i.e., within 500 m, rather than 1,000 or 2,000 m), and the Black Rail, a secretive species also expected to be fairly sedentary in its habits, responded most strongly to conditions within a 1,000-m radius. The Marsh Wren and Common Yellowthroat were most responsive to land-use characteristics within a 2,000-m radius. The wider-scale sensitivity of the latter two species may be related to the fact that they are less philopatric and are quite mobile during the non-breeding season, with the Common Yellowthroat apparently moving to wetlands outside the San Francisco Bay during the winter (Grinnell and Miller 1944).

Only the Black Rail exhibited a positive relationship with the proportion of tidal-marsh habitat in the surrounding landscape; it is apparently the most tidal-marsh dependent of the four species. However, when controlling for other variables, the proportion of natural upland and agriculture were more important to Black Rails than overall marsh cover (see below). Landscape variables other than tidal marsh were also more important for the other species we examined. Song Sparrows actually exhibited a negative relationship with the proportion of marsh within 500 m.

Song Sparrows were positively associated with natural uplands and negatively associated with tidal and non-tidal marsh and agriculture in the surrounding landscape, reflecting the upland edge and shrub affiliation of this species. Marsh Wrens were negatively associated with the proportion of salt ponds in the surrounding 2,000 m and positively associated with agriculture and natural uplands in the surrounding landscape, also reflecting the use of uplands by this species.

Common Yellowthroats, Marsh Wrens, and Black Rails all exhibited positive associations with the proportion of agricultural land use in the surrounding area, controlling for other variables. Because none of these species actually occur in agricultural fields or pastures, and given that this effect was primarily driven by San Pablo Bay, where agricultural land use is most prevalent, it may actually represent the absence of urban development, or the potential co-occurrence of agricultural lands with less

saline marsh conditions away from the bay edge (for Common Yellowthroats and Marsh Wrens). Alternatively, agricultural lands may actually contain suitable habitats such as riparian woodland (Common Yellowthroats) or freshwater wetland (used by both species). For the Black Rail, which was also positively associated with the proportion of surrounding natural uplands, agricultural lands (and natural uplands) may provide refugia from predation during high tides (when birds are forced out of the marsh onto higher elevations), known to be a period of significant mortality for this species (Evens and Page 1986).

#### CONSERVATION AND MANAGEMENT IMPLICATIONS

The specific local and landscape-level habitat associations quantified herein can provide land managers with the specific information needed to manage for or restore key habitat elements for specific bird species, e.g., gumplant for Song Sparrows, sedge species for Common Yellowthroats and Marsh Wrens, and numerous small channels for Black Rails and Common Yellowthroats.

The range of responses among species to local- and landscape-level habitat factors highlights the importance of preserving a heterogeneous mosaic of tidal-marsh habitat throughout the San Francisco Bay estuary, representing the entire salinity gradient and the resulting diversity of estuarine habitats. In addition, habitat diversity within a site, representing the full elevational and tidal inundation spectrum of a natural marsh, is equally important for providing the habitat elements needed by the full range of tidal-marsh-dependent species. Thus we suggest that large areas of contiguous tidal marsh and adjacent natural uplands be protected and restored, in order to preserve biological and physical heterogeneity at the ecosystem level.

Our results also suggest that landscape context is important for tidal-marsh birds. In particular, marshes surrounded by natural or agricultural

uplands appear to be more valuable than those surrounded by urbanization. This finding should be considered in the evaluation of bayland sites for potential tidal-marsh restoration, as a potential predictor of restoration success.

#### ACKNOWLEDGMENTS

We would like to thank the many field assistants and biologists who collected data for this study, especially J. Wood, E. Brusati, J. Hammond, J. Caudill, S. Cashen, A. Ackerman, S. Webb, E. Strauss, G. Downard, L. Hug, R. Leong, W. Neville, T. Eggert, C. Millett, and S. Macias. G. Geupel, T. Gardali, S. Zack, and J. Evens contributed greatly to the initiation of the study. V. Toniolo helped calculate GIS-based spatial metrics. We would also like to thank J. E. Maldonado and two anonymous reviewers for suggested improvements to the manuscript and to J. Evens for insights related to Black Rails. This study was made possible by grants from the Mary Crocker Trust, the USDI Fish and Wildlife Service Coastal Program, the Bernard Osher Foundation, Calfed Bay/Delta Program, and the Gabilan Foundation. We thank the following agencies and individuals for permission to access their property and for facilitating our field studies: USDI Fish and Wildlife Service (Don Edwards San Francisco Bay National Wildlife Refuge, with special thanks to J. Albertson, C. Morris, and M. Kolar; and San Pablo Bay National Wildlife Refuge, with special thanks to G. Downard, L. Vicencio and B. Winton), California Department of Fish and Game, California Department of Parks and Recreation, East Bay Regional Park District, Hayward Regional Shoreline, the City of Vallejo, Sonoma Land Trust, Solano County Farmlands and Open Space, Peninsula Open Space Trust, the City of Palo Alto, Wickland Oil Martinez, and Marin County Parks. This work was conducted under a memorandum of understanding with California Department of Fish and Game. This is PRBO contribution number 1090.