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Abstract:
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Avian Communities in Tidal Salt Marshes of San Francisco Bay: A Review of Functional Groups by Foraging Guild and Habitat Association

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ABSTRACT

The San Francisco Bay estuary is highly urbanized, but it supports the largest remaining extent of tidal salt marshes on the west coast of North America as well as a diverse native bird community. San Francisco Bay tidal marshes are occupied by more than 113 bird species that represent 31 families, including five subspecies from three families that we denote as tidal-marsh obligates. To better identify the niche of bird species in tidal marshes, we present a review of functional groups based on foraging guilds and habitat associations. Foraging guilds describe the method by which species obtain food from tidal marshes, while habitat associations describe broad areas within the marsh that have similar environmental conditions. For example, the ubiquitous song sparrows (Alameda *Melospiza melodia pusillula*, Suisun *M. m. maxillaris*, and San Pablo *M. m. samuelis*) are surface-feeding generalists that consume prey from vegetation and the ground, and they are found across the entire marsh plain into the upland–marsh transition. In contrast, surface-feeding California black rails (*Laterallus jamaicensis coturniculus*) are cryptic, and generally restricted in their distribution to the mid- and high-marsh plain. Although in the same family, the endangered California clapper rail (*Rallus longirostris obsoletus*) has become highly specialized, foraging primarily on benthic fauna within marsh channels when they are exposed at low tide. Shorebirds such as the black-necked stilt (*Himantopus mexicanus*) typically probe in mud flats to consume macroinvertebrate prey, and are generally restricted to foraging on salt pans within the marsh plain, in ponds, or on mud flats during transitional stages of marsh evolution. The abundance and distribution of birds varies widely with changing water depths and vegetation colonization during different stages of restoration. Thus, tidal-marsh birds represent a rich and diverse community in bay marshes, with niches that may be distinguished by the food resources they consume and the habitats that they occupy along the tidal gradient.

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KEY WORDS

Tidal marsh restoration, restoration stage, aerial forager, benthic forager, marsh-surface gleaner, aquatic forager, song sparrow, *Melospiza melodia*, California black rail, *Laterallus jamaicensis coturniculus*, California clapper rail, *Rallus longirostris obsoletus*, black-necked stilt, *Himantopus mexicanus*

INTRODUCTION

Development and human encroachment have greatly reduced the extent of tidal marshes in the San Francisco Bay estuary and altered or fragmented its remaining wetlands. Nearly 80% of tidal marsh habitats have been lost and >13,000 ha of wetlands have been converted to salt evaporation ponds (Nichols and others 1986; Goals Project 1999). Native bird communities that use these wetlands have been adversely affected, and populations of several species or subspecies are now threatened because of their reduced abundance and limited distribution (Harvey and others 1992; Goals Project 2000; Greenberg and others 2006a; Shuford and others 2008).

In the past two decades, hundreds of wetland restoration projects have been initiated to restore historic estuary wetlands to tidally-influenced marshes, including conversion of former salt ponds (Goals Project 1999; Steere and Schaefer 2001). However, wetland restoration sites may not be functionally equivalent to natural marshes in terms of suitability for tidal marsh-dependent wildlife. For example, Pacific cordgrass (*Spartina foliosa*) in a created wetland of southern California were less vigorous and failed to provide the vertical structure needed for nests of endangered light-footed clapper rail (*Rallus longirostris levipes*; Zedler 1993). Furthermore, tidal-marsh birds face numerous threats (see Takekawa and others 2006a) such as habitat fragmentation, invasive species, environmental contaminants, predation, and climate change. Sea-level rise may not result in a gradual upslope movement of tidal marshes to higher elevations because many tidal marshes are confined by levees in San Francisco Bay. Sea-level rise and extreme tide events will likely exacerbate the threats tidal-marsh birds already face by reducing the amount of tidal marsh and upland refugia available (Greenberg and others 2006b; Takekawa and others 2006a).

At present, San Francisco Bay tidal marshes support rich bird communities. Tidal marshes in San Francisco Bay support at least 113 bird species that represent 31 families, including five subspecies from three families that are tidal-marsh obligates: song sparrows (Alameda song sparrow *Melospiza melodia pusillula*, Suisun song sparrow *M. m. maxillaris*, and San Pablo song sparrow *M. m. samuelis*), salt marsh common yellowthroat (*Geothlypis trichas sinuosa*), and California clapper rail (*Rallus longirostris obsoletus*). Greenberg and others (2006a) noted that inhabitants of tidal marshes are disproportionately listed as endangered, threatened, or species of conservation concern more often than avian species in other habitats. Indeed, within San Francisco Bay nearly 25% of species that use tidal marshes and 50% of tidal marsh-associated species are designated with special conservation status (Table 1).

Tidal-marsh birds must be adapted to diurnal changes in tidal levels and salinity conditions. Birds that breed within tidal marshes typically elevate their nests to reduce the probability of flooding (Reinert 2006), but elevating their nests too high may result in increased visibility and predation (Greenberg and others 2006a). Birds with small breeding home ranges, such as the California black rail (*Laterallus jamaicensis coturniculus*), select habitats close to high tide refugia sites such as upland levees or tall vegetation along channels (Tsao and others 2009). In addition to behavioral adaptations to extreme tide events, tidal-marsh birds are physically adapted to salinity. For example, American avocet (*Recurvirostra americana*) chicks hatch with relatively large nasal salt glands so they can cope with their highly saline environment (Rubega and Oring 2004).

Some endemic species may be considered tidal marsh obligates if they are found principally in these salt marsh habitats, and are potentially well-adapted to live in them. For example, passerines such as Belding's savannah sparrow (*Passerculus sandwichensis beldingi*) that are found in tidal marshes of the Pacific coast south of Point Conception do not

Table 1 Avian species that use San Francisco Bay tidal marshes, the habitat elements they occupy, foraging strata, and special status designation

Family	Common Name	Scientific Name	Habitat Association[a]	Foraging Guild[b]	Special Status[c]
Anatidae	Canada Goose	*Branta Canadensis*	UT, MP, CH	AQ	
	Gadwall	*Anas strepera*	MP, CH, P	AQ	
	American Wigeon	*Anas Americana*	MP, CH, P	AQ	
	Mallard	*Anas platyrhynchos*	MP, CH, P	AQ	
	Blue-winged Teal	*Anas discors*	MP, CH, P	AQ	
	Cinnamon Teal	*Anas cyanoptera*	MP, CH, P	AQ	
	Northern Shoveler	*Anas clypeata*	MP, CH, P	AQ, B	CSC
	Northern Pintail	*Anas acuta*	MP, CH, P	AQ	
	American Green-winged Teal	*Anas crecca carolinensis*	MP, CH, P	AQ	
	Canvasback	*Aythya valisineria*	CH, P	AQ, B	CSC S2
	Redhead	*Aythya Americana*	CH, P	AQ, B	
	Greater Scaup	*Aythya marila*	CH, P	AQ, B	
	Lesser Scaup	*Aythya affinis*	CH, P	AQ, B	
	Surf Scoter	*Melanitta perspicillata*	CH	AQ, B	
	Bufflehead	*Bucephala albeola*	CH, P	AQ, B	
	Common Goldeneye	*Bucephala clangula*	CH, P	AQ, B	
	Common Merganser	*Mergus merganser*	CH, P	AQ	
	Red-breasted Merganser	*Mergus serrator*	CH, P	AQ	
	Ruddy Duck	*Oxyura jamaicensis*	MP, CH, P	AQ, B	
Phasianinae	Ring-necked Pheasant	*Phasianus colchicus*	UT	S	
Podicipedidae	Pied-billed Grebe	*Podilymbus podiceps*	CH, P	AQ	
	Horned Grebe	*Podiceps auritus*	CH, P	AQ	
	Eared Grebe	*Podiceps nigricollis*	CH, P	AQ	
	Western Grebe	*Aechmophorus oreccidentalis*	MP, CH, P	AQ	
	Clark's Grebe	*Aechmophorus clarkii*	MP, CH, P	AQ	
Pelecanidae	American White Pelican	*Pelecanus erythrorhynchos*	P	AQ	
	Brown Pelican	*Pelecanus occidentalis*	CH, P	AQ	
Phalacrocoracidae	Double-crested Cormorant	*Phalacrocorax auritus*	CH, P	AQ	CSC S3, WL
Ardeidae	American Bittern	*Botaurus lentiginosus*	MP, CH, P	AQ	CSC S3
	Great Blue Heron	*Ardea Herodias*	UT, MP, CH, P	AQ	CSC S4
	Great Egret	*Ardea alba*	UT, MP, CH, P	AQ	CSC S4
	Snowy Egret	*Egretta thula*	UT, MP, CH, P	AQ	CSC S4
	Green Heron	*Butorides virescens*	MP, CH, P	AQ	
	Black Crowned Night Heron	*Nycticorax nycticorax*	UT, MP, CH, P	AQ, B	CSC S3
Cathartidae	Turkey Vulture	*Cathartes aura*	MP, UT	A	
Pandionidae	Osprey	*Pandion haliaetus*	UT, MP, CH, P	AQ	CSC S3, WL
Accipitridae	White-tailed Kite	*Elanus leucurus*	UT, MP	A	CSC S3, FP
	Northern Harrier	*Circus cyaneus*	UT, MP	A	CSC S3, BSSC3
	Sharp-shinned Hawk	*Accipiter striatus*	UT, MP	A	CSC S3, WL
	Cooper's Hawk	*Accipiter cooperii*	UT, MP	A	CSC S3, WL
	Red-shouldered Hawk	*Buteo lineatus*	UT, MP	A	

Table 1 *Continued*

Family	Common Name	Scientific Name	Habitat Association[a]	Foraging Guild[b]	Special Status[c]
	Red-tailed Hawk	*Buteo jamaicensis*	UT, MP	A	
Falconidae	American Kestrel	*Falco sparverius*	UT, MP	A	
	Merlin	*Falco columbarius*	UT, MP	A	CSC S3, WL
	Peregrine Falcon	*Falco peregrines*	UT, MP, P	A	CSC S3, FD, CE, FP, BCC
Rallidae	Black Rail	*Laterallus jamaicensis coturniculus*	UT, MP	S	CSC S1, BCC, FP, CT
	California Clapper Rail	*Rallus longirostris obsoletus*	MP, CH, P	B	CSC S1, FE, CE, FP
	Virginia Rail	*Rallus limicola*	MP, P	S	
	Sora	*Porzana Carolina*	MP, P	S	
	American Coot	*Fulica Americana*	MP, CH, P	B	
Charadriidae	Black-bellied Plover	*Pluvialis squatarola*	MP, P	S	
	Snowy Plover	*Charadrius alexandrinus*	MP, P	S	CSC S2, FT, BCC
	Semipalmated Plover	*Charadrius semipalmatus*	MP, P	S	
Recurvirostridae	Black-necked Stilt	*Himantopus mexicanus*	MP, CH, P	B	
	American Avocet	*Recurvirostra americana*	MP, CH, P	AQ, B	
Scolopacidae	Spotted Sandpiper	*Actitis macularia*	MP, P	B, S	
	Greater Yellowlegs	*Tringa melanoleuca*	MP, P	B	
	Lesser Yellowlegs	*Tringa flavipes*	MP, P	B	
	Willet	*Catoptrophorus semipalmatus*	MP, CH, P	B	
	Whimbrel	*Numenius phaeopus*	MP, CH, P	B	
	Long-billed Curlew	*Numenius americanus*	MP, CH, P	B	CSC S2, BCC, WL
	Marbled Godwit	*Limosa fedoa*	MP, CH, P	B	
	Red Knot	*Calidris canutus*	P	B, S	
	Sanderling	*Calidris alba*	MP, P	B, S	
	Western Sandpiper	*Calidris mauri*	MP, P	B, S	
	Least Sandpiper	*Calidris minutilla*	MP, P	B, S	
	Dunlin	*Calidris alpine*	MP, P	B, S	
	Short-billed Dowitcher	*Limnodromus griseus*	MP, CH, P	B	
	Long-billed Dowitcher	*Limnodromus scolopaceus*	MP, CH, P	B	
	Wilson's Snipe	*Gallinago gallinago*	UT, MP	B	
	Wilson's Phalarope	*Phalaropus tricolor*	CH, P	AQ	
	Red-necked Phalarope	*Phalaropus lobatus*	CH, P	AQ	
Laridae	Bonaparte's Gull	*Larus Philadelphia*	CH, P	AQ	
	Mew Gull	*Larus canus*	CH, P	AQ	
	Ring-billed Gull	*Larus delawarensis*	CH, P	AQ	
	Western Gull	*Larus occidentalis*	CH, P	AQ	
	California Gull	*Larus californicus*	CH, P	AQ	CSC S2, WL
	Herring Gull	*Larus argentatus*	CH, P	AQ	
	Glaucous-winged Gull	*Larus glaucescens*	CH, P	AQ	
Sternidae	Least Tern	*Sterna antillarum*	CH, P	AQ	CSC S2S3, FE, CE, FP
	Caspian Tern	*Sterna caspia*	CH, P	AQ	CSC S4, BCC
	Forster's Tern	*Sterna forsteri*	CH, P	AQ	CSC S4,
Rynchopidae	Black Skimmer	*Rynchops niger*	CH, P	AQ	

Table 1 *Continued*

Family	Common Name	Scientific Name	Habitat Association[a]	Foraging Guild[b]	Special Status[c]
Columbidae	Mourning Dove	*Zenaida macroura*	UT	S	
Tytonidae	Barn Owl	*Tyto alba*	UT, MP	A	
Strigidae	Great Horned Owl	*Bubo virginianus*	UT, MP	A	
	Short-eared Owl	*Asio flammeus*	UT, MP	A	CSC S3, BSSC3
Trochilidae	Allen's Hummingbird	*Selasphorus sasin*	UT	A	
	Anna's Hummingbird	*Calypte anna*	UT, MP	A	
Alcedinidae	Belted Kingfisher	*Ceryle alcyon*	CH, P	AQ	BSSC3
Tyrannidae	Black Phoebe	*Sayornis nigricans*	UT, MP	A	
Corvidae	American Crow	*Corvus brachyrhynchos*	UT, MP	S	
	Common Raven	*Corvus corax*	UT, MP	S	
Hirundinidae	Tree Swallow	*Tachycineta bicolor*	UT, MP, P	A	
	Violet-green Swallow	*Tachycineta thalassina*	UT, MP, P	A	
	Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	UT, MP, P	A	
	Cliff Swallow	*Petrochelidon pyrrhonota*	UT, MP, CH, P	A	
	Barn Swallow	*Hirundo rustica*	UT, MP, P	A	
Troglodytidae	Marsh Wren	*Cistothorus palustris*	MP	S	
Motacillidae	American Pipit	*Anthus rubescens*	UT, MP	S	
Parulidae	Saltmarsh Common Yellowthroat	*Geothlypis trichas sinuosa*	UT, MP	S	CSC S2, BCC, BSSC3
Emberizidae	Bryant's Savannah Sparrow	*Passerculus sandwichensis alaudinus*	UT, MP	S	BSSC3
	Savannah Sparrow	*Passerculus sandwichensis*	UT, MP	S	
	Golden-crowned Sparrow	*Zonotrichia atricapilla*	UT, MP	S	
	White-crowned Sparrow	*Zonotrichia leucophrys*	UT, MP	S	
	Fox Sparrow	*Passerella iliaca*	UT, MP	S	
	Alameda Song Sparrow	*Melospiza melodia pusillula*	UT, MP	A, S	CSC S2, BCC, BSSC2
	San Pablo Song Sparrow	*Melospiza melodia samuelis*	UT, MP	A, S	CSC S2, BCC, BSSC
	Suisun Song Sparrow	*Melospiza melodia maxillaris*	UT, MP	A, S	CSC S2, BCC, BSSC
	Lincoln's Sparrow	*Melospiza lincolnii*	UT, MP	S	
Icteridae	Western Meadowlark	*Sturnella neglecta*	UT, MP	S	
	Brown-headed Cowbird	*Molothrus ater*	UT, MP	S	
	Red-winged Blackbird	*Agelaius phoeniceus*	UT, MP	S	
Fringillidae	House Finch	*Carpodacus mexicanus*	UT, MP	A	
	American Goldfinch	*Carduelis tristis*	UT	A	
	Lesser Goldfinch	*Carduelis psaltria*	UT, MP	A	

[a] Habitat Association: UT = upland transition and high marsh plain; MP = mid- and low-marsh plain; CH = tidal creeks and channels; P = pannes and ponds
[b] Foraging Guild: A = aerial; S = surface; B = benthic; AQ = aquatic
[c] Special Status: FE = Federal Endangered, FT = Federal Threatened FP = Federal Protected, FD = Federal Delisted, CE = California Endangered, CT = California Threatened; BSSC = Department of Fish and Game Bird Species of Special Concern, updated in Shuford and Gardali (2008); numeral following (1 to 3) indicates priority ranking from highest (1) to lowest (3); BCC = Fish and Wildlife Service Birds of Conservation Concern; WL = Department of Fish and Game Watch List; CSC = California Species of Concern (California Department of Fish and Game legal designation prior to 2008); Natural Heritage Status Ranking at the S (subnational) level for California (S1 = critically imperiled, S2 = imperiled, S3 = vulnerable to extirpation or extinction, S4 = statewide population apparently secure, factors exist to cause concern)

possess salt glands, but their kidney structure (high volume of medulla) may allow them to concentrate salts (Goldstein 2006). San Francisco Bay song sparrows are adapted to high salinities and can maintain their body mass in salt marshes, while riparian species such as the Marin song sparrow (*M. m. gouldii*) are less adapted for saline conditions (Basham and Mewaldt 1987).

FORAGING GUILDS

Diverse food resources are available in tidal marshes through terrestrial and marine food webs (Adam 1990; Kwak and Zedler 1997; Cloern and others 2002), and tidal-marsh birds are often omnivorous to take advantage of the various available food resources in these dynamic environments. Use of foraging guilds to describe bird communities reflects ecosystem productivity as it relates to a specific foraging community. Functional foraging guilds also help distinguish the way birds use the physical environment; here, we group birds into aerial, marsh surface, benthic, or aquatic foraging guilds (Table 1). Species can belong to more than one foraging guild, based on flexibility in their diet and behavior.

Aerial foragers, such as song sparrows, prey within and above tidal-marsh plant canopies. Virtually all of the passerines found in tidal marshes—including swallows (*Hirundinidae*), savannah sparrows (*Passerculus sandwichensis*), marsh wrens (*Cistothorus palustris*), salt marsh common yellowthroat, and red-winged blackbirds (*Agelaius phoeniceus*)—belong to this foraging guild. Aerial foragers commonly feed upon flying insects such as plant hoppers (*Prokelisia* spp., *Delphacidae*); leafhoppers (*Cicadellidae*); grasshoppers (*Acrididae*); mantids (*Mantidae*); bees and wasps (*Hymenoptera*); flies (*Ephydridae, Dolichopodidae*); and moths and butterflies (*Lepidoptera*), such as the Western pygmy-blue (*Brephidium exilis*) and the inchworm moth (*Perizoma custodiata*); but they may also consume plant seeds (Goals Project 2000). Northern harriers (*Circus cyaneus*), white-tailed kite (*Elanus leucurus*), red tailed hawks (*Buteo jamaicensis*), and owls (*Tytonidae and Strigidae*) are all tertiary aerial consumers that forage on small mammals, other birds, or insects. The white-tailed kite forages high above open marshes and grasslands (5 to 25 m above the ground) by rapidly beating its wings and hovering in place while scanning the ground for prey (Dunk 1995). The northern harrier has distinctive owl-like facial disks that help with directional hearing to locate prey (Rice 1982). When foraging, the northern harrier flies relatively close to the ground (<2 m) using both visual and auditory cues to capture prey (Rice 1982; Macwhirter and others 1996).

Marsh surface gleaners, such as the black rail, forage primarily at the marsh surface on invertebrate prey such as beetles (*Cicindela* spp., *Bembidion* spp.), spiders (*Pardosa* spp., *Phidippus* spp.), amphipods (*Traskorchestia* spp.), snails (*Myosotella* spp., *Assiminea* spp.), shore bugs (*Saldidae*), isopods (*Isopoda*), and on other items such as seeds (Takekawa and others unpublished data). Many gleaners have bills adapted to capture a wide range of prey resources. For example, song sparrows are gleaners that have longer and deeper bills than their closest non-tidal marsh relative (Grenier and Greenberg 2006), presumably as a response to selection for increased invertebrate diets over seeds that can be obtained on the sediment surface. Western meadowlarks (*Sturnella neglecta*) and red-winged blackbirds are also surface gleaners that are found in large flocks, feeding on insects and seeds on the ground. Canada geese (*Branta canadensis*) are primarily herbivores that feed on a wide variety of plants and aquatic vegetation. Their diet may also include agricultural grains.

Benthic foragers consume prey within marsh and channel surface sediments. As tidal waters recede, foraging habitats become exposed for benthivores such as black-necked stilts (*Himantopus mexicanus*) and clapper rail. Typical benthic macroinvertebrates consumed by birds in the tidal marsh are: horse mussel (*Geukensia demissa*), clams (*Corbula* spp., *Macoma* spp.), crustaceans (*amphipods [Corophium* spp.*], Cumaceae*), and annelids (*Capitellidae*). Although horse mussels comprise the majority of the clapper rail diet (Moffitt 1941), the rail also consumes crabs (*Hemigrapsus* spp., *Carcinus* spp., *Pachygrapsus crassipes*) and spiders (*Phidippus* spp., *Pardosa* spp., *Lycosid*)—one record reports a bird opportunistically

fed on rabbit carrion (Moffitt 1941). In contrast, northern shovelers (*Anas clypeata*) are dabbling ducks that use their spatula-shaped bill to filter and strain plant material, mollusks, crustaceans, and other small invertebrates from the water column and benthos (Dubowy 1996).

Shorebirds are benthic foragers, and are of special importance because each year hundreds of thousands of shorebirds winter in San Francisco Bay (Takekawa and others 2001; Warnock and others 2002). Based on these large shorebird populations, the estuary was designated as a Western Hemisphere Shorebird Reserve Network Site of Hemispheric Importance in 1989 (Morrison and others 2001; WHSRN 2010). One of the reasons bay tidal flats support these high numbers can be explained by resource partitioning between birds of different size with varied bill lengths and shapes. Some shorebirds are adapted to forage on the surface of mud flats (i.e., western sandpiper, *Calidris mauri*; American avocet), while others have long bills that can probe deeper into the substrate (long-billed curlew, *Numenius americanus*; marbled godwit, *Limosa fedoa*). American avocets have slightly upturned bills and primarily forage by scything: holding their bill open and moving it side to side on the surface of the sediment. They are reported to be generalists and consume most prey items of <63 mm (Robinson and others 1997). Long-billed curlews are the largest North American shorebird and have a long, decurved bill that is adapted to probing and pecking for crustaceans and other benthic invertebrates deep (10 to 15 cm) below the sediment surface (Dugger and Dugger 2002).

Aquatic foragers, such as herons and egrets (*Ardeidae*) and terns (*Sternidae*), consume aquatic organisms that dwell in channels or ponds such as crabs, threespine stickleback (*Gasterosteus aculeatus*), silversides (*Menidia* spp.), gobies (*Gobiidae*), prickly sculpin (*Cottus asper*), brine shrimp (*Artemia franciscana*), shrimp (*Palaemon* spp., *Crangon* spp.), and aquatic insects, including water boatmen (*Trichocorixa reticulate*) (Goals Project 2000). Ducks (*Anatidae*), grebes (*Podicipedidae*), and cormorants (*Phalacrocoracidae*) are aquatic foragers that search for aquatic vegetation, crustaceans, mollusks, fish, and other invertebrates. Dabbling ducks (such as American wigeon, *Anas americana*) forage primarily at the surface on aquatic vegetation, and consume insects, beetles, mollusks, and crustaceans during the breeding season (Mowbray 1999), while grebes, cormorants, and diving ducks (such as ruddy duck, *Oxyura jamaicensis*) submerge to forage underwater on pelagic or benthic prey. Pied-billed grebes (*Podilymbus podiceps*) nest in emergent aquatic vegetation, and forage in the open water or amongst aquatic vegetation. They are opportunistic and feed on large crustaceans, fish, insects, and other invertebrates (Muller and Storer 1999).

TIDAL-MARSH HABITATS

In addition to functional foraging guilds, the diversity of tidal-marsh birds is reflected in their spatial use of different habitats along an elevation and tidal gradient. Associating birds to their habitats is fundamental in identifying the functions and structures of landscapes critical to a bird's life cycle (Wiens 1994, 1996; Walters 1998). Habitat use integrates movements and behavior (home range, foraging strategy, breeding requirements), and marsh structure (elevation and canopy complexity), with driving processes (tidal fluctuations, global climate change), and biotic interactions (prey consumption, predation, and competition). Tidal marshes are characterized by distinct vegetation zones based on the degree of tidal inundation and the salinity tolerance of marsh plants (Josselyn 1983; Goals Project 1999).

Tidal-marsh habitats progress along a gradient from the upland–high marsh transition to the estuarine edge (as in Goals Project 1999). We group birds within these habitat types, reflecting our interpretation of how birds partition in tidal marshes. From higher to lower elevation, these habitats include: upland transition and high-marsh plain, mid- and low-marsh plain, tidal creeks and channels, and pans and ponds. We then provide examples using four different species—song sparrows, black rails, clapper rails, and black-necked stilts—describing their association with tidal-marsh habitats, foraging guilds, and habitat use.

Upland Transition and High-Marsh Plain

The upland transition demarcates the zone between the edge of the tidal marsh and the adjacent non-tidal habitat. In San Francisco Bay, marshes are often bordered by transitional high-elevation levees that separate human development from the marshes. At the upper end of the tidal marshes, the high marsh plain is San Francisco Bayland habitat within the historic tideline (Goals Project 1999) that is inundated infrequently above mean higher high water. The high marsh plain is dominated by common pickleweed (*Sarcocornia pacifica*, formerly *Salicornia virginica*) with coyote bush (*Baccharis pilularis*) and other characteristic vegetation extending across to the upland transition.

Song Sparrows

Song sparrows in bay marshes have differentiated into three subspecies, each of which is endemic and adapted to saline and brackish conditions (Marshall 1948; Marshall and Dedrick 1994; Chan and Arcese 2002). The three endemic subspecies segregate regionally: San Pablo song sparrow in San Pablo Bay (north of Sausalito on the west side and north of Point Richmond on the east side), Alameda song sparrow in the Central Bay and South Bay, and Suisun song sparrow in Suisun Bay (including the Carquinez Strait, Figure 1). Each subspecies is phenotypically distinct, but their genetic differentiation is ambiguous, especially between the San Pablo and Suisun subspecies (Chan and Arcese 2002). Grinnell and Miller (1944) characterized the tidal-marsh song sparrows as widespread and abundant throughout San Francisco Bay. Population viability analyses and simulations indicated that the historic population size of the San Pablo song sparrow was likely three times larger than at present (Takekawa and others 2006b), and larger populations may have been likely for other song sparrow subspecies (Spautz and Nur 2008a, 2008b; Chan and Spautz 2008).

Bay song sparrows are sedentary, year-round residents (i.e., non-migratory) except for the young of the year, which disperse within and among marshes (PRBO unpublished data). Unlike salt marsh common yellowthroats or black rails, which are present in some tidal marshes and absent in others (Nur and others 1997), song sparrows are ubiquitous throughout tidally-influenced marshes and have been documented in all tidally-influenced marshes ($n > 80$) where surveys have been conducted in San Francisco Bay (Spautz and others 2006).

Systematic, repeated surveys of song sparrows during breeding seasons between 1996 and 2006 reveal population trends that differ by San Francisco Bay region, and thus subspecies (Figure 2). Their "apparent density" refers to detection per area, uncorrected for detection probability. In the absence of variation in detection probability among years or locations, apparent density provides a good surrogate for absolute density. Apparent density of song sparrows varies spatially, among bays, among marshes, and within marshes (Figure 3; Spautz and others 2006; Stralberg and others 2009). In the Central and South bays, the apparent density of song sparrows has been increasing from 1996 to 2008 (5.8% per year, $P = 0.008$), whereas for San Pablo and Suisun bays there has been an overall downward trend (1.5% and 2.6% decreases per year, respectively, $P > 0.15$; SFEIT 2011). Moreover, between 2004 and 2008 the apparent abundance decreased for all three regions.

The estimated density (after accounting for detection probability) of a particular song sparrow subspecies may vary two-fold among high- and low-density marshes. For example, in the spring of 2000, song sparrow density was estimated at 5.2 ± 0.5 birds ha^{-1} in Central and South bays, 14.9 ± 1.2 birds ha^{-1} in San Pablo Bay, and 14.9 ± 1.8 birds ha^{-1} in Suisun Bay (PRBO unpublished data). Variation in density among marshes may reflect differences in habitat suitability, but other factors are also influential, including habitat preference, site fidelity, and reproductive success. Although it is valuable to identify habitat and landscape correlates of density, variation in density alone is not a sufficient indicator of habitat quality. Habitat quality requires determination of reproductive success, survival, and recruitment of young.

Song sparrows are commonly associated with marshes that have higher elevations dominated by common pickleweed, but are also found throughout

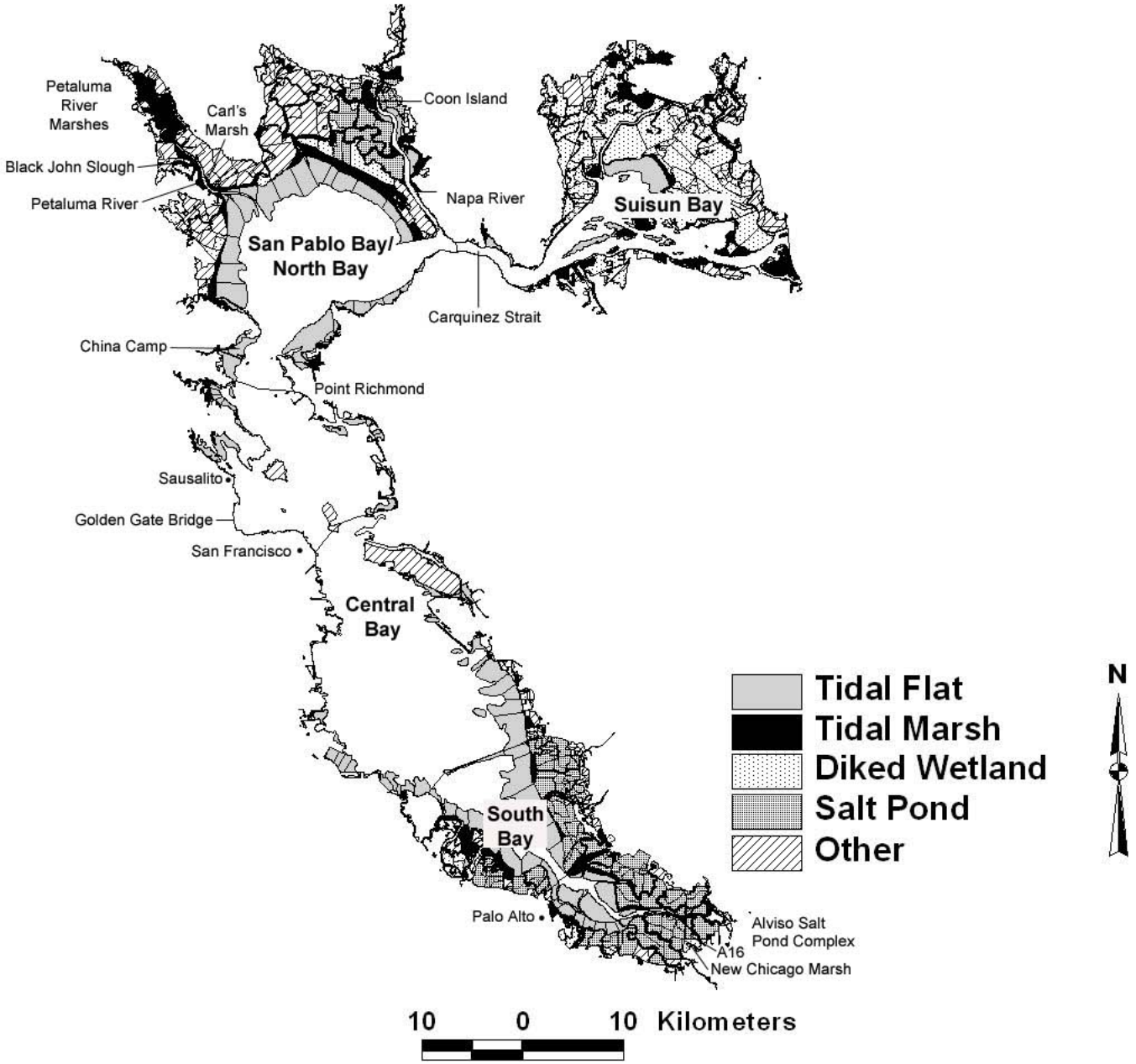

Figure 1 Mosaic of tidal salt marshes and related habitats within San Francisco Bay, including locations referenced within this paper. China Camp is part of the National Estuarine Research Reserve System. Habitat map created with EcoAtlas (SFEI 1998).

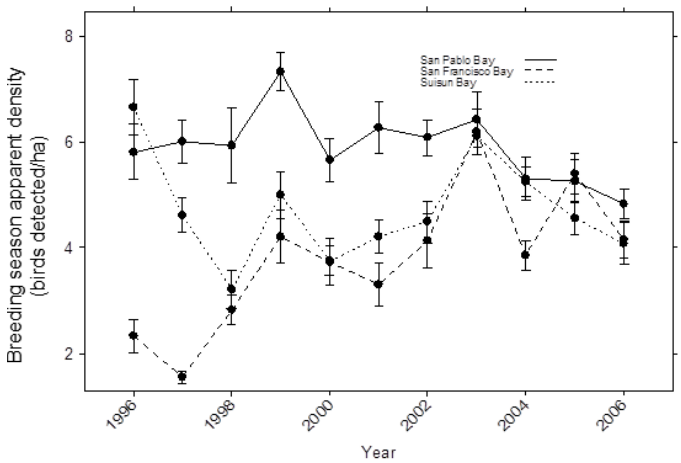

Figure 2 Song sparrow (Alameda *Melospiza melodia pusillula*, Suisun *M. m. maxillaris*, and San Pablo *M. m. samuelis*) breeding season density indices in the San Francisco Bay region from 1996 to 2006 (Liu and others 2007)

lower marshes characterized by Pacific cordgrass. They require vegetation of sufficient height to establish nests that avoid tidal flooding (>30 cm: Marshall 1948). They primarily nest along tidal channels and sloughs, and forage along channel edges and on the adjacent marsh plain, consuming invertebrates such as snails, amphipods, and insects, as well as seeds (Grenier 2004). Tidal-marsh song sparrows require fully-vegetated marshes yet avoid habitat where the vegetation is extremely dense (Marshall 1948).

Multivariate analysis of within-marsh and between-marsh variation in apparent density revealed that tidal-marsh song sparrows were most strongly and positively associated with gum plant (*Grindelia* spp.), as well as with coyote bush (Spautz and others 2006), while negatively associated with rushes (*Juncus* spp.), pond, and pan habitat types. In addition, apparent

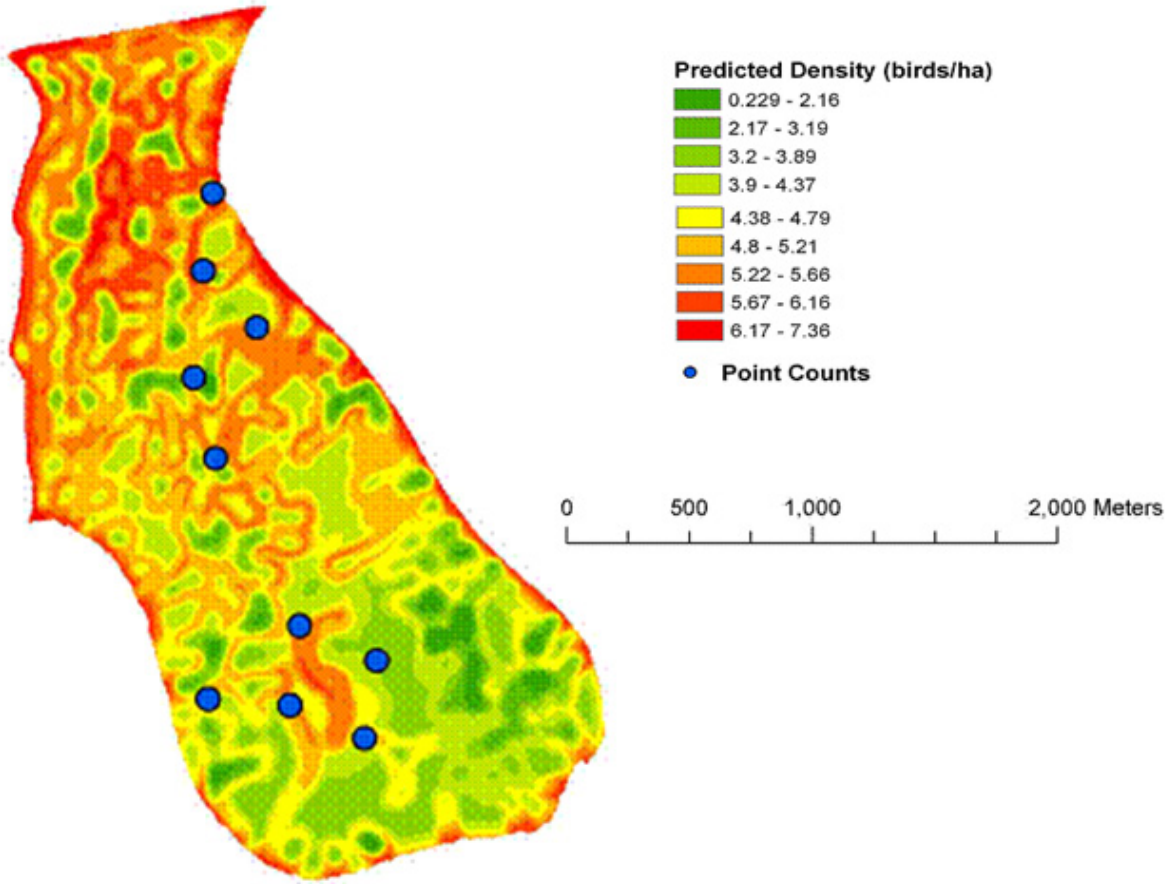

Figure 3 Predicted density of San Pablo song sparrows (*M. m. samuelis*) at Coon Island, lower Napa River (Stralberg and others 2010)

density of song sparrows was positively related to the size of the marsh (Spautz and others 2006). However, this relationship demonstrated diminishing returns: the largest marshes (top 10% in size) did not necessarily have the highest density of birds, which suggest that additional factors influence song sparrow density, or that densities may not always be optimal. Apparent density increased with distance from the water's edge (e.g., bayshore or river shore), consistent with their use of high marsh. Predictive models that included fine-scale (1-m) vegetation indices and geomorphology suggested that song sparrow abundance was positively associated with salinity and tules (*Bolboschoenus* spp., and *Schoenoplectus* spp., formerly *Scirpus* spp.; Stralberg and others 2009). Statistical models that related species abundance to spatial habitat relationships suggested that breeding bird abundance was positively associated with vegetation productivity (Normalized Difference Vegetation Index) as well as channel area, density, and proximity, which may reflect a preference for tall vegetative structure for nesting sites (Stralberg and others 2009). Overall, models were successful in predicting song sparrow abundance (Stralberg and others 2009).

Reproductive success also reflects variation in habitat and landscape characteristics. For example, song sparrow nests located in the invasive, non-native cordgrass (*Spartina alterniflora* and its hybrids) were less successful than nests in native plants (Nordby and others 2009). Nests in non-native *Spartina* at lower elevation were likely more susceptible to flooding. However, nests that were placed too high in vegetation were more susceptible to predation (Greenberg and others 2006a). Recent studies revealed that nest survival in tidal-marsh song sparrows was maximized when nest heights were 20 to 30 cm above the ground; nests closer to the ground were more susceptible to flooding and nests >30 cm were presumably more susceptible to predation (PRBO unpublished data).

Mid- and Low-Marsh Plain

The mid-marsh plain occurs between mean high water and mean higher high water and is inundated regularly. It is dominated by common pickleweed and also supports species that are less tolerant to inundation in the upper reaches of the marsh plain such as saltgrass (*Distichlis spicata*), fat-hen (*Atriplex triangularis*), and alkali heath (*Frankenia salina*; Goals Project 1999). Characteristic birds of the mid-marsh plain include black rail, northern harrier, and song sparrow. Within the mid-marsh plain, the habitat of black rail and song sparrow can be differentiated by the vertical strata they occupy. Black rails fly infrequently and spend most of their time within the marsh canopy. Song sparrows, especially males defending breeding territories, are more often found at the top of the vegetation.

The low-marsh plain is found along tidal creeks and channels and is inundated daily during high tides. Low-marsh vegetation is dominated by tall emergent species such as cordgrass or in more brackish waters by tules. Characteristic bird species of low marsh include clapper rail, willet (*Catoptrophorus semipalmatus*), and marsh wren (*Cistothorus palustris*). Canopy architecture of tall emergent vegetation is a critical feature for nesting birds, providing nest cover during high tides and flood tides. Sufficient plant height for nesting birds not only reduces the probability of nest flooding, but also provides sufficient cover against predators (Zedler 1993; Greenberg and others 2006b; Reinert 2006).

California Black Rail

California black rails occur in two distinct regions: the Colorado River region and northern California (Conway and Sulzman 2007; Evens and others 1991; Girard and others 2010). Roughly 80% to 90% of the northern California population is found in San Francisco Bay tidal marshes (Evens and others 1991; Goals Project 2000). Black rails are listed as a state threatened species (DFG 2008). Unlike song sparrows, black rails tend to run below and within wetland vegetation and seem reluctant to fly although short flights are common (Eddleman and others 1994). Detection is challenging because of their highly secretive nature and the variation in detection is influenced by distance from observer, sex, breeding stage, and time of day (Legare and others 1999). However, there appears to have been a drastic decline

in black rail populations since the 1900s (Eddleman and others 1994). This decline is largely from the loss of 80% of historical tidal marshes and fragmentation of the remaining tidal marshes. A recent increase in estuary-wide black rail populations (+3.2% annually from 1996 to 2008) may be a result of restoration efforts over the past 30 years—rail density is positively correlated with years since restoration (Wood 2009). The black rail occurs primarily in large, contiguous marshes dominated by common pickleweed, or in mature vegetated freshwater marshes (Ehrlich and others 1988; Evens and others 1991; Evens and Nur 2002), but peripheral upland vegetation or tall vegetation along channel edges provides refuge from predation during extreme high tides (Evens and Page 1986; Goals Project 2000; Tsao and others 2009).

Breeding black rails are found almost exclusively in mature, fully tidal marshes that are dominated by pickleweed and tules (Evens and others 1991; Spautz and others 2006), but younger marshes that are more prominently vegetated with cordgrass have been found to support rails during the non-breeding season (Evens and others 1991). Breeding black rails require a dense pickleweed canopy and an open understory for nesting, foraging, and movement (Evens and Page 1983). Black rail nests consist of a bowl with a canopy of dead or living plant matter (Flores and Eddleman 1993) that is approximately 45 to 70 cm above the nest (Ehrlich and others 1988). Some nests subject to inundation are thick (>12.7 cm) and comprise many layers resulting from frequent repair (Huey 1916). On the Petaluma River in northern San Pablo Bay, radio-marked black rails have relatively small breeding home ranges (average 95% fixed kernel home range of 0.65 ha; Figure 4; Tsao and others 2009). Levees and channel edges lined with taller vegetation such as coyote bush and gum plant serve as areas of refugia for black rails during extreme high tides (Evens and Page 1986).

Habitat structure (vegetation height, stem density, percent cover, and vegetation productivity) rather than plant species composition seem to better explain black rail habitat selection (Tsao and others 2009; Stralberg and others 2009). Other local and landscape factors that are associated with black rails include nearby tidal marsh, natural upland, and agricultural habitats, channels <1 m wide, marsh size (>8 ha), proximity to creeks and rivers (especially the mouth), and limited access by predators (Evens and Nur 2002; Spaultz and others 2006). Predictive modeling (Strahlberg and others 2009) suggests that channel area and vegetation diversity were negative predictors of black rail abundance, perhaps because this species may select more mature marshes with taller

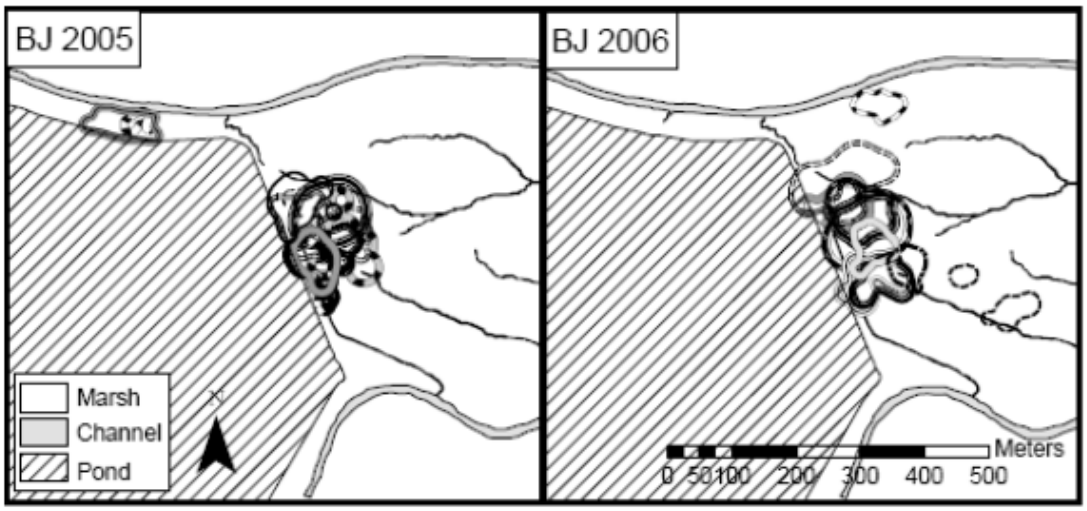

Figure 4 Ninety-five percent fixed kernel home ranges of breeding California black rails (*Laterallus jamaicensis coturniculus*) at Black John Slough on the Petaluma River. Each polygon represents a unique individual in 2005 (n = 10) and 2006 (n = 10; Tsao and others 2009).

vegetation to avoid nest flooding (Spautz and Nur 2002; Spautz and others 2006; Tsao and others 2009). Statistical models of habitat use support that black rails used areas dominated by pickleweed (Tsao and others 2009), which tend to have low plant diversity. Because black rails require more mature habitat features, habitat use of restored marshes may depend on site-specific processes of marsh development.

Black rails consume terrestrial insects, aquatic invertebrates, and seeds (Ehrlich and others 1988) typically found on the marsh surface. In the Petaluma River marshes of San Pablo Bay, black rail diet (regurgitated samples) comprised primarily of beetles and spiders (97% and 72% frequency of occurrence, respectively), with amphipods and snails found less often (44% and 28% frequency of occurrence, respectively; Takekawa and others unpublished data). Other taxa detected include flies (*Diptera*), leaf hoppers (*Cicadellidae*), shore bugs (*Saldidae* and *Macroveliidae*), and seeds. Nematodes, Hemiptera, Heteroptera, Hymenoptera, Orthoptera, and shaft lice (*Menopon* spp.) were found in <5% of samples.

Black rails are vulnerable to extreme high-tide events, which may flood nests and increase the probability of predation as individuals are forced to retreat to upland margins or areas with less cover during flood events (Evens and Page 1986). Furthermore, black rails exhibit strong site fidelity and seem to select for elements that provide high tide refugia, such as tall vegetation (>1 m in height) near channels or proximity to upland areas (Tsao and others 2009). Since most wetlands in this urbanized estuary are surrounded by levees with rather narrow upland transition zones, sea-level rise and extreme tide events might further reduce available high-tide refugia, and lead to increased predation exposure and risk of nest flooding.

Tidal Creeks and Channels

Tidal creeks and channels form a drainage network through low-marsh and mid-marsh plain areas within tidal marshes. Channels drain the marsh surface and serve as conduits for water, sediments, nutrients and channel biota, such as phytoplankton, zooplankton, nekton (small fish and shrimp), and benthic invertebrates. Some aquatic channel inhabitants can use the low marsh when it is flooded at high tide, including silversides, longjaw mudsuckers (*Gillichthys mirabilis*), and crabs. Herons and egrets are among the many waterbirds that feed on the small fish and benthic invertebrates found in tidal creeks, but perhaps no other tidal-marsh bird uses tidal creeks and channels to the extent of the clapper rail, a tidal-marsh obligate.

California Clapper Rail

The clapper rail is endemic to the tidal marshes of San Francisco Bay and populations have been affected by habitat loss, habitat degradation, hunting, and predation. Historically, the clapper rail population was thought to have been abundant, as "thousands" were reported to have been killed in a single day in 1859 for consumption in San Francisco and to feed gold miners in the Sierra Nevada Mountains (Wilbur and Tomlinson 1976). Sport and market hunting drastically reduced clapper rail numbers, but with the passage of the Migratory Bird Treaty Act in 1913 (Wilbur and Tomlinson 1976) clapper rail numbers improved (Grinnell and Miller 1944). More recently clapper rail numbers steadily declined since the mid-1900s, and in 1970, the clapper rail became a federally listed endangered species (35 Federal Register 16047; 13 October 1970).

Although population estimates of clapper rails include some survey data gaps, the evidence suggests that declining trends were real. In the 1970s, surveys estimated 4,200 to 6,000 birds were present, of which 55% resided in the South Bay (Albertson and Evens 2000). In the 1980s, clapper rail numbers had declined to between 1,200 and 1,500 birds, with 80% of the population in the South Bay (Harvey 1980). Based on surveys conducted in 1992 and 1993, the entire population of clapper rails was placed conservatively at <600 individuals (Collins and others 1994). By 1988, the introduced red fox (*Vulpes vulpes regalis*) was identified as one of the primary reasons for the clapper rail population decline (Foerster and others 1990). In 1991, a predator management program was initiated as the clapper rail population consisted of only 300 to 500 individuals (Albertson and Evens 2000). Clapper rail populations rebounded to

over 800 individuals in 1993, largely attributed to the predator management program (Albertson and Evens 2000). In the early 2000s, the clapper rail population increased to almost 1,400 individuals, with 75% of the population in the South Bay (Liu and others 2009). However, surveys following removal of invasive cordgrass in southern San Francisco Bay indicated declining populations (Liu and others 2009).

The clapper rail uses tidal channels for foraging and as corridors for travel, and clapper rail numbers may be positively correlated with channel density (Albertson and Evens 2000). Clapper rails primarily occur within the tidal inundation zone in emergent-marsh vegetation, including pickleweed, Pacific cordgrass, invasive cordgrass, gum plant, tules, and jaumea (*Jaumea carnosa*; Grinnell and others 1918; DeGroot 1927; Harvey 1988; Albertson and Evens 2000). Much of their remaining habitat is characterized as being isolated and relatively small, with a high edge-to-area ratio usually enveloped by industrial and urban areas (Albertson and Evens 2000).

Clapper rail habitat use is highly correlated with the presence of tidal sloughs and channels of varying widths and depths (DeGroot 1927; Harvey 1988; Foerster and others 1990; Schwarzbach and others 2006). Clapper rails use channels for movement through the marsh, as feeding areas, and as escape routes from predators (DeGroot 1927). Clapper rails have a relatively small annual home range (averaging <3 ha), with a smaller breeding home range (average <2 ha: Albertson 1995; U.S. Geological Survey, unpublished data). Radio-telemetry observations of clapper rails in several South Bay tidal marshes indicate that intra-daily movement (Figure 5)

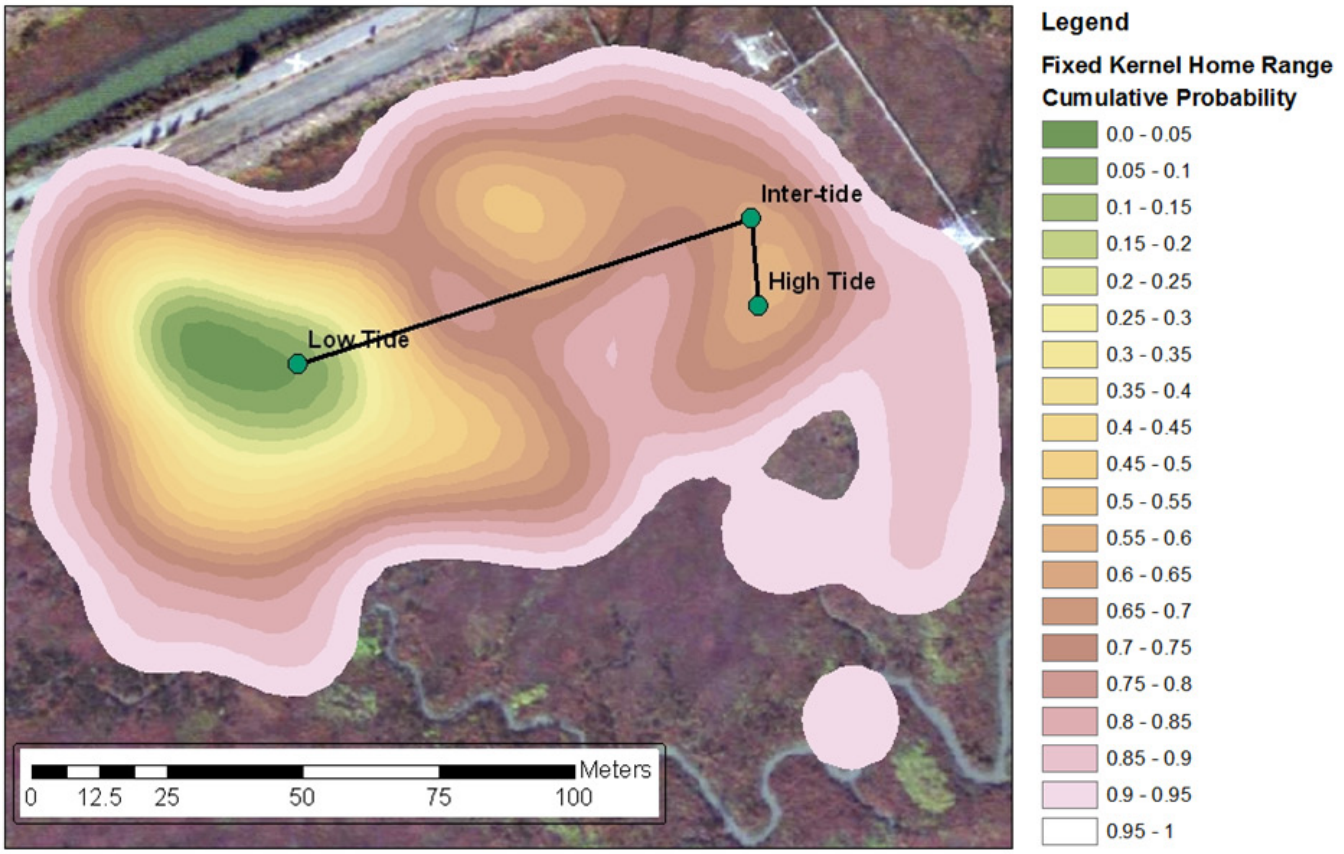

Figure 5 Example of an intra-daily movement of a California Clapper rail (*Rallus longirostris obsoletus*) within its annual home range (95% adaptive kernel, CVH smoothing parameter; U.S. Geological Survey unpublished data).

may be greater than inter-daily movement (Overton unpublished data), because movements among feeding, nesting, and roosting areas during varying tidal cycles account for the extensive intra-daily movements. Thus, rails may use a larger proportion of their seasonal or annual home range on a daily basis than otherwise might be expected.

Clapper rail nests consist of a nest bowl and canopy, and are commonly found close to tidal channels (<10 m width; DeGroot 1927; Zucca 1954; Harvey 1988; Foerster and others 1990). The nest bowl is built on top of a platform that is approximately 18 cm high and often contains woven cordgrass stems (Harvey 1988). The nest canopy is on average 57 cm tall and is commonly constructed of pickleweed, cordgrass, gum plant, and tules so that the nest platform is concealed. Although recent foraging studies have not been attempted in San Francisco Bay, previous research indicated rails primarily forage in the benthic zone on animal matter including the introduced horse mussel, crabs, clams (*Macoma balthica*) and spiders (Williams 1929; Moffitt 1941). Plant matter, primarily *Spartina* seeds, made up less than 15% of the food items by bulk found in 18 stomach samples collected near Palo Alto (Moffitt 1941). Current diet may be affected by more recent non-native invasive species commonly found in the estuary such as the overbite clam (*Corbula amurensis*).

Pans and Ponds

Salt pans are shallow depressions that fill with rain water or during highest tides. Salts are concentrated through evaporation, and vascular plant growth is inhibited, resulting in bare and exposed areas (Mitsch and Gosselink 2000). Salt pans vary in size, and some are large enough to support ponds with submerged vegetation, while others dry up entirely, forming completely bare patches within the tidal marsh. Natural salt pans were first developed into industrial salt ponds, in the mid–1800s (Goals Project 1999). By the mid–1900s, almost half of the South Bay's historical tidal marshes had been converted into salt ponds and approximately 4,050 ha of salt ponds were created in the North Bay. At peak production, salt ponds covered approximately 14,580 ha in San Francisco Bay (California Research Bureau 2002). Many waterfowl and shorebirds use salt ponds, especially as stopover sites during migration (Takekawa and others 2000, 2001, 2005) to consume the rich supply of invertebrates such as brine shrimp (*Artemia franciscana*) and brine flies (*Ephydra* spp.). Shorebirds such as American avocet and black-necked stilt also use salt ponds for breeding (Robinson and others 1999). Here we focus on the black-necked stilt, because the species often nests in or near salt pans within the tidal-marsh plain.

Black-Necked Stilt

Historically, black-necked stilts (hereafter stilts) were uncommon residents of San Francisco Bay (Grinnell and others 1918; Grinnell and Wythe 1927). Presently, stilts are common wintering and breeding residents in the Bay, possibly due to the expansive creation of artificial salt evaporation ponds from tidal marsh between the 1930s and 1950s (Gill 1977; Goals Project 1999). Stilt abundance in San Francisco Bay is highest in the fall (about 6,239 birds), followed by early winter (5,104), and the spring (1,088 birds; Stenzel and others 2002). Stilts are the second-most abundant breeding shorebird in San Francisco Bay after American avocets, and San Francisco Bay represents the largest breeding area for stilts on the Pacific coast (Page and others 1999; Stenzel and others 2002; Rintoul and others 2003). Stilts are most abundant in the South Bay (Stenzel and others 2002), where the breeding population has been estimated at 590 pairs (Rintoul and others 2003).

Stilts in San Francisco Bay breed predominantly in marshes but use salt ponds heavily for foraging during the breeding season. For example, during the pre-breeding, breeding, and post-breeding seasons, radio-marked stilts primarily used managed marshes (49%, 66%, and 63%) and salt ponds (32%, 22%, and 20%), followed by uplands (14%, 8%, and 9%), tidal marshes (2%, 3%, and 2%), sloughs (2%, <1%, and 1%), lagoons (1%, 1%, and 5%), and tidal flats (<1%, <1%, and <1%), respectively (Figure 6; Ackerman and others 2007; Ackerman and others unpublished data). Similarly, Hickey and others (2007) found that habitat use by radio-marked stilts captured on nests

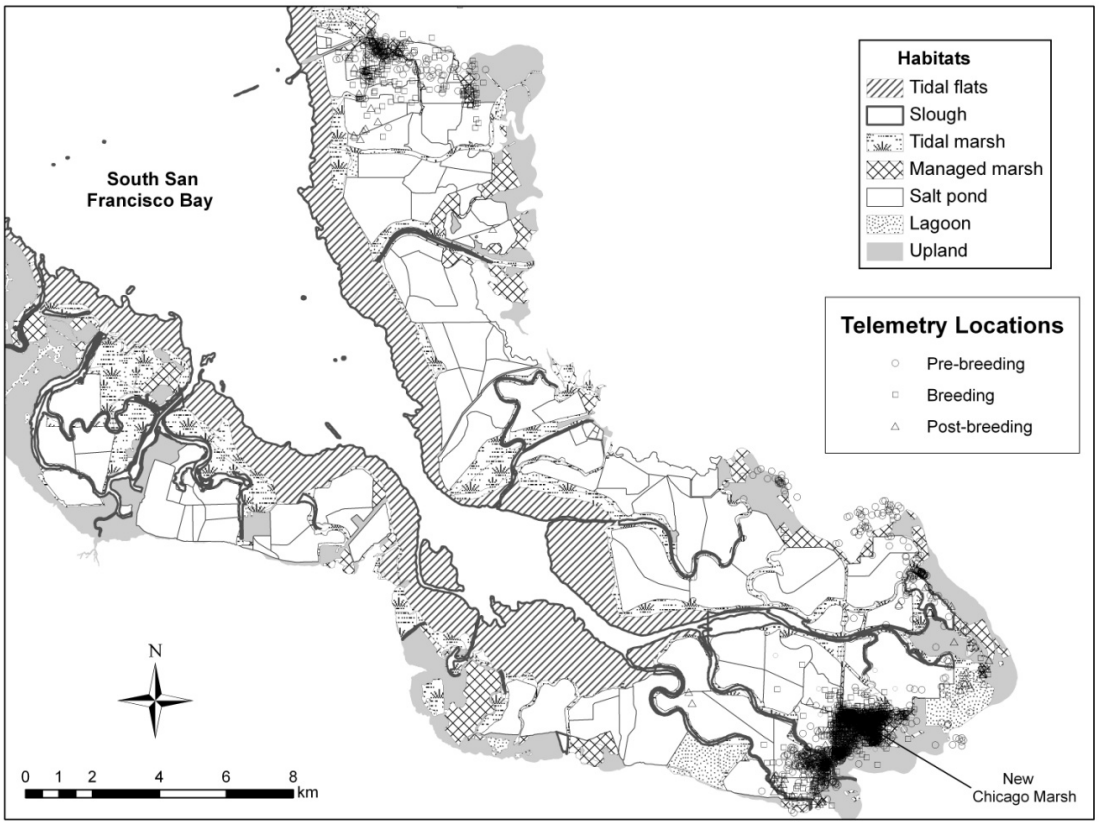

Figure 6 Locations of black-necked stilts (*Himantopus mexicanus*) radio-marked during the pre-breeding seasons in 2005 and 2006, South San Francisco Bay, California. Symbols depict the breeding stage in which the location was obtained, including pre-breeding (open circles), breeding (open triangles), and post-breeding (open squares; Ackerman and others 2007; Ackerman and others unpublished data). Habitat types depicted include salt ponds, managed marshes, tidal marshes, tidal flats, uplands, and open bay (SFEI 1998).

in the South Bay was highest in salt ponds (57%), followed by diked wetlands (20%), tidal marsh (12%), tidal flats (6%), and other wetlands (6%). Compared to habitat availability, both diked marshes and salt ponds were selected by stilts (Hickey and others 2007). During South Bay breeding surveys, Rintoul and others (2003) observed stilts predominantly used salt ponds (55%) and marshes (29%), followed by other wetland types (14%) and tidal flats (1%). Stilts are mainly aquatic foragers, consuming invertebrates such as brine shrimp and brine flies when foraging within ponds or pans, but they will also consume small fish and some seeds (Hamilton 1975; Robinson and others 1999).

Stilts generally nest in managed and diked marshes within short emergent vegetation, bare areas, or vegetated margins (Robinson and others 1999). Of 385 stilt nests monitored in the South Bay in 2006, 88% were in marshes, 12% were on islands within salt ponds, and <1% were on peninsulas within salt ponds; notably, no nests were found along salt pond levees (Ackerman unpublished data). Accordingly, 95% of the nests were associated with vegetation within 1 m of the nest bowl, with an average height of 15.2 ± 8.9 (SD) cm (Ackerman unpublished data). A particularly important nesting area for stilts in San Francisco Bay is New Chicago Marsh (Rintoul and others 2003; Ackerman and others 2007), which is adjacent to the Alviso Salt Pond Complex. Nest monitoring efforts in New Chicago Marsh detected 101, 302, and 183 stilt nests in 2005, 2006, and 2007, respectively, although search efforts varied among years (Ackerman unpublished data). In 2005, radio-marked stilt chicks that were hatched in New Chicago Marsh moved toward the adjacent A16 salt

pond when brine flies were abundant, but this pattern was not observed in 2006 after A16 was breached and salinity levels and potentially invertebrate abundance decreased (Ackerman and others unpublished data). Few other studies have monitored stilt nests in San Francisco Bay, but Rintoul and others (2003) observed that of 137 stilt nests found in the South Bay, 21% were in marshes, 69% were around salt ponds, and 9% were in other wetland habitats.

RESTORATION STAGE

San Francisco Bay's landscape is rapidly changing because of tidal-marsh restoration efforts, and avian communities vary widely in response to those changing conditions. Multi-species management in this urbanized estuary has become a difficult balancing act that requires weighing the costs and benefits of converting habitats for threatened tidal-marsh species with reduced habitat for numerous species that depend on salt ponds (Stralberg and others 2009). Tidal marsh restorations represent transitional habitat types as subtidal areas become suitable for vegetation colonization with adequate sediment supply (Woo and others 2007; Athearn and others 2009). Subsequently, habitat use by different foraging guilds or nesting birds may reflect the habitat succession associated with restoration stage. For example, newly inundated aquatic areas become available to diving ducks and dabblers, and will transition to tidal flats within a few years or decades with adequate sediment inputs. Tidal flats are heavily used by foraging shorebirds during low tide and are also used by diving benthivores (i.e., greater scaup *Aythya marila*, lesser scaup *Aythya affinis*, and ruddy duck) when the flats are submerged by the tides.

In sediment-rich areas, continued sedimentation favors plant colonization in the tidal flats. As a low-marsh habitat develops dominated by tall emergent cordgrass, tules, or sedges (*Cyperaceae*), increased vegetative structure allows for greater habitat and foraging partitioning for aerial foragers at the expense of foraging opportunities for benthic foragers. For example, vegetative marshes have greater habitat availability for nesting marsh wrens and song sparrows (Marshall 1948), but growth of denser vegetation then supports few shorebirds (Stralberg and others 2003; Patten and O'Casey 2007; Stralberg and others 2009). Small mammals found within the marsh plain can colonize and subsequently provide prey resources to raptors that soar above the marshes. In marshes with greater vegetative cover and height, black rails may colonize the marsh plain, as long as suitable high marsh and upland transition zones are nearby. Finally, establishment of channel networks and tall vegetative cover in more mature marshes will result in available foraging habitat and conditions suitable for clapper rails (Foin and others 1997).

Song sparrows are ubiquitous within both young restoration sites and older historical marshes alike. Their relative abundance is not influenced by vegetation composition or obvious micro-habitat features (percent channel, width of channel, or distance to water) but is positively related to vegetation cover (Nur and others 1997). Nest survival for song sparrows varies by year and is influenced by edaphic and hydrologic conditions as well as species interactions. In an unseasonably wet spring, song sparrow nest success at Carl's Marsh, a relatively young marsh (breached in 1994), was over twice that at China Camp, a historic tidal marsh. Over 50% of nest failures at China Camp were caused by flooding, compared to only 21% at Carl's Marsh (Liu and others 2007). On the other hand, nest failures from predation were greater at Carl's Marsh (45%), compared to China Camp.

Black rails are found almost exclusively in mature marshes that are dominated by pickleweed and tules (Evens and others 1991; Spautz and Nur 2002), although some younger marshes vegetated with Pacific cordgrass have been found to support rails during the non-breeding season (Evens and others 1991). Since their breeding home ranges are relatively small (0.65 ha; Tsao and others 2009), varied topography that provide a dense pickleweed canopy and an open understory for nesting, foraging, and movement seem to be preferred (Evens and Page 1983). Also preferred are areas with more complex habitat structure (vegetation height, stem density, and percent cover: Tsao and others 2009). Tidal-marsh restoration with particular attention to upland transition zones will increase habitat availability for black rail.

Clapper rails inhabit the most mature tidal salt marshes with well-developed cordgrass, vegetative cover, and creek and channel networks. Clapper rails are not usually found in young restoration sites, and it can take years or decades for the appropriate emergent vegetative cover and channels to develop (Foin and others 1997). Considerable time may be needed for creek and channel networks to develop naturally (Wallace and others 2005; Woo and others 2007) or for constructed channels to equilibrate (Zeff 1999; Williams and others 2002). Clapper rail recovery efforts can be difficult because it may take multiple years before colonization, and detections and densities can vary from year to year (Foin and others 1997; Liu and others 2007). Other factors can contribute to clapper rail reproductive success, including contaminants, predation, and flooding events (Schwarzbach and others 2006).

Black-necked stilts have benefited from the existing habitat mosaic of salt pond and tidal marsh. Although they were rather uncommon in San Francisco Bay historically, today they are the second most abundant breeding shorebird in San Francisco Bay (Stenzel and others 2002; Rintoul and others 2003). Stilts forage in salt ponds yet primarily nest in adjacent managed and diked marshes, and to a lesser extent, islands within salt ponds (Robinson and others 1999; Ackerman and others unpublished data). Large-scale restoration and conversion of salt pond to tidal marsh will increase available nesting habitat for stilts at the expense of available foraging habitat. For species that depend on multiple habitat types such as stilts, the overall population response to restoration is not clear. Landscape-scale analyses of population viabilities may help determine an extent of tidal-marsh restoration that benefits multiple species.

Restoration effectiveness relies on a site's ability to provide suitable prey resources, cover, and, for breeding birds, habitat for successful reproduction. Restoration is also a process of succession dynamics with habitats in transition. Habitat availability for wildlife will vary through time, depending on foraging strategies, prey availabilities, cover requirements, and habitat use during species' life stages. Understanding the mechanisms that govern habitat use and habitat requirements should improve restoration designs to maximize wildlife use of habitat mosaics through time.

CONCLUSIONS

Birds have distinct niches in tidal marshes of San Francisco Bay based on their foraging guilds and habitat associations. Rather than representing a singular, monotypic habitat type, birds respond to a composite of different resources within the tidal marsh. In addition, species show distinct responses to habitat features that vary with the evolution of a site. Urbanization and flood protection have resulted in a much more static system, and perhaps a less diverse avian community that may not be able to respond to the combined threats of sea-level rise, habitat degradation and fragmentation, invasive species and predation, and other environmental stressors.

Despite the severe loss of historic marshlands, restoration has resulted in an increase in tidal-marsh habitat and generally a large response by birds (i.e., waterbirds). However, the avian community in early restoration is mostly transitional, and the species abundance and diversity will likely decrease over time in favor of endemic tidal-marsh birds such as the black rail and the clapper rail that require mature marshes. Although the historical mosaic of tidal marshes in San Francisco Bay has changed through time, providing a wide range of habitats, current conditions are more restricted because regional development now surrounds tidal marshes. Rather than upslope migration of marshes to higher elevations, sea-level rise may eliminate tidal marshes and upland refugia zones adjacent to urban development. Thus, conservation of tidal-marsh birds will require protection of existing marshes or expansion into new areas. Future research should be directed at predicting habitat alteration and fragmentation in tidal marshes caused by sea-level rise, and linking them to changes in vital rates of bird populations, thereby identifying which species are most at risk.

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