Wintering site fidelity and movement patterns of Western Sandpipers *Calidris mauri* in the San Francisco Bay estuary

SARAH E. WARNOCK* & JOHN Y. TAKEKAWA

U.S. National Biological Service, California Pacific Science Center, 6924 Tremont Road, Dixon, CA 9[illegible]9648, USA

Western Sandpipers *Calidris mauri* are the most numerous shorebird species in the San Francisco Bay estuary during winter. A sample of 106 Western Sandpipers was captured in mist nets and radio-marked with 1-g transmitters to examine their wintering site fidelity and movements. Differences in distances moved, home range extent and core area size were examined by age, sex, season, site, time of day and tide. All birds remained in the south San Francisco Bay region during winter and exhibited strong site fidelity, with a mean home range of 22.0 km^2 or only 8% of the study area. First-year birds had larger home ranges (26.6 ± 3.6 km^2) than adults (17.2 ± 2.5 km^2) in winter, but home range sizes of males and females were not significantly different in any period. Home range sizes were similar between seasons, but core areas were smaller in spring (6.3 ± 1.2 km^2) than in early (9.6 ± 4.0 km^2) or late (11.6 ± 1.6 km^2) winter. Movements and home range size were similar for radio-marked birds located during day and night. The high degree of regional and local site fidelity demonstrated that the mixture of natural mud flats and artificial salt ponds in southern San Francisco Bay provided sufficient resources for large wintering populations of Western Sandpipers.

Wetlands in California have been reduced to less than 6% of their original extent during the past 150 years (Gilmer *et al.* 1982, Nichols *et al.* 1986). Nearly 90% of the remaining coastal wetlands are found within the San Francisco Bay estuary (Josselyn 1983). Historically, the mud flats of San Francisco Bay were bordered by vast expanses of vegetated salt marsh. Beginning in 1862, much of the natural marsh was diked for agricultural and urban use or flooded for evaporation ponds used in commercial salt production (Ver Planck 1958). Despite degradation and loss of natural habitats (Nichols *et al.* 1986), the estuary supports one of the largest concentrations of wintering and migrating shorebirds on the Pacific coast of North America (Kjelmyr *et al.* 1991).

Western Sandpipers *Calidris mauri* are the most abundant shorebird in the San Francisco Bay estuary, with several hundred thousand in mid-winter and over one-half million birds during spring migration (Kjelmyr *et al.* 1991, Page *et al.* 1992). Western Sandpipers have been studied extensively on the breeding grounds (Holmes 1971, 1972, 1973) and during migration (Butler *et al.* 1987, Gill & Handel 1990), but few studies have examined their wintering ecology. Shorebird studies (Recher 1966, Kelly & Cogswell 1979, Holway 1990) in the San Francisco Bay estuary have been limited by the difficulty in following marked individuals in such a large area. Development of miniature radio transmitters has improved opportunities to conduct research on marked shorebirds (Yalden 1991, Warnock & Warnock 1993) because individuals may be located from a distance of several kilometres in all weather conditions. Further, we were able to follow marked individuals at night, an activity period on which little research has previously been conducted.

We studied the wintering ecology of Western Sandpipers in south San Francisco Bay during the winter and spring of 1991–1992. In this paper, we describe site fidelity, spatial distribution and movement patterns of a radio-marked population and examine the effects of temporal, spatial and demographic factors on the movement distances and home range.

STUDY AREA

The San Francisco Bay estuary (Fig. 1) is located in central California (38.5°N, 122.3°W) and is one of the largest estuaries (1200 km^2) on the Pacific coast of North America (Conomos 1979, Monroe & Kelly 1992). Research was conducted in south San Francisco Bay (Fig. 1), where the estuary is characterized by a deep-water channel, broad mud flats and remnant tidal salt marsh, bordered by industrial salt evaporation ponds and urban development.

* Present address: 521 Imperial Boulevard, Reno, NV 89503, USA.

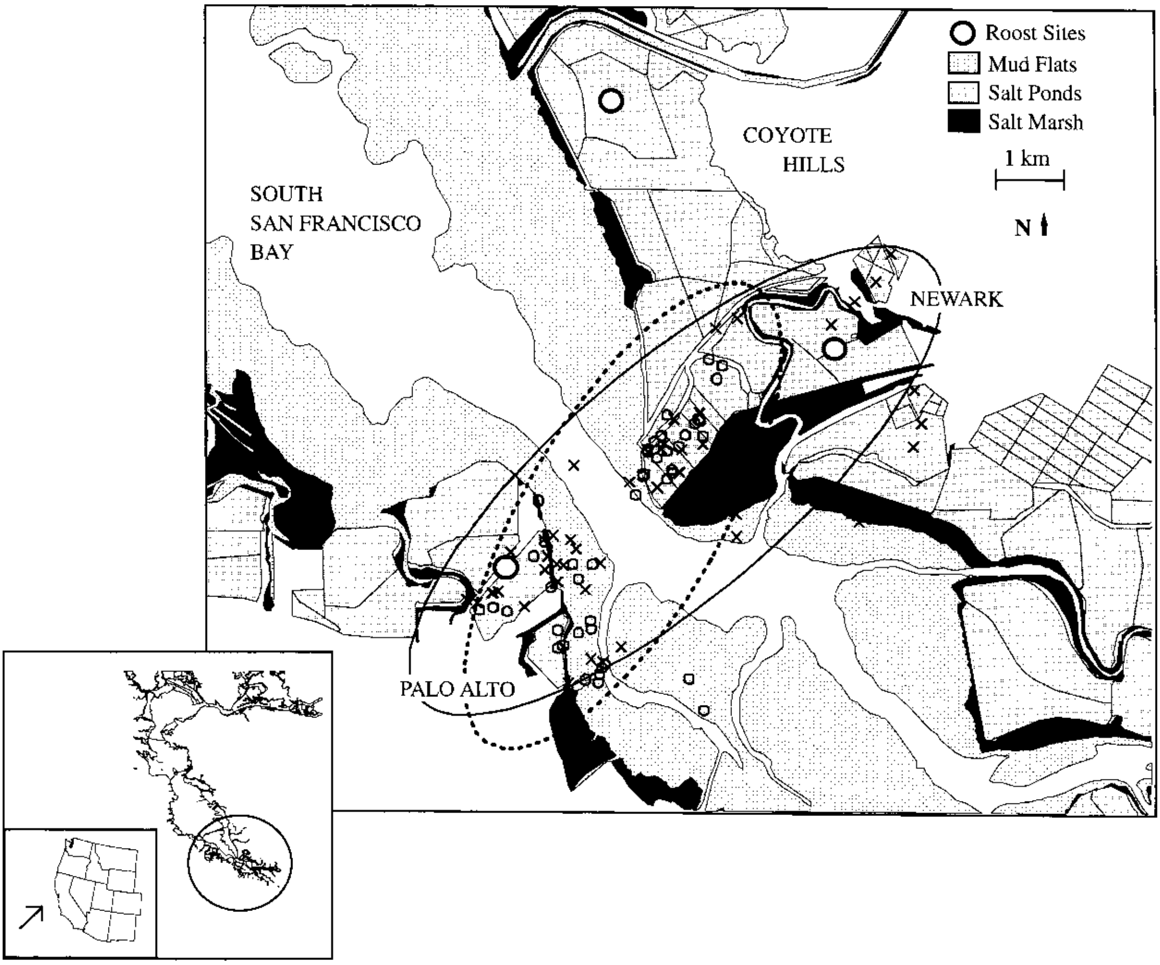

Figure 1. The San Francisco Bay estuary and the South Bay study area. Western Sandpipers were captured and radio-marked at three roost sites: Newark, Palo Alto and Coyote Hills. Radio locations for adult (#6129, o) and first-year (#5574, ×) birds are presented. Home ranges of the adult (– – –) and first-year (——) birds are also indicated.

METHODS

Capture and marking

Western Sandpipers were caught in mist nets set during daytime high tides at three of the major south San Francisco Bay roosting sites located about 5 km apart (Fig. 1). The birds were caught in early winter (November 1991), late winter (January 1992) and spring (April 1992). Birds were marked with U.S. Fish and Wildlife Service rings, ultraviolet-resistant colour rings with a green flag-band, measured and weighed. Sex was determined from bill length (Page & Fearis 1971). Individuals were classified as in their first year of life or as adult on the basis of presence (first year) or absence (adult) of chestnut-coloured inner median wing-coverts (Prater *et al.* 1977). Equal numbers of first-year and adult birds were marked at each site. Birds captured during spring were not aged because the inner covert characteristic was not considered reliable for age determination at that time of year.

Larger individuals (>25 g) were fitted with radio transmitters with unique frequencies. Transmitters (Model BD-2, Holohil Systems Ltd, Woodlawn, ON) weighed approximately 1 g and were glued to the Western Sandpipers with a waterproof epoxy (Titan Corporation, Lynnwood, WA) about 5 mm anterior of the uropygial gland (Warnock & Warnock 1993). Retention time with this method of attachment was at least 7 weeks. Transmitter batteries had an expected lifespan of 30 days and a range of 3–4 km on the ground and 7–9 km from a 120-m hill. Most birds were caught, processed and released within 15 min.

Radio tracking

After a 3-day adjustment period, the location of each bird was recorded within 1 h of each low and high tide, for a maximum of four locations per day. Tides were classified into low tides (<0.76 m at the Golden Gate Bridge) when mud flats were widely available and high tides (>1.30 m) when mud flats were inundated. We also classified early and late winter locations into day (0600–1800h) and night (1800–0600h) periods. The average day period included 1 h before sunrise and 1 h after sunset during the winter. Each radio-marked bird was relocated for up to 38 days. Aerial telemetry surveys were conducted at periodic intervals to locate missing birds.

Ground locations were obtained by observers in vehicles equipped with dual-Yagi null-peak telemetry systems. An effort was made to locate each radio-marked individual during every tide. Truck location and azimuth and bird azimuth were entered directly into a laptop computer, and bird locations were computed in Universal Transversal Mercator (UTM) coordinates using a modified version of the XYLOG and UTMTEL programs (Dodge & Steiner 1986, Dodge *et al.* 1986). Two or more bearings were used to estimate the location of each radio-marked individual.

Statistical analyses

Two different measurements were used to examine site fidelity and movement patterns of the marked Western Sandpipers. The distance a bird moved from roosting to feeding was measured by calculating the distance between an individual's location at high tide and its location on the following low tide. We assumed that movements of a marked bird were independent of other birds, and we averaged the movements of each individual for analysis.

Movement patterns through the tracking period were also quantified by determining the home range of radio-marked individuals. Following Burt (1943), we defined the home range of Western Sandpipers as the areas used in their normal activities of feeding and roosting, including areas between roosting and foraging sites. Areas within the home range that contained the maximum number of locations and exceeded a uniform distribution were defined as core use areas (Samuel & Green 1988). The weighted (95%) bivariate elliptical home ranges and core use areas (Samuel & Garton 1985) were computed from radiotelemetry locations with the program HOME RANGE (Ackerman *et al.* 1990). the HOME RANGE procedure eliminated outlier locations that could potentially result in excessively large home ranges (Samuel & Garton 1985).

Home range estimates were calculated for radio-marked Western Sandpipers with more than 20 locations because home range size has been shown to stabilize at or near that sample size (Anderson 1982, Jaremovic & Croft 1987). Distribution of locations from each radio-marked bird was tested for goodness of fit to a bivariate normal distribution with the Cramer-von Mises test (Samuel & Garton 1985).

Analysis of variance (ANOVA) tests, adjusted for unbalanced sample sizes (general linear model procedure: Zar 1984, SAS Institute, Inc. 1989), were used to examine for differences between groups. A two-way ANOVA test was used to examine for age and sex differences. Separate one-way ANOVA tests were used to test seasonal and site differences. Significance values for the multiple ANOVA tests were adjusted by the Sidak procedure (Sidak 1967). When ANOVA test results were significant ($P < 0.05$), differences between means were examined with a least-significant-difference (LSD) test (Milliken & Johnson 1984).

Variations in home range size by night and day in early and mid-winter and by tidal levels across all seasons were examined by paired *t*-tests (Zar 1984). Relationships between daily movements (km) and tidal amplitude (m) and period (h) were examined in a linear regression analysis (Zar 1984) for adult and first-year birds. Means ± s.e. are reported for each comparison.

RESULTS

Capture and marking

A sample of 106 Western Sandpipers was radio-marked: 29 in early winter, 27 in mid-winter and 50 in spring. In early winter, seven radio-marked birds were found dead within 3 days of release. Following the first marking attempts, survival of radio-marked individuals was improved by marking and releasing them as quickly as possible (15 min). None of the birds was found dead during the remainder of the study, and radio-marked birds were regularly observed roosting and feeding among large flocks of unmarked birds. One transmitter failed, and three transmitters could not be relocated because of local radio interference at their frequencies.

Regional movements

Almost all (99/106; 96%) of the radio-marked birds were relocated during the study. None of the birds was found outside of the south San Francisco Bay study area during the winter tracking sessions, despite comprehensive aerial and ground searches conducted in nearby Bolinas Lagoon, Suisun Marsh, Sacramento–San Joaquin River Delta and Central Valley wetland areas. Before leaving the San Francisco Bay estuary to migrate north, individuals radio-marked during the spring tracking session remained within the South Bay and were not located in other areas of the bay prior to migration. A large proportion (80%) of the birds radio-marked in spring was found several thousand kilometres north in staging areas on the coast of British Columbia and Alaska within 2–22 days of release (C. Iverson, unpubl. data).

Local movements

The average distance Western Sandpipers moved between feeding and roosting areas was 2.2 ± 0.1 km (Table 1). Most birds used roosting areas within a short distance of the site where they were captured. Home ranges were calculated for 21 Western Sandpipers during early winter, 20 during late winter and 18 in spring. Despite the conservative nature of the Cramer-von Mises test (Jaremovic & Croft 1987), radio locations for nearly all individuals fitted a bivariate normal distribution. The distribution adequately described the home

Table 1. *Mean distances moved between high and low tides, 95% weighted bivariate home ranges and core use areas for radio-marked Western Sandpipers in south San Francisco Bay*

	Movement (km)			Home range (km²)			Core area (km)		
Comparison	Mean	s.e.	*n*	Mean	s.e.	*n*	Mean	s.e.	*n*
Age									
Adult	2.4	0.1	257	17.2	2.5	20	11.8	1.5	20
First year	2.0	0.1	307	26.6	3.6	21	8.8	0.8	21
Sex									
Male	2.1	0.1	197	19.4	2.7	12	9.7	1.3	12
Female	2.2	0.7	475	23.1	3.1	29	10.7	1.1	29
Season									
Early winter	2.3	0.1	213	24.6	2.3	21	9.6	0.9	21
Late winter	2.1	0.8	351	19.3	4.1	20	11.6	1.6	20
Spring	2.3	0.2	108	23.4	1.2	18	6.3	1.2	18
Site									
Newark	2.5	0.1	363	30.0	3.3	26	12.2	1.1	26
Palo Alto	2.4	0.2	113	25.0	5.7	11	8.5	1.4	11
Coyote Hills	1.7	0.1	196	12.1	1.4	22	5.8	1.0	22
Time									
Day	2.2	0.1	406	13.6	2.3	12	6.5	1.4	12
Night	2.2	0.1	266	16.3	3.3	12	6.6	1.1	12
Tide									
Low	—	—	—	12.6	3.0	12	5.2	1.0	12
High	—	—	—	9.3	2.5	12	4.6	1.1	12
Overall	2.2	0.1	672	22.0	0.7	59	9.5	1.0	59

range of most radio-marked Western Sandpipers ($P > 0.05$) during early winter (83%), mid-winter (90%) and spring (89%). Mean home range size for all birds was 22.0 ± 0.7 km^2 or about 8% of the total study area (Table 1). Mean core areas (9.5 ± 1.0 km^2) accounted for 3% of the total study area. All birds had core use areas encompassing 50–72% of their radio locations.

Age and sex differences

There were no significant age and sex interactions for movements ($F_{1,44} = 1.91$, n.s.) or home range size ($F_{1,37} = 4.37$, n.s.). Adults did not move significantly farther than first-year birds between roosting and feeding areas ($F_{1,44} = 1.91$, n.s.; Fig. 1). First-year birds had larger home ranges than did adults during winter ($F_{1,44} = 4.37$, $P < 0.05$), but core areas were not significantly different in size ($F_{1,37} = 2.94$, n.s.). It was not possible to examine differences in home range size during the spring because first-year and adult birds could not be separated reliably. The distances moved by male and female Western Sandpipers were not significantly different in any season ($F_{1,44} = 0.20$, n.s.). Males and females also had similarly sized home ranges ($F_{1,37} = 0.91$, n.s.) and core areas ($F_{1,37} = 0.46$, n.s.).

Seasonal differences

Radio-marked birds moved similar distances ($F_{2,84} = 0.12$, n.s.) in early winter (2.3 ± 0.1 km), late winter (2.1 ± 0.1 km) and spring (2.3 ± 0.2 km). Additionally, mean home range sizes for birds in early winter (24.6 ± 2.3 km^2), mid-winter (19.3 ± 4.1 km^2) and spring (23.4 ± 1.2 km^2) did not differ significantly ($F_{2,56} = 0.69$, n.s.). Core area size, however, did differ between seasons ($F_{2,56} = 3.76$, $P < 0.03$). Core areas were smaller ($P < 0.05$) in spring (6.3 ± 1.2 km^2) than in early (9.6 ± 4.0 km^2) or late winter (11.6 ± 1.6 km^2) (Table 1).

Site differences

Birds from different sites moved similar distances between roosting and foraging areas ($F_{2,84} = 0.15$, n.s.). However, differences in home range size (Table 1) were detected ($F_{2,56} = 11.9$, $P < 0.001$) among birds from different capture sites. The LSD tests indicated that Western Sandpipers captured at Coyote Hills had smaller home ranges ($P < 0.05$) than did birds captured at either Newark or Palo Alto. Significant size differences ($F_{2,56} = 9.47$, $P < 0.001$) were found between core use areas, but only birds from Newark and Coyote Hills

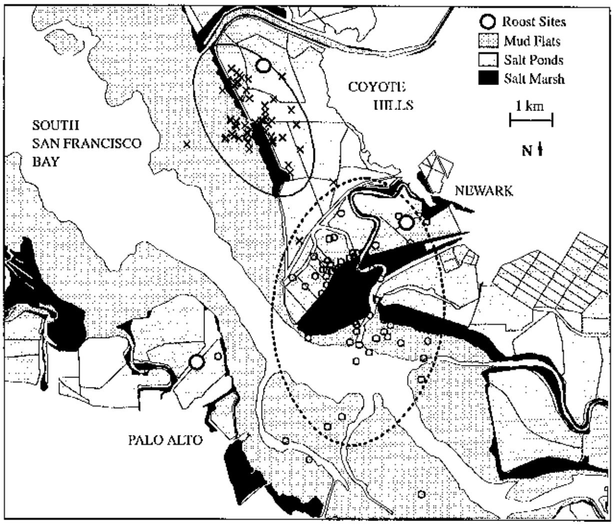

Figure 2. Differences in home range of two Western Sandpipers captured at different sites in south San Francisco Bay. Examples are provided for a sandpiper from Coyote Hills (#6035, ——) and Newark (#5217, - - -) areas. Radio locations are shown for the birds at Coyote Hills (×) and Newark (○).

(Fig. 2) had separable core areas ($P < 0.05$) in multiple comparison tests.

Time and tide differences

There was no difference ($t_{10} = 0.94$, n.s.) in distance moved between day (2.2 ± 0.08 km) and night (2.2 ± 0.09 km) locations (Fig. 3). Home range ($t_{10} = 0.36$, n.s.) and core use area ($t_{10} = 0.53$, n.s.) of Western Sandpipers were also not significantly different between day and night periods. Mean home range size for Western Sandpipers at low tide (12.6 ± 3.0 km^2) tended to be larger than home ranges at high tide (9.3 ± 2.5 km^2) (Fig. 4), although differences were not statistically significant. The sizes of the low (5.2 ± 1.0 km^2) and high (4.6 ± 1.1 km^2) tide core use areas were similar.

Movements and tidal amplitude

A linear regression analysis (Fig. 5) showed that variation in movements of Western Sandpipers was not related to the time period between low and high tides ($F_{1,669} = 0.05$, n.s.). Tidal amplitude was a significant factor ($F_{1,669} = 53.8$, $P < 0.001$) in determining movement distances, but as little of the variation in movements ($r^2 = 0.07$) was explained, this made only a small contribution to explaining movement distances.

DISCUSSION

Studies of shorebird movements have revealed varying degrees of site fidelity among species and individuals during

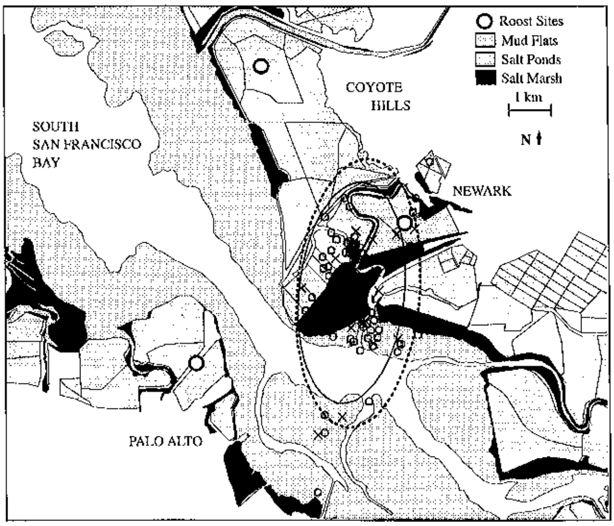

Figure 3. Day (- - -) and night (——) home ranges for Western Sandpiper #5447 in south San Francisco Bay. Radio locations for day (×) and night (○) are shown.

the nonbreeding period (Pienkowski & Evans 1984, Myers 1986). We found that radio-marked Western Sandpipers exhibited strong site fidelity in the south San Francisco Bay region during the course of our study and were consistently located at or short distances from established roost sites. There was little mixing of birds from different roost sites, even though the roosts were separated by as little as 5 km.

Other calidrid species wintering in coastal California estuaries make daily movements of up to 25 km to take advantage of newly exposed mud flats created by tidal lags among nearby estuaries (Myers 1986, Ruiz *et al.* 1987).

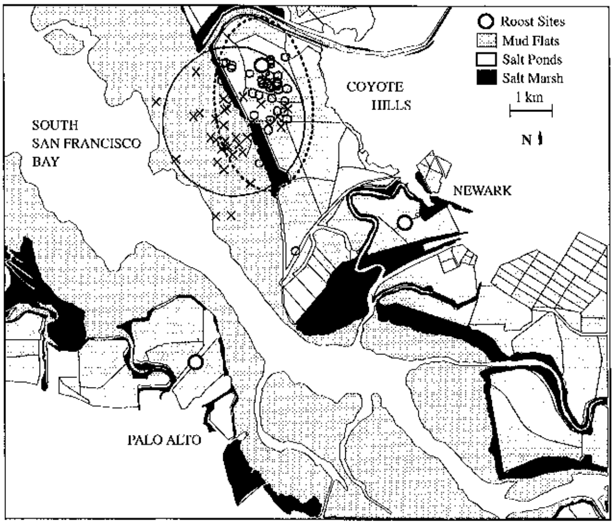

Figure 4. Low (——) and high (- - -) tide home ranges and radio locations (× = low tide, ○ = high tide) for Western Sandpiper #5515 in south San Francisco Bay.

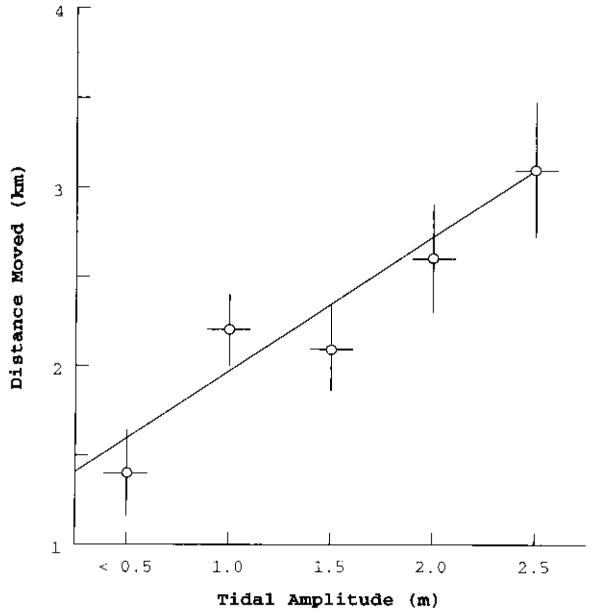

Figure 5. Relationship of tidal amplitude to movement distances of radiomarked Western Sandpipers. Means and 95% confidence intervals are shown for data grouped at 0.5-m intervals. A linear model ($r^2 = 0.07$) was estimated as: $Y = 0.66X + 1.48$, where Y is the distance moved (km) and X is the amplitude (m) between high and low tide.

Weather may also be a major factor influencing movements of shorebirds (Davidson 1981, Warnock *et al.* 1995), as strong winds and rainfall can result in decreased prey availability (Evans 1976, Pienkowski 1981). The radio-marked Western Sandpipers, however, showed no tendency to move between widely separated foraging areas. During the winter months, south San Francisco Bay has calm weather conditions on an average of 12 days per month, compared with 1.5 days per month in the North Bay region (Conomos 1979). The mild microclimate of the South Bay may explain both the strong site fidelity of Western Sandpipers and the large number of birds which use the region.

Moreover, the lack of long distance movements by the radio-marked Western Sandpipers indicates that the South Bay area apparently provides an adequate mixture of roosting and feeding sites. Because flight is energetically costly (Castro & Myers 1989), availability of feeding areas in close proximity to roosting sites reduces energy use by Western Sandpipers.

Although home ranges of the sandpipers were generally small, patterns of variation in home range size were detected. First-year birds had larger winter home ranges than did adults. Adult Western Sandpipers may have located profitable foraging areas and repeatedly returned to those sites, similar to foraging behaviour reported for Dunlin *Caladris alpina* (Warnock 1990). In several shorebird species, adults exclude first-year birds from dense foraging areas (Groves 1978, van der Have *et al.* 1984, Goss-Custard & leV. dit Durell 1987), forcing them to explore peripheral areas. Western Sandpipers are often territorial on their wintering grounds and aggressively defend mud flat foraging areas over several days (Recher & Recher 1969).

Home range sizes were similar in both winter and spring. There was no indication that birds were gradually expanding their home ranges prior to migration. Birds radio-marked during spring had smaller core use areas. Higher spring densities and decreased food availability (Goss-Custard 1984) may contribute to factors making it energetically efficient for individuals to defend a small foraging patch of mud flat (Recher & Recher 1969, Myers *et al.* 1979). Birds captured at the Coyote Hills site (Figs 1 and 2) had the smallest home ranges, probably because feeding and roost areas were in closest proximity at that site.

Nocturnal foraging by shorebirds varies among species and seasons (McNeil *et al.* 1992) but was common in Western Sandpipers in San Francisco Bay during winter. There were no differences in their nocturnal and diurnal movements or home ranges, and birds were located on mud flats on both moonlit and dark nights. Darkness apparently had little effect on flights of Western Sandpipers from roosting to feeding areas, although their ability to fly at night may have been aided by artificial light from the surrounding urban areas. Close proximity of the salt pond roosting areas to the mud flat foraging areas also may have facilitated feeding at night.

Distance travelled between high and low tide roosting and feeding areas was significantly related to tidal amplitude (Table 1). The larger the amplitude from high to low tide, the farther the birds flew to feed near the edge of the receding tide. Several studies have indicated that many *Calidris* species, including Western Sandpipers, forage mainly at the edge of the receding tideline where there is a high concentration of invertebrate activity (Recher 1966, Stenzel & Page 1988).

A consequence of the small home range areas used by Western Sandpipers in the South Bay is an increased potential for repeated contaminant exposure for birds feeding in polluted areas. San Francisco Bay is a highly urbanized estuary (Nichols *et al.* 1986) with several point sources of industrial and municipal discharge. Elevated concentrations of selenium, silver, copper, mercury and cadmium have been reported in waterfowl at certain sites in the South Bay (Ohlendorf *et al.* 1986), and it is likely that other species with strong wintering site fidelity like Western Sandpipers are also at risk.

The ability to exploit alternative wintering strategies gives shorebirds the flexibility necessary to maximize over-winter survivorship under changing habitat conditions. The high degree of site fidelity to south San Francisco Bay observed in Western Sandpipers indicates that the combination of tidal mud flats and commercial salt ponds which dominate the region currently provides adequate resources for the resident wintering sandpipers.

We thank D. Barnum, K.-M. Exo, D. Gilmer, C. Kitting, B. Kus, S. Opp, L. Stenzel and N. Warnock for providing helpful comments on the manuscript. We are grateful to technicians E. Burns and N. Bish and volunteers J. Albertson, J. Dinsdale, J. Griffin, P. Griffin, R. Griffin, S. Matsuoka, M. Parker, K. Reynolds, S. Spisak and M. Staughton for assistance in capturing and tracking birds. M. Casazza, J. Day and D. Orthmeyer conducted aerial telemetry surveys. K. Gonzalez, W. Newton, W. Perry and M. Samuel kindly assisted with analyses, while R. Coleman, D. Roster and J. E. Takekawa provided administrative support. This study was supported by the Northern Prairie and California Pacific Science Center.

REFERENCES

Ackerman, B.B., Leban, F.A., Samuel, M.D. & Garton, E.O. 1990. User's Manual for Program Home Range, 2nd ed. Technical Report No. 15. Moscow, Idaho: Forestry, Wildlife, and Range Experiment Station, University of Idaho.

Anderson, D.J. 1982. The home range: A new nonparametric estimation technique. Ecology 63: 103–112.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24: 346–352.

Butler, R.W., Kaiser, G.W. & Smith, G.E.J. 1987. Migration chronology, length of stay, sex ratio, and weight of Western Sandpipers (*Calidris mauri*) on the south coast of British Columbia. J. Field Ornithol. 58: 103–111.

Castro, G. & Myers, J.P. 1989. Flight range estimates for shorebirds. Auk 106: 474–476.

Conomos, T.J. (ed.). 1979. San Francisco Bay: The urbanized estuary. San Francisco, Calif.: Pacific Division, American Association for the Advancement of Science.

Davidson, N.C. 1981. Survival of shorebirds (Charadrii) during severe weather: The role of nutritional reserves. *In* Jones, N.V. & Wolff, W.J. (eds) Feeding and Survival Strategies of Estuarine Organisms: 231–249. New York: Plenum Press.

Dodge, W.E. & Steiner, A.J. 1986. XYLOG: A Computer Program for Field Processing Locations of Radio-tagged Wildlife. Technical Report No. 4. Washington, D.C.: U.S. Department of the Interior, Fish and Wildlife Service.

Dodge, W.E., Wilkie, D.S. & Steiner, A.J. 1986. UTMTEL: A laptop computer program for location of telemetry "finds" using Loran-C. Unpublished report. Amherst, Mass.: U.S. Fish and Wildlife Service, Massachusetts Cooperative Research Unit.

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: 112–139.

Gill, R.E. & Handel, C.M. 1990. The importance of subarctic intertidal habitats to shorebirds: A study of the central Yukon–Kuskokwim Delta, Alaska. Condor 92: 709–725.

Gilmer, D.S., Miller, M.R., Bauer, R.D. & LeDonne, J.R. 1982. California's Central Valley wintering waterfowl: Concerns and challenges. Trans. North Am. Wildl. Nat. Resour. Conf. 47: 441–452.

Goss-Custard, J.D. 1984. Intake rates and food supply in migrating and wintering shorebirds. *In* Burger, J & Olla, B.L. (eds) Behavior of Marine Animals, Vol. 6: 230–270. New York: Plenum Press.

Goss-Custard, J.D. & leV. dit Durell, S.E.A. 1987. Age related effects in Oystercatchers *Haematopus ostralegus* feeding on mussels *Mytilus edulis*. I. Foraging and interference. J. Anim. Ecol. 56: 521–536.

Groves, S. 1978. Age-related differences in Ruddy Turnstone foraging and aggressive behavior. Auk 95: 95–103.

Holmes, R.T. 1971. Density, habitat, and the mating system of the Western Sandpiper (*Calidris mauri*). Oecologia 7: 191–208.

Holmes, R.T. 1972. Ecological factors influencing the breeding season schedule of Western Sandpipers (*Calidris mauri*) in subarctic Alaska. Am. Midl. Nat. 87: 472–491.

Holmes, R.T. 1973. Social behavior of breeding Western Sandpiper (*Calidris mauri*). Ibis 115: 107–123.

Holway, D.A. 1990. Patterns of winter shorebird occurrence in a San Francisco Bay salt marsh. West. Birds 21: 51–64.

Jaremovic, R.V. & Croft, D.B. 1987. Comparison of techniques to determine Eastern Grey Kangaroo home range. J. Wildl. Mgmt 51: 921–930.

Josselyn, M. 1983. The Ecology of San Francisco Bay Tidal Marshes: A community profile. Technical Report No. FWS/OBS-83/23. Washington, D.C.: U.S. Fish and Wildlife Service.

Kelly, P.R. & Cogswell, H.L. 1979. Movements and habitat use by wintering populations of Willets and Marbled Godwits. *In* Pitelka, F.A. (ed.) Shorebirds in Marine Environments. Studies in Avian Biology 2: 69–82. Lawrence, Kans.: Allen Press, Inc.

Kjelmyr, J., Page, G.W., Shuford, W.D. & Stenzel, L.E. 1991. Shorebird Numbers in Wetlands of the Pacific Flyway: A summary of spring, fall, & winter counts in 1988, 1989, and 1990. Unpublished report. Bolinas, Calif.: Point Reyes Bird Observatory.

McNeil, R., Drapeau, P. & Goss-Custard, J.D. 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. Biol. Rev. 67: 381–419.

Milliken, G.A. & Johnson, D.E. 1984. Analysis of Messy Data, Vol. 1, Designed experiments. New York: Van Nostrand Reinhold Co.

Monroe, M.W. & Kelly, J. 1992. State of the Estuary. Report of the San Francisco Estuary Project. Oakland, Calif.: U.S. Environmental Protection Agency.

Myers, J.P. 1986. Structure in Sanderling (*Calidris alba*) populations: The magnitude of intra- and interyear dispersal during the nonbreeding season. Proc. Int. Orn. Congr. XIX: 604–615.

Myers, J.P., Connors, P.G. & Pitelka, F.A. 1979. Territoriality in non-breeding shorebirds. Studies in Avian Biol. 2: 231–246.

Nichols, F.H., Cloern, J.E., Luoma, S.N. & Peterson, D.H. 1986. The modification of an estuary. Science 231: 567–573.

Ohlendorf, H.M., Lowe, R.W., Kelly, P.R., Harvey, T.E. & Stafford, C.J. 1986. Selenium and heavy metals in San Francisco Bay diving ducks. J. Wildl. Mgmt 50: 64–70.

Page, G.W. & Fearis, B. 1971. Sexing Western Sandpipers by bill length. Bird-Banding 4: 82–88.

Page, G.W., Shuford, W.D., Kjelmyr, J.E. & Stenzel, L.E. 1992. Shorebird Numbers in Wetlands of the Pacific Flyway: A summary of counts from April 1988 to January 1992. Unpublished report. Bolinas, Calif.: Point Reyes Bird Observatory.

Pienkowski, M.W. 1981. How foraging plovers cope with environmental effects on invertebrate behaviour and availability. *In* Jones, N.V. & Wolff, W.J. (eds) Feeding and Survival Strategies of Estuarine Organisms: 179–182. New York: Plenum Press.

Pienkowski, M.W. & Evans, P.R. 1984. Migratory behavior of shorebirds in the Western Palearctic. *In* Burger, J. & Olla, B.L. (eds) Behavior of Marine Animals, Vol. 6: 73–123. New York: Plenum Press.

Prater, A.J., Marchant, J.H. & Vourinen, J. 1977. Guide to the Identification and Ageing of Holarctic Waders. Tring: British Trust for Ornithology.

Recher, H.F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47: 393–407.

Recher, H.F. & Recher, J.A. 1969. Some aspects of the ecology of migrant shorebirds. II. Aggression. Wilson Bull. 81: 140–154.

Ruiz, G.M., Connors, P.G., Griffin, S.E. & Pitelka, F.A. 1987. Structure of a wintering Dunlin population. Condor 91: 562–570.

Samuel, M.D. & Garton, E.O. 1985. Home range: A weighted normal estimate and tests of underlying assumptions. J. Wildl. Mgmt 49: 513–519.

Samuel, M.D. & Green, R.E. 1988. The revised test procedure for identifying core areas within the home range. J. Anim. Ecol. 57: 1067–1068.

SAS Institute, Inc. 1989. SAS/STAT User's Guide, Version 6. Cary, N.C.: SAS Institute, Inc.

Sidak, Z. 1967. Rectangular confidence regions for the means of multivariate normal distributions. J. Am. Stat. Assoc. 62: 626–633.

Stenzel, L.E. & Page, G.W. 1988. Results of the 16–18 April 1988 Shorebird Census of San Francisco and San Pablo Bays. Unpublished report. Stinson Beach, Calif.: Point Reyes Bird Observatory.

van der Have, T.M., Nieboer, E. & Boere, B.C. 1984. Age-related distribution of Dunlin in the Dutch Wadden Sea. *In* Evans, P.R., Goss-Custard, J.D. & Hale, W.G. (eds) Coastal Waders and Wildfowl in Winter: 160–176. Cambridge: Cambridge University Press.

Ver Planck, W.E. 1958. Salt in California. Bulletin No. 175. Sacramento, Calif.: California Division of Mines.

Warnock, N. 1990. Apparent age-segregation of Dunlin within Bolinas Lagoon—A preliminary study. Wader Study Group Bull. 60: 27–30.

Warnock, N. & Warnock, S. 1993. Attachment of radio-transmitters to sandpipers: Review and methods. Wader Study Group Bull. 70: 28–30.

Warnock, N., Page, G.W. & Stenzel, L.E. 1995. Non-migratory movements of Dunlin on their California wintering grounds. Wilson Bull. 107: 131–139.

Yalden, D.W. 1991. Radio-tracking of Golden Plover *Pluvialis apricaria* chicks. Wader Study Group Bull. 63: 41–44.

Zar, J.H. 1984. Biostatistical Analysis, 3rd ed. Englewood Cliffs, N.J.: Prentice-Hall, Inc.

Submitted 18 October 1994; revision accepted 6 March 1995