SARAH CONNORS, Moss Landing Marine Laboratories, Moss Landing, California 95039; sarah.connors@yahoo.com

ABSTRACT: At Elkhorn Slough, an estuary on Monterey Bay, California, the number of shorebirds using muted tidal wetlands at high and low tide differs significantly. At all seasons, small sandpipers are significantly more abundant in muted tidal wetlands at high tide. In contrast, numbers of the Black-necked Stilt (*Himantopus mexicanus*) and American Avocet (*Recurvirostra americana*) do not differ significantly by tide except in winter, when they are more abundant at high tide. Manipulation of water level by adjustment of tide-gate settings enhances the suitability of muted tidal wetlands for many species. These areas provide an additional habitat dimension within the slough, enabling shorebirds to feed and roost at high tide when fully tidal mudflats are unavailable.

Intertidal mudflats provide important feeding areas for coastal shorebirds along the Pacific Flyway. The mixed semidiurnal tidal regime along the Pacific coast (two high and two low tides of different elevations in 24 hours), however, limits shorebirds' access to their prey as the extent of exposed mudflats varies (Recher 1966). Shorebirds exploit multiple strategies for foraging, particularly when their demand for energy is high (Evans 1979, Connors et al. 1981, Schneider and Harrington 1981). One important strategy is to shift to alternative foraging areas when the intertidal zone is flooded at high tide. Alternative foraging habitats include coastal beaches (Burger et al. 1977, Connors et al. 1981), agricultural fields and pastures (Colwell and Dodd 1995, Rottenborn 1996, Long and Ralph 2001), and impoundments where the tides are muted, such as salt-evaporation ponds (Masero and Perez-Hurtado 2001, Parsons 2002, Warnock et al. 2002, Strong 1990).

Many coastal wetlands have areas where the tide is restricted, either naturally or more often because of diking and restoration. The benefit of these areas to shorebirds during migration and winter has been little studied. In addition to offering alternative sites for foraging, muted tidal habitat can provide greater protection from human disturbance and wind than other high-tide roosts such as coastal beaches (Davidson and Evans 1986, Helmers 1993). For coastal wetlands to be managed successfully and maximize habitat quality for birds, baseline information on seasonal and daily patterns of use of various habitats within these wetlands is needed.

Elkhorn Slough supports one of the largest concentrations of shorebirds in California's coastal wetlands (Page et al. 1992). Elkhorn Slough's wetland complex includes both mudflats exposed to full tidal influence and impoundments where tidal flow is restricted. I evaluated shorebird use of muted tidal habitat and tested the hypothesis that it supports a greater number of shorebirds at high tide than at low tide.

METHODS

Study Area

Elkhorn Slough's wetlands comprise several mudflats to which the flow of tidal water is restricted through culverts. I studied three of these areas: North Marsh, the salt ponds, and Moro Cojo Slough (Figure 1). North Marsh, bordering the main channel of Elkhorn Slough and within Elkhorn Slough National Estuarine Research Reserve, covers 42.2 ha and contains elevated areas of pickleweed marsh (*Salicornia virginica*) interspersed with

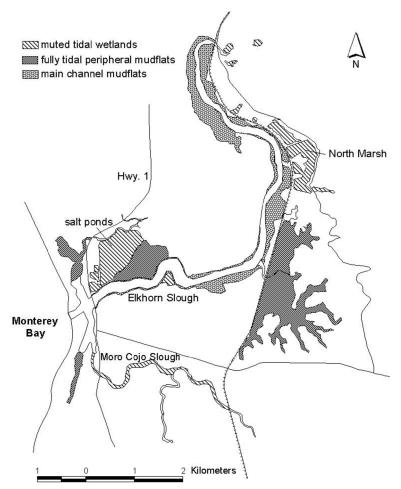


Figure 1. Mud habitat within Elkhorn Slough's wetlands on Monterey Bay, California, in 1999 and 2000.

bare mudflat (approximately 14 ha). This site receives water from Elkhorn Slough through four culverts. Salinity readings taken throughout the year ranged from 18 to 56 parts per thousand (ppt). This area was closed to the public during my study.

The salt ponds, bordering the lower portion of Elkhorn Slough and encompassing approximately 49 ha, were used as evaporation ponds for salt mining from 1916 until 1973 (Gordon 1996). During my study, this site was an important nesting area for the Snowy Plover (*Charadrius alexandrinus*) and was closed to the public to reduce disturbance to it and other nesting birds. The salt ponds consist of four principal ponds, each with tide gates. Manipulation of the water level during the breeding season (managed by PRBO Conservation Science) provides exposed mud for foraging, roosting, and nesting shorebirds. The ponds' salinity, influenced by rainfall and evaporation, ranges from brackish to hypersaline.

Moro Cojo Slough, less than 2 km to the south of Elkhorn Slough, is exposed to minimal tidal influence at its connection with Moss Landing Harbor, where the tide is restricted through culverts. This site covers approximately 5.4 ha of mudflats from the harbor to the railroad tracks 3.5 km to the east. The channel is bordered by salt marsh, agricultural land, and rangeland actively grazed by cattle. Salinity readings ranged from 2 to over 100 ppt throughout the year, influenced by distance from the harbor, rainfall, and evaporation.

Data Collection

From 1 March 1999 through 30 June 2000 I surveyed the three study sites for shorebirds two to three times monthly within a 6-hour period around low tide and a 6-hour period around high tide on the same day, using 8×40 binoculars and a spotting scope with a 20–60 zoom lens. I followed the same routes consistently on foot at North Marsh and the salt ponds. I used a kayak at Moro Cojo Slough when the water level permitted; otherwise, I surveyed this site on foot. The duration of surveys depended on the number of birds in the area. All shorebirds on mudflats were counted and identified to species when visibility permitted. The Dunlin (Calidris alpina), Western Sandpiper (C. mauri), and Least Sandpiper (C. minutilla) were counted as "peeps" when visibility was compromised. At high tide I recorded behavior, categorizing it as feeding, roosting (including preening), or "other." I placed water-depth gauges, consisting of posts 2 inches in diameter with alternating black and white bands 2 inches wide, at each study site to record the water's depth on each survey. I did not survey when high water made a study site unavailable to small shorebirds; consequently, the number of surveys varied by site.

Data Analysis

I categorized my results by season: winter (1 December to 28 February), spring (1 March to 30 May), and fall (1 July to 30 November). I evaluated statistically only species that made up 5% or more of the total counted in a study area in all seasons combined. Red-necked Phalaropes (*Phalaropus lobatus*) were relatively abundant for a brief period during fall only and so were not evaluated statistically. Only counts that totaled at least 10% of each

species' peak count within a season were included in data analysis. Data from the three sites were combined for statistical analysis. I used a paired *t* test to compare abundances of shorebirds at high and low tides. When the data were not normally distributed, I used the Wilcoxon signed-rank test. The level of significance was defined as p < 0.05. I evaluated abundances rather than density because the change in the extent of mudflat between high and low tide was minimal. In spring, to reduce disturbance to nesting Snowy Plovers, I surveyed the salt ponds from their outer boundaries but did not include these data in analyses because of compromised visibility.

RESULTS

Shorebird Abundance and Diversity

During high-tide surveys from 1 March 1999 to 1 July 2000 I recorded 25 species of shorebirds totaling 166,142 individuals. During low-tide surveys I recorded 22 species (a subset of those recorded at high tide) totaling 21,939 individuals. Four species occurred year round: the American Avocet (*Recurvirostra americana*), Black-necked Stilt (*Himantopus mexicanus*), Killdeer (*Charadrius vociferus*), and Snowy Plover. All others were migrants. Small sandpipers were the most abundant shorebirds, accounting for 77% of all birds recorded (unidentified peeps 27%, Least Sandpiper 26%, Western Sandpiper 17%, Dunlin 6%). The greatest count of peeps during high tide at a site was more than 12,000 individuals on 18 January 2000 at the salt ponds.

Species following peeps in order of abundance were dowitchers (*Limnodromus scolopaceus* and *L. griseus*, not differentiated; 6%), American Avocet (5%), Black-necked Stilt (3%), and Red-necked Phalarope (3%). All three study sites were similar in the number of shorebird species recorded (North Marsh and Moro Cojo Slough: 19; salt ponds: 20), though the composition of the assemblages differed subtly.

High Tide vs. Low Tide

Eighty-eight percent of all shorebirds recorded during the study were observed at high tide. At all seasons the abundance of sandpipers of the genus *Calidris* at high tide significantly exceeded numbers at low tide (Table 1, Figure 2). In winter the abundances of Black-necked Stilts and American Avocets were significantly greater at high tide than at low tide, but in fall and spring there was no significant difference (Table 1, Figure 2).

In contrast to the difference in shorebird abundance by tide phase, the overall number of species recorded at each study site at high and low tide did not differ markedly (Table 2).

Behavior

The principal behaviors of shorebirds during high tide at all seasons were feeding and roosting (Figure 3). During fall and winter most of the small sandpipers were roosting (73% and 66% respectively). In contrast, during spring (pre-migration) 60% were feeding. Of the larger shorebirds, most avocets, stilts, and dowitchers were feeding at high tide in all seasons (Figure 3).

	Na	t ^b	Zc	Р
Fall				
Black-necked Stilt	26	_	0.7113	>0.05
American Avocet	16	_	1.4230	>0.05
Dowitchers	20	_	0.2407	>0.05
Dunlin	8	2.4813	_	< 0.05
Western Sandpiper	22	_	3.1039	< 0.01
Least Sandpiper	22	4.4782	_	< 0.001
All peeps combined	22	—	4.0007	< 0.0001
Winter				
Black-necked Stilt	11	_	2.7603	< 0.01
American Avocet	11	2.7323	_	< 0.05
Dowitchers	8	4.0678	_	< 0.01
Dunlin	11	_	2.8896	< 0.01
Western Sandpiper	11	_	2.8480	< 0.01
Least Sandpiper	11	5.7701	_	< 0.001
All peeps combined	11	4.4019	_	< 0.01
Spring				
Black-necked Stilt	15	_	0.2558	>0.05
American Avocet	14	_	0.0314	>0.05
Dowitchers	11	2.3884	_	< 0.05
Western Sandpiper	11	1.8593	_	>0.05
Least Sandpiper	11		1.4240	>0.05
All peeps combined	11	2.3922		< 0.05

Table 1Results of Statistical Tests Comparing ShorebirdAbundance at High and Low Tide in Muted Tidal Habitat atElkhorn Slough, California, 1999–2000

^aNumber of surveys included in the analysis.

^bResults of paired t tests.

^cResults of Wilcoxon signed-rank tests.

DISCUSSION

Habitat Use at Different Tides

This study emphasizes the value of muted tidal habitat in coastal wetlands for shorebirds as foraging and roosting grounds during migration and winter, particularly at high tide when intertidal mudflats are unavailable. Over 75% of all shorebirds using this habitat were small sandpipers, a proportion similar to that in the larger Elkhorn Slough wetland complex during winter (68%), spring (65%), and fall (77%) of 1999 (Connors 2003). Earlier surveys at Elkhorn Slough also found small sandpipers to be the most abundant species, accounting for over 80% of all shorebirds at all seasons (Ramer et al. 1991).

The importance of muted tidal habitat for shorebirds may depend largely on its proximity to intertidal feeding grounds. Muted tidal areas at Elkhorn Slough are less than 2 km from the principal feeding area along the main

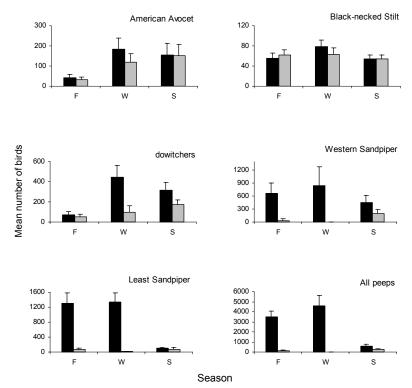


Figure 2. Mean number of shorebirds recorded during surveys at consecutive high and low tides (\pm standard error) at muted tidal wetlands at Elkhorn Slough from March 1999 through June 2000. F, fall; W, winter; S, spring. Black bar, high tide; gray bar, low tide; see Table 1 for values of *N*.

channel of the slough. Over 80% of all shorebirds recorded during this study were observed at North Marsh or the salt ponds, both sites immediately adjacent to the main channel. Connors (2003) found the abundance of small sandpipers decreasing dramatically in February 2000, possibly because of the flooding of most muted tidal areas after substantial rainfall in January. Commuting to more distant high-tide roosts may have been too costly, resulting in the birds' relocating to another complex of wetlands. The less time spent in transit between intertidal foraging areas at low tide and foraging or roosting sites at high tide, the less energy is expended in transportation costs and time that could be spent feeding or resting. Farmer and Parent (1997) determined that the more disconnected a wetland complex, the less likely are Pectoral Sandpipers to move among foraging and roosting sites. They concluded that, with increasing distance between sites in a wetland system, the less energetically beneficial is the complex for shorebirds and the shorter the period that migrating birds will reside in the area.

	High tide	Low tide	
North Marsh (N = 23)			
Unidentified peeps	0.42	American Avocet	0.27
Least Sandpiper	0.17	Dowitchers	0.21
Western Sandpiper	0.16	Least Sandpiper	0.12
Dowitchers	0.07	Black-necked Stilt	0.12
Dunlin	0.06	Red-necked Phalarope	0.12
American Avocet	0.05	Western Sandpiper	0.07
Marbled Godwit	0.02	Marbled Godwit	0.04
Black-necked Stilt	0.02	Dunlin	0.02
Red-necked Phalarope	0.02	Willet	0.01
Total number of shorebirds	88,655	Semipalmated Plover	0.01
Moro Cojo Slough ($N = 21$)		Total number of shorebirds	13,005
Least Sandpiper	0.49	Western Sandpiper	0.24
Unidentified peeps	0.12	Red-necked Phalarope	0.21
Western Sandpiper	0.09	Black-necked Stilt	0.20
Dowitchers	0.08	Dowitchers	0.11
Black-necked Stilt	0.06	American Avocet	0.10
Red-necked Phalarope	0.06	Least Sandpiper	0.08
Dunlin	0.05	Killdeer	0.03
American Avocet	0.03	Dunlin	0.01
Killdeer	0.01	Greater Yellowlegs	0.01
Total number of shorebirds	23,899	Total number of shorebirds	7505
Salt Ponds $(N = 8)$			
Least Sandpiper	0.35	Black-necked Stilt	0.26
Western Sandpiper	0.25	American Avocet	0.19
Unidentified peeps	0.20	Least Sandpiper	0.14
Dunlin	0.10	Red-necked Phalarope	0.09
Marbled Godwit	0.03	Snowy Plover	0.07
Willet	0.01	Willet	0.06
American Avocet	0.01	Long-billed Curlew	0.06
Black-bellied Plover	0.01	Greater Yellowlegs	0.04
Black-necked Stilt	0.01	Black-bellied Plover	0.02
Semipalmated Plover	0.01	Killdeer	0.02
Snowy Plover	0.01	Dowitchers Sourdeuling	0.01
Total number of shorebirds	53,588	Sanderling	0.01
	-	Semipalmated Plover	0.01 0.01
		Unidentified peeps	0.01
		Total number of shorebirds	1429

Table 2Proportions of Shorebirds by Tide at Sites with Muted Tides atElkhorn Slough, California, 1 March 1999–1 July 2000a

^aSpecies with proportions <0.01 are not shown; *N*, number of surveys conducted. Species whose scientific names are not in the text: Black-bellied Plover (*Pluvialis squatarola*), Semi-palmated Plover (*Charadrius semipalmatus*), Willet (*Tringa semipalmata*), Greater Yellowlegs (*Tringa melanoleuca*), Long-billed Curlew (*Numenius americanus*), Marbled Godwit (*Limosa fedoa*), Sanderling (*Calidris alba*).

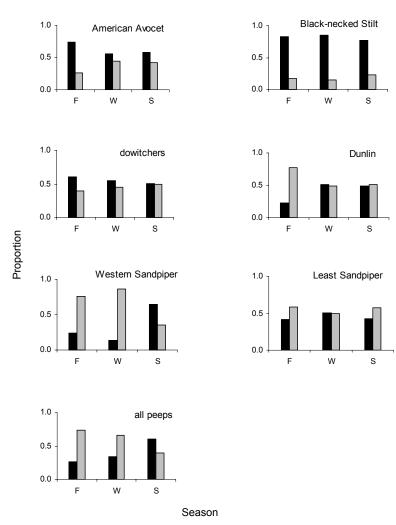


Figure 3. Proportion of total number of shorebirds recorded during high-tide surveys that were feeding (black bar) and roosting (gray bar) at muted tidal wetlands at Elkhorn Slough from March 1999 through June 2000. F, fall; W, winter; S, spring; see Table 1 for values of N.

At all seasons I found shorebird use of muted tidal areas to be most pronounced during high tide. The reduced tidal amplitude at these sites provides birds a place to feed and rest at high tide. Strong (1990) observed a similar pattern at Elkhorn Slough's salt ponds in the late 1980s. Davidson and Evans (1986) reported comparable results at man-made peripheral wetlands

in England, with most shorebird species present in far greater numbers at high tide than at low tide.

Species diversity at muted tidal sites at Elkhorn Slough does not differ markedly by tidal phase; species composition, however, does. Small *Calidris* sandpipers dominate the shorebird assemblage on high tides, then relocate to the intertidal zone as the tide recedes. Warnock et al. (2002) observed a similar pattern of shorebird species composition on salt ponds in San Francisco Bay, where *Calidris* sandpipers dominate at high tide (constituting 46% and 55% of all birds in two consecutive years) but account for less than 5% of all birds at low tide.

Some shorebirds at Elkhorn Slough, primarily residents, use muted tidal areas throughout the tide cycle, implying that this habitat meets their daily requirements for feeding and roosting. Stilts and avocets use muted tidal wetlands surrounding Elkhorn Slough throughout the tide cycle during fall and spring and nest in this habitat. Similarly, Velasquez and Hockey (1992) found little difference in the abundance of resident waterbirds on saltpans between high and low tide but migrants to be markedly more abundant at high tide than at low tide.

Muted tidal wetlands offer two principal benefits to migratory shorebirds: providing an alternative place to feed when intertidal mudflats are inaccessible and a place to rest during interludes between foraging at low tide. The behavior of the most abundant shorebirds using muted tidal wetlands, the small sandpipers, was not consistent throughout the year. In fall and winter (July through February), the majority of *Calidris* sandpipers roosted at high tide. During spring (March through May), however, they spent most of their time feeding. Potential causes of this pattern during spring are shortage of available food at low tide in the intertidal zone, time constraints during feeding on intertidal mudflats, seasonal increases in energy demands, and seasonal variations in availability of prey in muted tidal habitat (Evans 1976, Evans and Dugan 1984, Schneider and Harrington 1981, Velasquez and Hockey 1992). Masero and Perez-Hurtado (2001) documented a greater proportion of Redshanks (Tringa totanus) foraging in peripheral wetlands before migration than in winter, coinciding with a decrease in the biomass of prev in adjacent intertidal habitat. Shorebirds' demand for energy increases during migration. Birds that arrive at their breeding grounds in optimal condition can use surplus fat and protein to accelerate egg production (Davidson and Evans 1988). If a bird cannot meet its caloric needs during the diurnal low tide cycle, it may enhance its intake by foraging at night or in habitats exposed at high tide. A study of the composition and seasonal availability of prev in muted tidal wetlands at Elkhorn Slough may elucidate corresponding patterns of shorebird behavior.

Management Considerations

Water depth at muted tidal sites is influenced by rainfall, evaporation, and extent of tidal exchange and can be manipulated to provide habitat for various species of birds. Awareness of shorebirds' migratory schedule, which varies considerably by species, is needed to manage water levels successfully and enhance habitat for shorebirds.

Management of water level may also be influenced by other variables

unique to a site. For example, during late spring, summer, and early fall, a thick layer of algae (*Ulva* sp. and *Enteromorpha* sp.) formed on the water surface in North Marsh, providing an alternative feeding and roosting substrate for small shorebirds. Deeper water was maintained when algae were present, providing habitat for other birds such as ducks and herons while still supporting short-legged species such as the Western and Least Sandpipers. The presence of algal mats on the water surface may have increased foraging success for some shorebirds. Allen (1992) found more amphipod crustaceans within algal mats overlying mudflats than on mudflats without algae.

Various studies have examined the site fidelity of migrating and breeding shorebirds (Gratto et al. 1985, Warnock and Takekawa 1996, Takekawa et al. 2002). Although many shorebirds maintain some degree of site fidelity during migration and winter (Kelly and Cogswell 1979, Smith and Houghton 1984), they also use suitable habitat opportunistically as soon as it becomes available (Rundle and Fredrickson 1981, Skagen and Knopf 1994). Minor adjustments in water depth at muted tidal sites can make a tremendous difference in habitat availability to small shorebirds (Helmers 1992, Safran et al. 1997, Collazo et al. 2002, pers. obs.) and can attract migrants quickly.

Boettcher et al. (1994) found that variation in bottom topography and gradual flow of water into an impoundment create a variety of microhabitats. At North Marsh, a given water level provides a diversity of water depths suiting a broad assemblage of species. Whereas small sandpipers use mudflats covered by up to 5 cm of water, some larger shorebirds such as avocets and stilts feed in water as deep as 17 cm (Helmers 1992, Boettcher et al. 1995, Isola et al. 2000).

Water-level adjustments have longer-lasting benefits if they are made in small increments. Small shorebirds tend to feed along the receding water's edge; thus, a gradual drawdown provides suitable feeding habitat for a longer period of time (Rundle and Fredrickson 1981, Fredrickson and Taylor 1982). Velasquez (1992) found that if water level is decreased gradually, both shorebird abundance and diversity increase. Alternatively, managing for a relatively constant water level reduces the risk of flooding nests and may serve other purposes as well, including reduction of mosquito populations (P. Ghormley, N. Salinas Valley Mosquito Abatement District, pers. comm.). By June at Elkhorn Slough, migrant shorebirds have vacated the region, and resident species have established nests. Gradual drawdowns, which benefit small migratory shorebirds, are not critical at this time. Rather, managing for stable water levels would be a strategy appropriate to preclude flooding of resident birds' nests. As migrants begin to return to the slough in July, drawdowns can commence in anticipation of the arrival of large numbers of small sandpipers.

The conservation and management of muted tidal wetlands can enhance a coastal wetland system by providing an additional habitat dimension for migrating and wintering birds. Mudflats with restricted tidal flow are an important component of Elkhorn Slough's wetlands for most shorebirds. Use of these sites at high tide underscores their value for shorebirds. With knowledge of patterns of shorebirds' habitat use, seasonal requirements, and regional habitat limitations, mudflats with muted tidal flow can be managed effectively to optimize habitat quality for shorebirds.

ACKNOWLEDGMENTS

Funding was provided by a NOAA National Estuarine Research Reserve graduate fellowship, the Thomas Harvey Scholarship Fund, the Dr. Earl and Ethel Myers Oceanographic and Marine Biology Trust, a Packard Foundation scholarship, and a Marianna Pisano scholarship. Much thanks to Jim Harvey for guidance in all aspects of this study, Carleton Eyster for field assistance and ongoing encouragement, the Elkhorn Slough staff, particularly Becky Christensen and Kerstin Wasson, and Alan Baldridge, Greg Cailliet, Richard Callas, Jim Harvey, Tim Manolis, Skyli McAfee, Steven Morgan, Lewis Oring, Gary Page, Lynne Stenzel, Nils Warnock, and Kerstin Wasson for perceptive comments on earlier drafts of the manuscript.

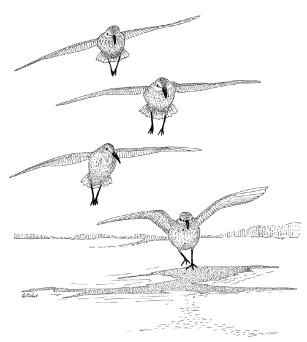
LITERATURE CITED

- Allen, J. K. 1992. Benthic invertebrates living in macroalgal mats on intertidal mudflats of Elkhorn Slough, California. M.S. thesis, San Jose State University.
- Boettcher, R., Haig, S. M., and Bridges, W. C., Jr. 1994. Behavioral patterns and nearest neighbor distances among nonbreeding avocets. Condor 96:973–986.
- Boettcher, R., Haig, S. M., and Bridges, W. C., Jr. 1995. Habitat-related factors affecting the distribution of nonbreeding American Avocets in coastal South Carolina. Condor 97:68–81.
- Burger, J., Howe, M. A., Hahn, D. C., and Chase, J. 1977. Effects of tide cycles on habitat selection and habitat partitioning by migrating shorebirds. Auk 94:743–758.
- Collazo, J. A., O'Harra, D. A., and Kelly, C. A. 2002. Accessible habitat for shorebirds: Factors influencing its availability and conservation implications. Waterbirds 25 (Spec. Publ. 2):13–24.
- Colwell, M. A., and Dodd, S. L. 1995. Waterbird communities and habitat relationships in coastal pastures of northern California. Conserv. Biol. 9:827-834.
- Connors, P. G., Myers, J. P., Connors, C., and Pitelka, F. A. 1981. Interhabitat movements by Sanderlings in relation to foraging profitability and the tidal cycle. Auk 98:49–64.
- Connors, S. 2003. Shorebird distribution in a changing environment: Patterns at Elkhorn Slough. M.S. thesis, San Jose State University.
- Davidson, N. C., and Evans, P. R. 1986. The role and potential of man-made and man-modified wetlands in the enhancement of the survival of overwintering shorebirds. Colonial Waterbirds 9:176–188.
- Davidson, N. C., and Evans, P. R. 1988. Prebreeding accumulation of fat and muscle protein by Arctic-breeding shorebirds. Proc. Int. Ornithol. Congress 19:342–352.
- Evans, P. R. 1976. Energy balance and optimal foraging strategies in shorebirds: Some implications for their distributions and movements in the non-breeding season. Ardea 64: 117–139.
- Evans, P. R. 1979. Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal invertebrate prey, in Cyclic Phenomena in Marine Plants and Animals (E. Naylor and R. G. Hartnoll, eds.), pp. 357–366. Pergamon Press, Oxford, England.
- Evans, P. R., and Dugan, P. J. 1984. Coastal birds: Numbers in relation to food resources, in Coastal Waders and Wildfowl in Winter (P. R. Evans, J. D. Goss-Custard, and W. G. Hale, eds.), pp. 8–28. Cambridge Univ. Press, Cambridge, England.

- Farmer, A. H., and Parent, A. H. 1997. Effects of the landscape on shorebird movements at spring migration stopovers. Condor 99:698–707.
- Fredrickson, L. H., and Taylor, T. S. 1982. Management of seasonally flooded impoundments for wildlife. U.S. Dept. Interior, Fish & Wildlife Serv. Resource Publ. 148.
- Gordon, B. L. 1996. Monterey Bay Area: Natural History and Cultural Imprints, 3rd ed. Boxwood Press, Pacific Grove, CA.
- Gratto, C. L., Morrison, R. I. G., and Cooke, F. 1985. Philopatry, site tenacity, and mate fidelity in the Semipalmated Sandpiper. Auk 102:16–24.
- Helmers, D. L. 1992. Shorebird management manual. Western Hemisphere Shorebird Reserve Network, P. O. Box 1770, Manomet, MA 02345.
- Helmers, D.L. 1993. Enhancing the management of wetlands for migrant shorebirds. Trans. N. Am. Wildlife Nat. Resources Conf. 58:335–344.
- Isola, C. R., Colwell, M. A., Taft, O. W., and Safran, R. J. 2000. Interspecific differences in habitat use of shorebirds and waterfowl foraging in managed wetlands of California's San Joaquin Valley. Waterbirds 23:196–203.
- Kelly, P. R., and Cogswell, H. L. 1979. Movements and habitat use by wintering populations of Willets and Marbled Godwits. Studies Avian Biol. 2:69–82.
- Long, L. L., and Ralph, C. J. 2001. Dynamics of habitat use by shorebirds in estuarine and agricultural habitats in northwestern California. Wilson Bull. 113:41–52.
- Masero, J. A., and Perez-Hurtado, A. 2001. Importance of the supratidal habitats for maintaining overwintering shorebird populations: How redshanks use tidal mudflats and adjacent saltworks in southern Europe. Condor 103:21–30.
- Page, G. W., Shuford, W. D., Kjelmyr, J. E., and Stenzel, L. E. 1992. Shorebird numbers in wetlands of the Pacific Flyway: A summary of counts from April 1988 to January 1992. Point Reyes Bird Observatory, 3820 Cypress Dr. #11, Petaluma, CA 94954.
- Parsons, K. C. 2002. Integrated management of waterbird habitats at impounded wetlands in Delaware Bay, U.S.A. Waterbirds 25 (Spec.Publ. 2):25–41.
- Ramer, B. A., Page, G. W., and Yoklavich, M. M. 1991. Seasonal abundance, habitat use, and diet of shorebirds in Elkhorn Slough, California. W. Birds 22:157–174.
- Recher, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47:393–407.
- Rottenborn, S. C. 1996. The use of coastal agricultural fields in Virginia as foraging habitat by shorebirds. Wilson Bull. 108:783–796.
- Rundle, W. D., and Fredrickson, L. H. 1981. Managing seasonally flooded impoundments for migrant rails and shorebirds. Wildlife Soc. Bull. 9:80–87.
- Safran, R. J., Isola, C. R., Colwell, M. A., and Williams, O. E. 1997. Benthic invertebrates at foraging locations of nine waterbird species in managed wetlands of the northern San Joaquin Valley, California. Wetlands 17:407–415.
- Schneider, D. C., and Harrington, B. A. 1981. Timing of shorebird migration in relation to prey depletion. Auk 98:801–811.
- Skagen, S. K., and Knopf, F. L. 1994. Migrating shorebirds and habitat dynamics at a prairie wetland complex. Wilson Bull. 106:91–105.
- Smith, P. W., and Houghton, N. T. 1984. Fidelity of Semipalmated Plovers to a migration stopover area. J. Field Ornithol. 55:247–249.

- Strong, C. 1990. Bird use of the Moss Landing Wildlife Management area, April 1988 to April 1989. Report to Santa Clara Valley Audubon Society, 22221 McClellan Rd., Cupertino, CA 95014.
- Takekawa, J. Y., Warnock, N., Martinelli, G. M., Miles, A. K., and Tsao, D. C. 2002. Waterbird use of bayland wetlands in the San Francisco Bay estuary: Movements of Long-billed Dowitchers during the winter. Waterbirds 25 (Spec. Publ. 2):93–105.
- Velasquez, C. R. 1992. Managing artificial saltpans as a waterbird habitat: Species' responses to water level manipulation. Colonial Waterbirds 15:43–55.
- Velasquez, C. R., and Hockey, P. A. R. 1992. The importance of supratidal foraging habitats for waders at a south temperate estuary. Ardea 80:243–253.
- Warnock, N., Page, G. W., Ruhlen, T. D., Nur, N., Takekawa, J. Y., and Hanson, J. T. 2002. Management and conservation of San Francisco Bay salt ponds: Effects of pond salinity, area, tide, and season on Pacific Flyway waterbirds. Waterbirds 25 (Spec. Publ. 2):79–92.
- Warnock, S. E., and Takekawa, J. Y. 1996. Wintering site fidelity and movement patterns of Western Sandpipers *Calidris mauri* in the San Francisco Bay estuary. Ibis 138:160–167.

Accepted 1 May 2008



Western Sandpipers

Sketch by George C. West