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SPACE USE AND HABITAT SELECTION OF MIGRANT AND RESIDENT AMERICAN AVOCETS IN SAN FRANCISCO BAY

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Abstract. San Francisco Bay is a wintering area for shorebirds, including American Avocets (*Recurvirostra americana*). Recently, a new resident population of avocets has emerged, presumably because of the development of tidal marshes into salt-evaporation ponds. In habitat restoration now underway, as many as 90% of salt ponds will be restored to tidal marsh. However, it is unknown if wintering and resident avocets coexist and if their requirements for space and habitat differ, necessitating different management for their populations to be maintained during restoration. We captured and radio-marked wintering avocets at a salt pond and a tidal flat to determine their population status (migrant or resident) and examine their space use and habitat selection. Of the radio-marked avocets, 79% were migrants and 21% were residents. At the salt pond, residents' fidelity to their location of capture was higher, and residents moved less than did migrants from the same site. Conversely, on the tidal flat, fidelity of residents to their site of capture was lower, and residents' home ranges were larger than those of migrants from the same site. Habitat selection of migrants and residents differed little; however, capture site influenced habitat selection far more than the birds' status as migrants or residents. Our study suggests that individual avocets have high site fidelity while wintering in San Francisco Bay, although the avocet as a species is plastic in its space use and habitat selection. This plasticity may allow wintering migrant and resident avocets to adapt to habitat change in San Francisco Bay.

Key words: American Avocet, habitat selection, home range, Recurvirostra americana, *San Francisco Bay, site fidelity, space use.*

Uso del Espacio y Selección de Hábitat de Individuos Migrantes y Residentes de *Recurvirostra americana* en la Bahía de San Francisco

Resumen. La Bahía de San Francisco es un área de invernada para aves playeras, incluyendo a *Recurvirostra americana*. Recientemente, una nueva población residente de *R. americana* emergió, posiblemente como resultado de la conversión de pantanos mareales a estanques de evaporación salina. Mediante proyectos de restauración de hábitat que se encuentran en curso, se espera que hasta el 90% por ciento de los estanques salinos sean restaurados a pantanos mareales. Sin embargo, se desconoce si los individuos invernantes y residentes de *R. americana* coexisten y si sus requerimientos de espacio y hábitat difieren de manera que necesiten un manejo distinto para que sus poblaciones se mantengan durante la restauración. Capturamos y marcamos con transmisores de radio individuos encontrados en un estanque salino y en una planicie mareal para determinar sus estatus poblacionales (migrante o residente) y para estimar sus usos del espacio y selección del hábitat. De los individuos marcados con radios, el 79% eran migrantes y el 21% residentes. En el estanque salino, la fidelidad de los individuos residentes a su sitio de captura fue mayor y los residentes se movieron menos que los migrantes del mismo sitio. Por el contrario, en la planicie mareal, la fidelidad de los residentes a su sitio de captura fue menor y los ámbitos hogareños de los residentes fueron mayores que los de los migrantes del mismo sitio. Sin embargo, la selección de hábitat por parte de individuos migrantes y residentes difirió poco, pues el sitio de captura influenció la selección de hábitat mucho más que lo que lo hizo el estatus de las aves como migrantes o residentes. Nuestros datos sugieren que los individuos de esta especie presentan una alta fidelidad al sitio mientras pasan el invierno en la Bahía de San Francisco, aunque la especie es plástica en su uso del espacio y selección del hábitat. Esta plasticidad podría permitir que las aves migrantes y residentes se adapten a los cambios en el hábitat en la Bahía de San Francisco.

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INTRODUCTION

Establishment of a new breeding population in a range in which a species formerly only wintered is rare and has been associated with anthropogenic habitat alterations (Leck 1980, Ingold and Galati 1997). During the past century, a resident population of the American Avocet (*Recurvirostra americana*), previously a common winter visitor only, has become established in San Francisco Bay. The first breeding of the avocet in San Francisco Bay was recorded in 1926 (Gill 1977), but by 1952 the species was a common resident (Sibley 1952). The establishment of this new population has been attributed to the development of tidal marshes into commercial salt ponds (Gill 1977). Stenzel et al. (2002) estimated avocet numbers in the estuary at 23 200 in the winter and 4300 in the spring, suggesting that approximately 20% of the total number of avocets that use San Francisco Bay are residents. However, because wintering avocets have not been individually marked, there has been no confirmation that breeding avocets are year-round residents.

In the South San Francisco Bay (South Bay), salt ponds are used by over a million waterbirds each year and are important to both migrant and resident shorebirds (Takekawa et al. 2001, Warnock et al. 2002). These ponds are nontidal, often provide abundant food (Takekawa et al. 2006a), and include topographic features such as levees and islands that waterbirds use for roosting and nesting (Warnock et al. 2002). Approximately 75% of avocets that breed in the South Bay nest in salt ponds (Rintoul et al. 2003, Demers et al. 2008). However, as part of the South Bay Salt Pond Restoration Project, federal and state agencies are planning to convert as many as 90% of decommissioned salt ponds into tidal marsh while maintaining a few highly managed ponds for foraging and nesting waterbirds (USFWS and CDFG 2007). The restoration of tidal marsh is expected to benefit endemic marsh obligates, but the effects of habitat change on other species, including the avocet, are more difficult to determine. Subsequently, as the availability of pond habitat is reduced and the amount of tidal habitat increases, avocets will need to be managed to maintain current population levels, as required by the goals of the restoration project (USFWS and CDFG 2007).

However, it is unknown to what extent wintering migrant and resident populations coexist and, if they do coexist, if they have differential spatial and habitat requirements during the period of overlap. Space and habitat use may be attributed to the distribution of resources on the landscape (Brown and Orians 1970, Brown 1975, Schoener 1983), site fidelity (Smith 1976, White and Garrott 1990), and interactions with conspecifics (With 1994, Leonard et al. 2008). If the spatial and habitat needs of migrants and residents do differ, then understanding these differences is necessary if an adequate refuge system is to be provided (Madsen 1998a, b), as migrant and resident avocets may require different management strategies for their populations to be maintained during the restoration project.

Therefore, to determine the population status of wintering avocets (i.e., migrant or resident), examine differences between the populations in space use and habitat selection, and apply these results in the context of the South Bay Salt Pond Restoration Project, we captured and radio-marked wintering avocets at a salt pond in which they breed and on a tidal flat in the South Bay. Salt ponds provide foraging, roosting, and breeding sites for avocets, so we predicted that resident avocets captured at the salt pond would restrict their movements around salt ponds and have strong site fidelity. This prediction arises because most resident avocets nest in salt ponds and there are energetic costs associated with locating other suitable habitats (Morris 1987). Winter visitors may also use salt ponds for foraging or roosting, but they may experience aggression from residents that defend territories in which they feed (Gibson 1971). Thus, migrants from the salt pond may explore alternative habitats with less competition from residents, such as tidal flats at low tide, to satisfy their requirements for foraging. These explorations may result in larger movements within a home range, especially if migrants exploit tidal flats that are available only part of the day and have more plasticity in their habitat selection than do resident avocets. We predicted that migrants captured at the tidal flat, with presumably less competition from territorial residents, would have strong site fidelity to that site. Conversely, if resident birds were captured on the tidal flat, they should have less site fidelity and use more space as they explore other habitats for potential breeding sites. To examine space use, we estimated the home-range size and linear movements of individual avocets, and we used their distance from the capture site as a proxy of site fidelity. Additionally, we examined habitat selection of individual avocets at two spatial scales (Manly et al. 2002).

METHODS

STUDY AREA

We captured and radio-tracked avocets in South San Francisco Bay, California, an area we defined as south of the San Mateo Bridge (Fig. 1). Major wetland habitats in this region include salt ponds, tidal flats, managed marshes (nontidal, with controlled water levels), diked marshes (nontidal, behind levees), and tidal marshes. We captured roosting avocets at a salt pond (pond A8) and a tidal flat (Coyote Creek Lagoon). Pond A8 is a former salt-evaporation pond and is adjacent to other salt ponds, tidal marsh, and upland habitats (Fig. 1). During this study, pond A8 was the largest avocet breeding colony in the South Bay (Ackerman et al. 2007). Coyote Creek Lagoon is a tidal flat adjacent to diked marsh and tidal marsh habitats (Fig. 1).

CAPTURE AND MARKING

We captured avocets with rocket nets (Dill and Thornsberry 1950, Hill and Frederick 1997) between 15 and 30 March 2005 and between 16 February and 16 March 2006. As part of a larger study examining contaminant levels of San Francisco

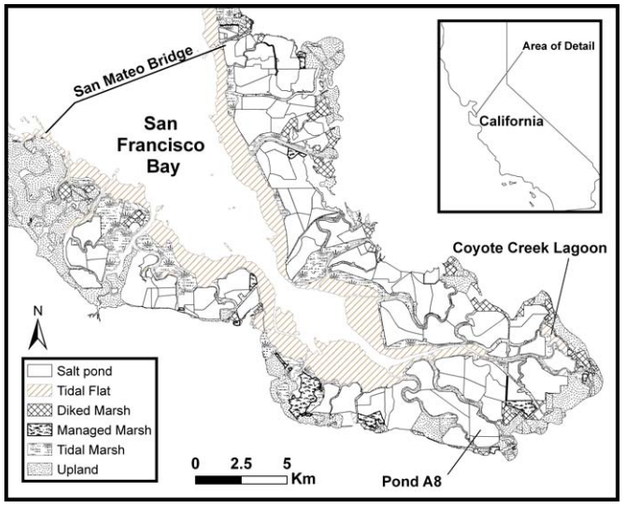

FIGURE 1. Locations of captured American Avocets and habitat types in South San Francisco Bay, California. Avocets were captured in a former salt pond (pond A8) and a tidal flat (Coyote Creek Lagoon).

Bay avifauna (Ackerman et al. 2007), we chose only female avocets for radio-marking, sexing them by bill dimorphism as described by Hamilton (1975). We attached radio transmitters (Advanced Telemetry Systems, model A2470, Isanti, MN) with epoxy to U.S. Geological Survey leg bands placed on the tibia (e.g., Plissner et al. 2000). We also marked avocets with UV-resistant Darvic color bands (A. C. Hughes, Ltd., Hampton Hill, UK) for individual identification. Total mass of the transmitter and bands was <4 g, or approximately 2% of the bird's mass (mean = 340 ± 2.2 g).

RADIO TELEMETRY

We tracked avocets with truck-mounted null-peak telemetry systems (AVM Instrument Company, Livermore, CA). Because avocets are active both day and night (Dodd and Colwell 1998, Johnson et al. 2003, Kostecke and Smith 2003), we tracked them during the morning (sunrise to 3 hr after sunrise), midday (3 hr after sunrise to 3 hr before sunset), evening (sunset to 3 hr before sunset), and night (all hours after sunset and before sunrise). Of the 2047 observations, 40% were during midday, 22% in the morning, 16% in the evening, and 22% at night. We also surveyed biweekly from an airplane to confirm the absence of avocets in the estuary.

We recorded the avocets' locations with at least two azimuths from telemetry-mounted trucks at known Universal Transverse Mercator (UTM) coordinates. We used LOAS 3.0.1 (Ecological Software Solutions, Urnash, Switzerland) to estimate the locations or recorded the locations directly on maps from visual resightings (4% of locations). Observers recorded azimuths within 15 min of each other to minimize error caused by birds moving. To minimize autocorrelation of spatial data, we recorded consecutive locations at least 1 hr apart, and 98% of observations were separated by >3 hr (e.g., Haig et al. 2002). In another shorebird study in San Francisco Bay with a similar system of transmitters and trucks, Warnock and Takekawa (1995) reported the average error of a telemetry location as 58 m, with error polygons of 1.1 ha (or <1% of the average habitat polygon in the South Bay). To reduce error in space-use estimation and habitat use, we excluded locations with large error polygons (>3 ha) from analyses.

MIGRANTS, RESIDENTS, AND CAPTURE LOCATION

We classified avocets as either resident or migrant on the basis of telemetry data and waterbird surveys. We considered avocets to be residents if they stayed in South San Francisco Bay throughout the breeding season (March–July), and we defined them as migrants if their last known telemetry location coincided with the departure of the majority of avocets from the bay, as determined by salt-pond surveys (Miles et al. 2004, Takekawa et al. 2006b) and baywide shorebird surveys (Stenzel et al. 2002). We confirmed the absence of avocets in the estuary on the basis of surveys from both the ground and the air, and we located migrants at inland breeding sites opportunistically on the basis of aerial telemetry conducted by others. We used migrants' median departure date as the ending date for analyses of space use and habitat selection by both winter visitors and residents. We also categorized wintering avocets as captured on a salt pond or tidal flat.

SPACE-USE ANALYSES

We used Home Range Tools for ArcGIS (Rodgers et al. 2005) in ArcGIS 9.1 (ESRI 2005) to calculate 95% fixed-kernel home ranges (Worton 1995). We define a fixed-kernel home range as the area, or group of areas, encompassing 95% of the probability distribution for each individual bird. We chose a kernel method because it consistently produces reliable results with low bias (Seamann and Powell 1996, Swihart and Slade 1997), measures the intensity of use within a range (Kernohan et al. 2001), and excludes large areas that are not used by the animal (White and Garrott 1990). We used Animal Space Use 1.1 (Horne and Garton 2007) to calculate a smoothing parameter for each home range. We used likelihood cross-validation for smoothing parameter because likelihood cross-validation tends to outperform least-squares cross-validation, producing a better fit with less variability, especially with sample sizes <50 (Horne and Garton 2006).

Because variation in numbers of observed locations may affect home-range estimates (Seaman et al. 1999), we determined the minimum number of locations required to create a fixed-kernel home range by consecutively removing random locations and recalculating home ranges for each avocet to create a plot of area vs. sample size (i.e., area-observation curve; Millspaugh and Marzluff 2001). We determined the minimum number of locations ($n = 10$) required for estimation of a home

range on the basis of the number of locations at which the area-observation curve reached an asymptote.

We used Hawth's Tools for ArcGIS (Beyer 2004) in ArcGIS 9.1 to calculate the linear distance between consecutive locations (i.e., linear movements) and the distance from the capture site. Because we recorded observations more than once a day, we evaluated the potential bias arising from multiple daily observations of movements by consecutively removing from analyses locations less than 1, 2, 4, 8, and 16 hr apart (Demers 2007). These removals did not significantly alter calculations of average distance, so in the analyses we used all locations >1 hr apart.

HABITAT CLASSIFICATION

We analyzed habitat selection of avocets by overlaying telemetry data with the EcoAtlas 1.50b (San Francisco Estuary Institute 1998) habitat layer in ArcGIS 9.1. The EcoAtlas delineates habitat types in San Francisco Bay with individual vector polygons. We classified habitat polygons within the study area into the following nine wetland categories; percentage of each habitat type is in parentheses: (1) salt ponds (37%): shallow, unvegetated ponds currently or formerly used for salt production; (2) managed marshes (2%): nontidal marshes actively managed for wildlife; (3) diked marshes (3%): nontidal marshes surrounded by levees but without active water management; (4) seasonal wetlands (1%): areas retaining water in the winter and spring but dry by summer (e.g., depressions and ditches); (5) treatment basins (2%): wastewater- or stormwater-storage basins; (6) tidal flats (16%): unvegetated mudflats exposed during low tides; (7) tidal channels (1%): tidally influenced sloughs and rivers; (8) tidal marshes (11%): areas dominated by wetland vegetation and subject to daily tidal flooding; and (9) bay (27%): tidally influenced open waters.

HABITAT-SELECTION ANALYSES

We calculated habitat-selection ratios (S) for each avocet by dividing the observed use of a habitat by the expected use of that habitat (Manly et al. 2002, Ackerman et al. 2009). We conducted this analysis on two orders of selection, adapted from Johnson (1980) to reduce biases introduced by defining habitats available to animals (Lopez et al. 2004, McCleery et al. 2006, Ackerman et al. 2009) and to provide insights into animal–habitat relationships that may not be detectable at one level of selection (McDonald et al. 2005). Johnson (1980) proposed selection orders, recognizing that habitat is selected hierarchally. For instance, selection of habitats within a home range is of a higher order than the selection of habitats on a regional scale because it is conditional on the latter (Johnson 1980). Therefore, we examined habitat selection at the regional scale (location to study area) and within each avocet's home range (location to range).

Location-to-study area scale. For each avocet, we determined habitat-selection ratios at the location-to-study area scale by dividing the observed use by the expected use for each habitat type. We calculated the ratios as $S = u_h/(n_x \times p_h)$, where u_h = the number of locations in a habitat type for an individual avocet, n_x = total number of radio locations for the individual, and p_h = proportion of habitat for the entire study area.

Location-to-range scale. We examined habitat selection within each avocet's home range by comparing the number of locations in each habitat to the proportion of that habitat within each avocet's home range. We calculated the selection ratios as $S = u_r/(n_t \times p_r)$ where u_r = the number of locations in a habitat within an individual avocet's home range, n_t = the total number of radio locations within that avocet's home range, and p_r = proportion of habitat inside the avocet's home range.

To calculate selection ratios, we used 95% fixed-kernel home ranges. We avoided zeros in the numerator and denominator of the formulae by adding 0.001 to habitat use and availability (Lopez et al. 2004, McCleery et al. 2006, Ackerman et al. 2009). Selection ratios >1 indicated selection of a given habitat, ratios <1 indicated avoidance, and ratios equal to 1 indicated use in proportion to availability (Manly et al. 2002).

STATISTICAL ANALYSES

In SAS 9.1.2 (SAS Institute 2004), we used three-factor analysis of variance (ANOVA) to test for differences in home-range size and three-factor repeated-measures ANOVA to compare differences in linear movements and distance from capture site. The mixed models included year (2005, 2006), capture site (salt pond, tidal flat), population (migrant, resident), and population-by-site interactions. We controlled for year effects and tested for differences between capture sites and populations with least-squares means-comparison tests. To meet the assumptions of normality, we $\log_{10}$-transformed telemetry data prior to analysis. To test if habitat-selection ratios were significantly different from 1, we calculated lower and upper simultaneous 95% confidence limits, using the Bonferroni inequality to control for type I error (Manly et al. 2002). We present all data, including space-use data transformed to yield a normal distribution, as means ± 1 SE in order to facilitate interpretation of results.

RESULTS

POPULATION STATUS

In 2005 and 2006, we radio-marked 87 female avocets, 39 at the salt pond (SP) and 48 at the tidal flat (TF). Of the SP avocets, 27 were migrants and 12 were residents; of TF avocets, 42 were migrants and 6 were residents. Of the overall sample, 69 avocets (79%) were migrants and 18 (21%) were residents. Among migrants, prior to their departure, we obtained sufficient locations for space-use analyses from 48 individuals (19 SP, 29 TF), and we obtained a sufficient number of locations for all 18 residents (12 SP, 6 TF). We obtained a total of 2047 locations with a mean number of 28.9 ± 1.6 locations per individual (range 15–55) and tracked each avocet for a mean

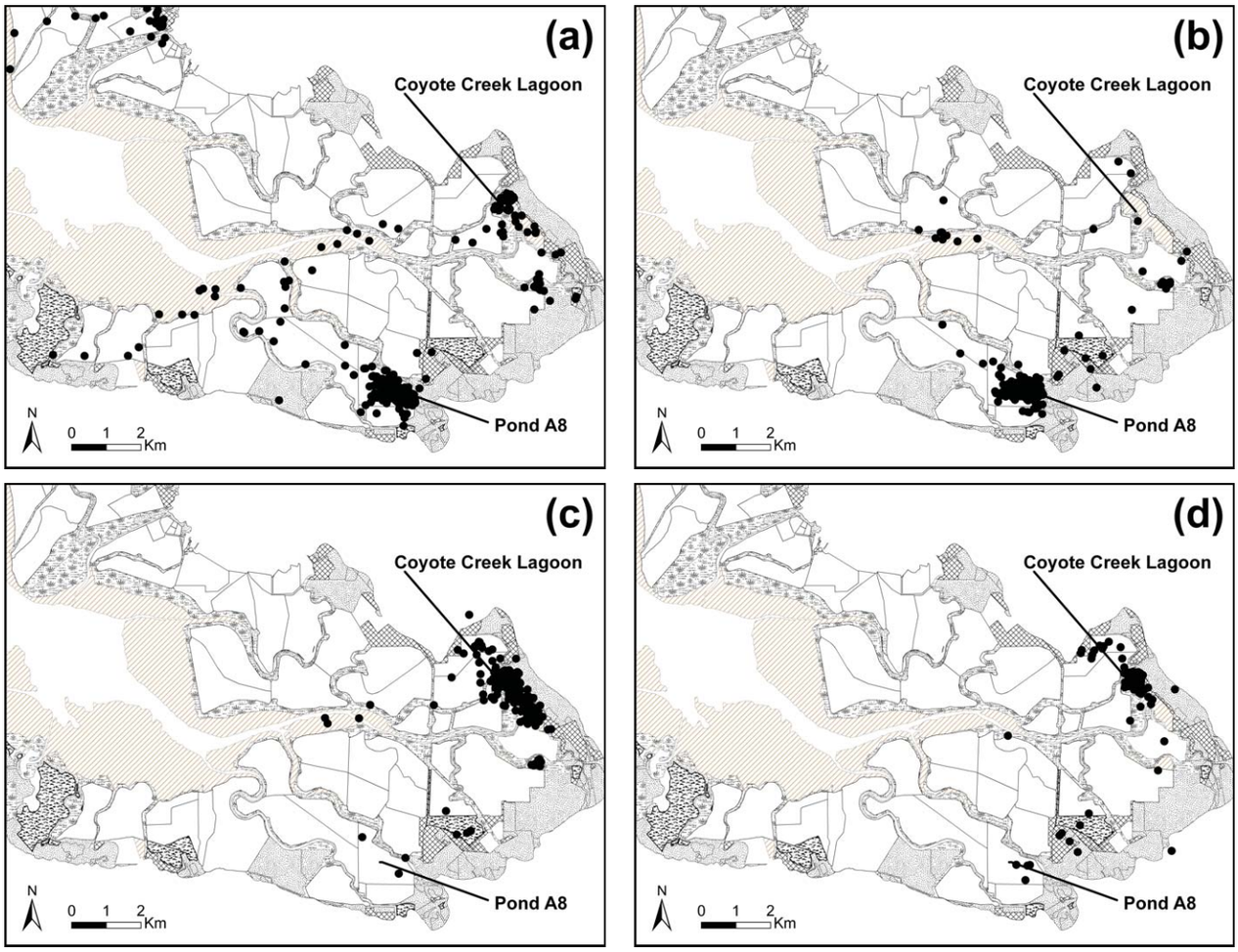

FIGURE 2. Telemetry locations of salt-pond migrant (2a), salt-pond resident (2b), tidal-flat migrant (2c), and tidal-flat resident (2d) American Avocets captured in South San Francisco Bay, California.

29.9 ± 1.6 days (Fig. 2). The median departure dates for migratory avocets were 15 April 2005 (± 2.3 days) and 6 April 2006 (± 3.2 days; Fig. 3), and these departure dates coincided with the reduction in avocet numbers counted in salt ponds (Fig. 3).

SPACE USE

We found significant interactions between capture site and population for home ranges ($F_{1, 60}$ = 5.4, P = 0.02), linear movements ($F_{1, 966}$ = 11.8, P = 0.001), and distance from capture site ($F_{1, 966}$ = 24.3, P < 0.001). Therefore, to isolate the effects of capture site on space-use variables, we compared capture sites independently.

Home ranges. The mean home range of SP migrants (1271 ± 290 ha) did not differ from that of SP residents (879 ± 220 ha; t_{60} = 0.2, P = 0.85; Fig. 4). However, the mean home range of TF migrants (472 ± 132 ha) was significantly smaller than that of TF residents (1482 ± 358 ha; t_{60} = 2.8, P = 0.006).

Linear movements. Linear movements of SP migrants (2689 ± 478 m) were greater than those of SP residents (991 ± 172 m; t_{966} = 3.8, P < 0.001; Fig. 4). However, linear movements of TF migrants (942 ± 287 m) did not differ from those of TF residents (1260 ± 262 m; t_{966} = 1.2, P = 0.25).

Distance from capture site. Distances for SP migrants (3413 ± 712 m) were greater than for SP residents (1295 ± 395 m; t_{966} = 5.1, P < 0.001; Fig. 4). Conversely, distances for TF migrants (849 ± 170 m) were smaller than for TF residents (1539 ± 479 m; t_{966} = 2.0, P = 0.045).

HABITAT SELECTION

Migrant and resident avocets primarily used the same habitat they were captured in, although migrants from both capture sites used tidal flats more than did residents and residents used more salt ponds than did migrants (Table 1). Habitat selection varied by selection order and capture location (Table 2).

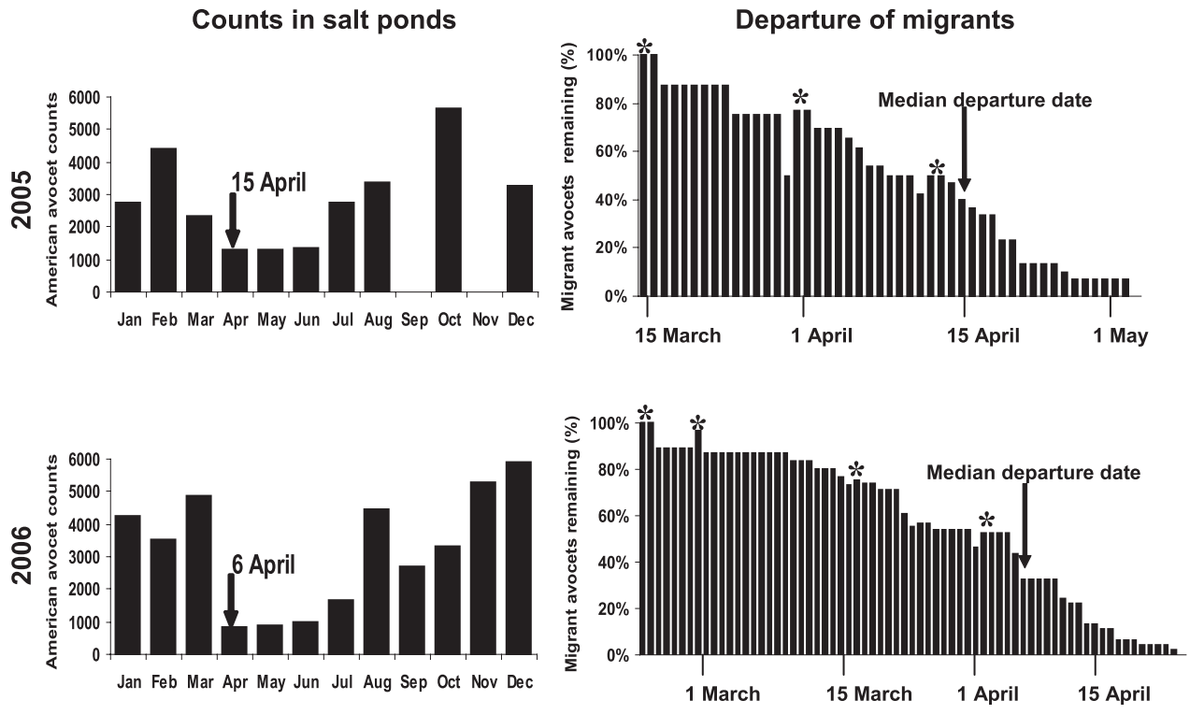

FIGURE 3. Counts of American Avocets during monthly surveys of the Alviso salt-pond complex of South San Francisco Bay and dates of departure of migrants in 2005 and 2006. Migrants' departure dates were determined by last known telemetry locations. The median departure dates for 2005 and 2006 are indicated above the histogram. Asterisks indicate captures of avocets, where radio-marked birds were added to the sample.

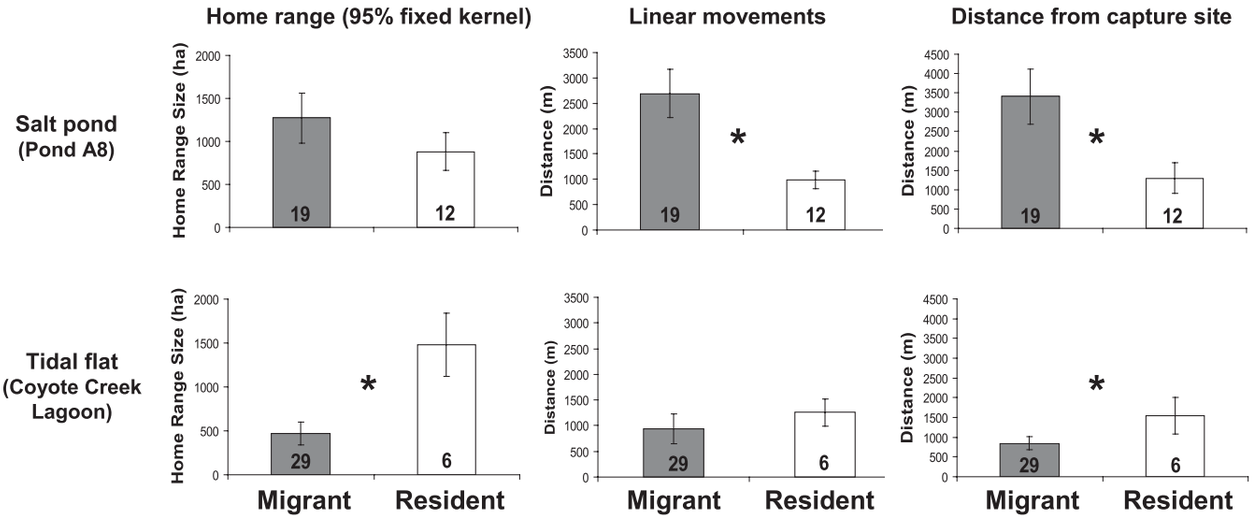

FIGURE 4. Home ranges, linear movements, and distance from capture site of migrant and resident American Avocets captured at two locations in South San Francisco Bay. Sample sizes (number of birds) are shown in each histogram. All data were log-transformed prior to analyses but are shown here as untransformed means ± SE. Asterisks indicate significant differences.

TABLE 1. Proportions of telemetry locations by habitat type of migrant and resident American Avocets captured at a salt pond (migrants: $n = 19$; residents: $n = 12$) and a tidal flat (migrants: $n = 29$; residents: $n = 6$) in South San Francisco Bay, California. Proportion of habitat availability in South San Francisco Bay is given in parentheses under each habitat type.

		Habitat								
Capture site	Population	Salt pond (0.37)	Managed marsh (0.02)	Diked marsh (0.03)	Seasonal wetland (0.01)	Treatment basin (0.02)	Tidal flat (0.16)	Tidal channel (0.01)	Tidal marsh (0.11)	Bay (0.27)
Salt pond	Migrant	0.67	0.01	0.08	0.00	0.01	0.14	0.01	0.08	0.00
	Resident	0.78	0.01	0.07	0.00	0.00	0.08	0.01	0.05	0.00
Tidal flat	Migrant	0.09	0.01	0.17	0.00	0.00	0.67	0.01	0.05	0.00
	Resident	0.18	0.01	0.19	0.00	0.01	0.59	0.00	0.02	0.00

Location-to-study area scale. At the study-area spatial scale, SP migrants and residents selected only salt ponds (migrants: $S = 2.14$; residents: $S = 2.46$), whereas TF migrants and residents selected diked marsh (migrants: $S = 5.37$; residents: $S = 4.58$) and tidal flats (migrants: $S = 4.57$; residents: $S = 4.08$). SP migrants avoided seasonal wetlands ($S = 0.02$) and bay ($S < 0.01$), and SP residents avoided treatment basins ($S = 0.20$) and bay ($S < 0.01$). TF migrants avoided salt ponds ($S = 0.28$), seasonal wetlands ($S = 0.01$), treatment basins ($S = 0.12$), and bay ($S < 0.01$), whereas TF residents avoided seasonal wetlands ($S = 0.02$), tidal channel ($S < 0.01$), and bay ($S < 0.01$).

Location-to-range scale. Within home ranges, there was no selection of habitats by SP migrants or residents, whereas TF migrants and residents selected tidal flats (migrants: $S = 2.83$; residents: $S = 7.10$). SP migrants avoided seasonal wetlands ($S = 0.58$) and treatment basins ($S = 0.56$), and SP residents avoided treatment basins ($S = 0.45$) and tidal marsh ($S = 0.50$). TF migrants avoided salt ponds ($S = 0.50$) and seasonal wetlands ($S = 0.69$). TF residents avoided salt ponds ($S = 0.46$), seasonal wetlands ($S = 0.02$), tidal channels ($S = 0.01$), and tidal marsh ($S = 0.09$).

DISCUSSION

POPULATION STATUS

From our radio-marked sample of avocets captured in South Francisco Bay, we determined that 79% were migrants and 21% were residents, similar to the proportion of migrants and residents inferred from previous estuary-wide surveys (Stenzel et al. 2002), the first confirmation that avocets wintering in the South Bay are a mix of migrants and residents. Also, the residents in our study appear to be year-round residents, rather than migrants from other wintering populations, although it is possible that some local breeders winter elsewhere. It is still unknown to what extent wintering migrants represent reproductively isolated populations from multiple other breeding sites. However, we did opportunistically locate two SP migrants near Los Banos, California (120 km southeast), and another near Fallon National Wildlife Refuge, Nevada (225 km northeast), suggesting that migrants that winter in the South Bay breed at multiple inland sites. Nonetheless, since migrant and resident avocets coexist at least part of the year in the South Bay, managers should consider that habitat change resulting

TABLE 2. Habitat selection (S) and avoidance (A) of migrant and resident American Avocets captured at a salt pond (migrants: $n = 19$; residents: $n = 12$) and a tidal flat (migrants: $n = 29$; residents: $n = 6$) in South San Francisco Bay, California. Dashes represent use of the habitats in proportion to its availability.

			Habitat								
Spatial order	Capture site	Population	Salt pond	Managed marsh	Diked marsh	Seasonal wetland	Treatment basin	Tidal flat	Tidal channel	Tidal marsh	Bay
Location-to-study area	Salt pond	Migrant	S	—	—	A	—	—	—	—	A
		Resident	S	—	—	—	A	—	—	—	A
	Tidal flat	Migrant	A	—	S	A	A	S	—	—	A
		Resident	—	—	S	A	—	S	A	—	A
Location-to-range	Salt pond	Migrant	—	—	—	A	A	—	—	—	—
		Resident	—	—	—	—	A	—	—	A	—
	Tidal flat	Migrant	A	—	—	A	—	S	—	—	—
		Resident	A	—	—	A	—	S	A	A	—

from restoration activities may affect more than one population of this species.

SPACE USE AND HABITAT SELECTION

We detected differences between migrants' and residents' use of space at the two capture sites. Although home ranges of SP residents and migrants did not differ, SP residents demonstrated higher site fidelity and made smaller linear movements than did migrants. TF migrants, conversely, had stronger fidelity to their capture site and maintained much smaller home ranges than did their resident counterparts. Migrants and residents differed somewhat in their habitat use, as migrants from both capture sites used tidal flats more than did residents, and residents used more salt ponds than did migrants. However, and somewhat surprisingly, capture site influenced habitat selection far more than did population status. The most appreciable difference was between TF migrants and residents at the study-area spatial scale, as TF migrants avoided salt ponds and TF residents selected them in proportion to their availability.

The avocets' observed patterns of space and habitat use may be attributed to resource distribution among habitats in the South Bay, the benefits of site fidelity, and, to some extent, conspecific interactions. For instance, because the breeding colony at the former salt-evaporation pond (pond A8) provides habitat for foraging, roosting, and breeding, it may be energetically profitable for SP residents to restrict their movements to that area, since they should have an increased knowledge of important resources within their home range (Powell 2000). The benefits of site fidelity were expressed in their subsequent choice of nesting locations, which were located within their winter home ranges (Demers et al. 2008). Of the 10 SP residents that nested, seven nested within pond A8, the others in a nearby managed marsh (1.5 km to the east) and a tidal basin (4 km to the east). Although SP migrants had similar home range sizes, they demonstrated less site fidelity and moved farther as a result of their more frequent use of tidal flats in San Francisco Bay and other salt ponds to the north and west. These longer movements may be associated with pre-breeding aggressive behaviors (Gibson 1971, Hamilton 1975, Robinson et al. 1997) of more territorial resident birds. Our own observations confirmed that paired avocets aggressively drove conspecifics from the site prior to nest initiation. Since migrants likely engage in hyperphagia prior to migration, it may not be energetically beneficial for migrants to compete with territorial residents when other foraging habitat is available.

In contrast, migrants from the tidal flat would not have similar agonistic behaviors, and possibly experienced less overall competition for resources, since there is no breeding habitat at that site. Instead TF residents nested in other habitats, including two salt ponds (pond A22 1.5 km to the northwest and pond A8 6 km to the southwest) and a managed marsh (4 km to the south), accounting for home ranges and distances from the capture site larger than those of TF migrants. Of our sample of radio-marked birds, the TF migrants had the smallest home ranges and the most site fidelity. Optimal-foraging theory suggests that home-range sizes are adjusted to minimize energy expenditure while maximizing resource acquisition (Stephens and Krebs 1983, Stephens et al. 2007), which may be possible with less agonistic behavior from resident conspecifics on the tidal flat. Additionally, previous studies of shorebirds have detected high site fidelity and restricted space use when food and safe roosting sites are nearby (Warnock 1990, Warnock and Takekawa 1995, Leyrer et al. 2006). Likewise, our telemetry and visual observations revealed that TF migrants foraged on the tidal flat of Coyote Creek Lagoon at low tide and roosted in the adjacent diked marsh at high tide. This juxtaposition of important habitats is beneficial for shorebirds since it reduces the need for extended flight, which is energetically costly for shorebirds (Castro and Myers 1989),

IMPLICATIONS FOR RESTORATION

Our study suggests that the conversion of salt ponds to tidal marsh, as part of the South Bay Salt Pond Restoration Project, will not affect coexisting wintering migrant and resident avocets differently. Despite the observed differences between migrant and resident avocets' use of space, capture site was the strongest influence on habitat selection of avocets wintering in the South Bay. This fidelity to a particular habitat likely aids in saving energy when a bird decides which habitats to use, as a previously useful habitat may be more likely to provide sufficient resources than an unexplored habitat (Hillen et al. 2009). Although individual avocets have high site fidelity, our study shows that the avocet as a species is plastic in its space use and habitat selection. This plasticity has allowed the species to establish a new breeding population in San Francisco Bay and will likely allow wintering avocets to adapt to habitat change during the early phases of restoration in the South Bay. However, the South Bay Salt Pond Restoration Project will ultimately result in less habitat available to wintering avocets, and other wintering waterbirds, as up to 90% of former commercial salt ponds will be restored to tidal marsh, a habitat we found that avocets did not select. To mitigate for the loss of pond habitat, the first phase of the restoration includes four highly managed ponds for waterbirds with variable water depths and islands (USFWS and CDFG 2007). With this overall decrease in the extent of ponds, refuge managers will need to support higher densities of birds in managed ponds and on tidal flats, possibly resulting in reduced habitat quality (Fretwell and Lucas 1970, Emlin 1985). Also, as the availability of pond habitat in the South Bay is reduced, wintering avocets may make greater use of tidal flats, like Coyote Creek Lagoon, for foraging. Therefore, we suggest that managers provide suitable roosting sites in close proximity, if not directly adjacent, to foraging sites, as our study suggests that wintering avocets are able to minimize their use of space when suitable habitats are close by.

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LITERATURE CITED

Ackerman, J. T., C. A. Eagles-Smith, G. H. Heinz, S. E. Wainwright-De La Cruz, J. Y. Takekawa, T. L. Adelsbach, A. K. Miles, D. J. Hoffman, S. E. Schwarzbach, T. H. Suchanek, and T. C. Maurer [online]. 2007. Mercury in birds of the San Francisco Bay-Delta: trophic pathways, bioaccumulation and ecotoxicological risk to avian reproduction. U. S. Geological Survey, Western Ecological Research Center, Davis, CA, and U. S. Fish and Wildlife Service, Environmental Contaminants Division, Sacramento, CA. <http://www.werc.usgs.gov/ProductDetails.aspx?ID=3472> (11 February 2009).

Ackerman, J. T., J. D. Bluso-Demers, and J. Y. Takekawa. 2009. Postfledging Forster's Tern movements, habitat selection, and colony attendance in San Francisco Bay. Condor 111:100–110.

Beyer, H. L. [online]. 2004. Hawth's analysis tools for ArcGIS. <http://www.spatialecology.com/htools> (11 February 2009).

Brown, J. L., and G. H. Orians. 1970. Spacing patterns in mobile animals. Annual Review of Ecology, Evolution, and Systematics. 1:239–262.

Brown, J. L. 1975. The evolution of behavior. Norton, New York.

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

Demers, S. [online]. 2007. Space use of American Avocets in South San Francisco Bay. M.Sc. thesis, Humboldt State University, Arcata, CA. <http://humboldt-dspace.calstate.edu/handle/2148/207> (11 February 2009).

Demers, S. A., M. A. Colwell, J. Y. Takekawa, and J. T. Ackerman. 2008. Breeding stage influences space use of female American Avocets in San Francisco Bay, California. Waterbirds 31:365–371

Dill, H. H., and W. H. Thornsberry. 1950. A cannon projected net trap for capturing waterfowl. Journal of Wildlife Management 14:132–137.

Dodd, S. L., and M. A. Colwell. 1998. Environmental correlates of diurnal and nocturnal foraging patterns of nonbreeding shorebirds. Wilson Bulletin 110:182–189.

Emlen, J. M. 1985. The assessment of frequency- and density-dependent influences on fitness in natural populations. American Naturalist 125:507–520.

Environmental Systems Research Institute (ESRI) 2005. ArcGIS version 9.1. ESRI, Redlands, CA.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distributions in birds. I. Theoretical development. Acta Biotheoretica 19:16–36.

Gibson, F. 1971. The breeding biology of the American Avocet (*Recurvirostra americana*) in central Oregon. Condor 73:444–454.

Gill, R. E. 1977. Breeding avifauna of the South San Francisco Bay estuary. Western Birds 8:1–12.

Haig, S. M., L. W. Oring, P. M. Sanzenbacher, and O. W. Taft. 2002. Space use, migratory connectivity, and population segregation among Willets breeding in the western Great Basin. Condor 104:620–630.

Hamilton, R. B. 1975. Comparative behavior of the American Avocet and the Black-necked Stilt (Recurvirostridae). Ornithological Monographs 17.

Hill, M. R. J., and R. B. Frederick. 1997. Winter movements and habitat use by Greater Snow Geese. Journal of Wildlife Management 61:1213–1221.

Hillen, J., A. Kiefer, and M. Veith. 2009. Foraging site fidelity shapes the spatial organization of a population of female western barbastelle bats. Biological Conservation 142:817–823.

Horne, J. S., and E. O. Garton. 2006. Likelihood cross-validation versus least-squared cross-validation for choosing the smoothing parameter of kernel home-range analysis. Journal of Wildlife Management 70:641–648.

Horne, J. S., and E. O. Garton [online]. 2007. <http://www.cnr.uidaho.edu/population_ecology/animal_space_use> (11 February 2009).

Ingold, J., and R. Galati. 1997. Golden-crowned Kinglet (*Regulus satrapa*), no. 301. *In* A. Poole and F. Gill [eds.], The birds of North America. Academy of Natural Sciences, Philadelphia.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, M., J. P. Beckmann, and L. W. Oring. 2003. Diurnal and nocturnal behavior of breeding American Avocets. Wilson Bulletin 115:176–185.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements, p. 125–166. *In* J. J. Millspaugh and J. M. Marzluff [eds.], Radio tracking and animal populations. Academic Press, San Diego.

Kostecke, R. M., and L. M. Smith. 2003. Nocturnal behavior of American Avocets in playa wetlands on the southern high plains of Texas, USA. Waterbirds 26:192–195.

Leck, C. F. 1980. Establishment of new population centers with changes in migration patterns. Journal of Field Ornithology 51:168–173.

Leonard, T. D., P. D. Taylor, and I. G. Warkentin. 2008. Landscape structure and spatial scale affect space use by songbirds in naturally patchy and harvested boreal forests. Condor 110:467–481.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

Leyrer, J., B. Spaans, M. Camara, and T. Piersma. 2006. Small home ranges and high site fidelity in Red Knots (*Calidris c. canutus*) wintering on the Banc d'Arguin, Mauritania. Journal of Ornithology 147:376–384.

Lopez, R. R., N. J. Silvy, R. N. Wilkins, P. A. Frank, M. J. Peterson, and M. N. Peterson. 2004. Habitat-use patterns of the Florida Key deer: implications of urban development. Journal of Wildlife Management 68:900–908.

Madsen, J. 1998a. Experimental refuges for migratory waterfowl in Danish wetlands. I. Baseline assessment of the disturbance effects of recreational activities. Journal of Applied Ecology 35:386–397.

Madsen, J. 1998b. Experimental refuges for migratory waterfowl in Danish wetlands. II. Tests of hunting disturbance effects. Journal of Applied Ecology 35:398–417.

Manly, B. F., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical

design and analysis for field studies. Kluwer Academic, Dordrecht, the Netherlands.

McCleery, R. A., R. R. Lopez, N. J. Silvy, and S. N. Kahlick. 2006. Habitat use of fox squirrels in an urban environment. Journal of Wildlife Management 71:1149–1157.

McDonald, L. L., J. R. Alldredge, M. S. Boyce, and W. P. Erickson. 2005. Measuring availability and vertebrate use of terrestrial habitats and foods, p. 465–488. *In* C. E. Braun [ed.], Techniques for wildlife investigations and management. 6th ed. Wildlife Society, Bethesda, MD.

Miles, A. K., J. Y. Takekawa, D. H. Schoellhamer, S. E. Spring, N. D. Athearn, G. G. Shellenbarger, and D. C. Tsao [online]. 2004. San Francisco Bay estuary salt ponds progress report 2001–2003, Priority Ecosystem Science Program, USGS/USFWS (CNO) Science Support Program. U. S. Geological Survey, Davis and Vallejo, CA. <www.southbayrestoration.org/pdf_files/USGS%20South%20Bay%20Salt%20Ponds%202003.pdf> (11 February 2009).

Millspaugh, J. J., and J. M. Marzluff. 2001. Radio tracking and animal populations. Academic Press, San Diego.

Morris, D. W. 1987. Spatial scale and the cost of density-dependent habitat selection. Evolutionary Ecology 1:379–388.

Plissner, J. H., S. M. Haig, and L. W. Oring. 2000. Postbreeding movements of American Avocets and implications for wetland connectivity in the western Great Basin. Auk 117:290–298.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators, p. 65–110. *In* L. Boitani and T. K. Fuller [eds.], Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York.

Rintoul, C., N. Warnock, and G. W. Page. 2003. Breeding status and habitat use of Black-necked Stilts and American Avocets in South San Francisco Bay. Western Birds 34:2–14.

Robinson, J. A., L. W. Oring, J. P. Skorupa, and R. Boettcher. 1997. American Avocet (*Recurvirostra americana*), no 275. *In* A. Poole and F. Gill [eds.], The birds of North America. Academy of Natural Sciences, Philadelphia.

Rodgers, A. R., A. P. Carr, L. Smith, and J. G. Kie. 2005. HRT: Home range tools for ArcGIS. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

SAS Institute [online]. 2004. SAS OnlineDoc, Version 9.1.2. SAS Institute, Inc., Cary, NC. <http://v8doc.sas.com/sashtml/> (11 February 2009).

Sanzenbacher, P. M., and S. M. Haig. 2002. Regional fidelity and movement patterns of wintering Killdeer in an agricultural landscape. Waterbirds 25:16–25.

Schoener, T. W. 1983. Simple models of optimal feeding-territory size: a reconciliation. American Naturalist 127:608–629.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

San Francisco Estuary Institute. 1998. Bay Area EcoAtlas narrative documentation, EcoAtlas beta release, version 1.5b4. San Francisco Estuary Institute, Oakland, CA.

Sibley, C. G. 1952. Birds of the South San Francisco Bay region. San Jose State College, 44 p. mimeograph.

Smith, S. M. 1976. Ecological aspects of dominance hierarchies in Black-capped Chickadees. Auk 93:95–107.

Stenzel, L. E., C. M. Hickey, J. E. Kjelmyr, and G. W. Page. 2002. Abundance and distribution of shorebirds in the San Francisco Bay area. Western Birds 33:69–98.

Stephens, D. W., and J. R. Krebs. 1983. Foraging theory. Princeton University Press, Princeton, NJ.

Stephens, D. W., J. S. Brown, and R. C. Ydenberg. 2007. Foraging behavior and ecology. University of Chicago Press, Chicago.

Swihart, R. K., and N. A. Slade. 1997. On testing for independence of animal movements. Journal of Agricultural, Biological, and Environmental Statistics 2:48–63.

Takekawa, J. Y., C. T. Lu, and R. T. Pratt. 2001. Bird communities in salt evaporation ponds and baylands of the northern San Francisco Bay estuary. Hydrobiologia 466:317–328.

Takekawa, J. Y., A. K. Miles, D. H. Schoellhamer, N. D. Athearn, M. K. Saiki, W. D. Duffy, S. Kleinschmidt, G. G. Shellenbarger, and C. A. Jannusch. 2006a. Trophic structure and avian communities across a salinity gradient in evaporation ponds of the San Francisco Bay estuary. Hydrobiologia 567:307–327.

Takekawa, J. Y., N. D. Athearn, B. J. Hattenbach, and A. K. Schultz [online]. 2006b. Bird monitoring for the South Bay salt pond restoration project. Data summary report, U. S. Geological Survey, Vallejo, CA. <http://www.southbayrestoration.org/pdf_files/USGS_SouthBaySP_Birds_2006.pdf> (11 February 2009).

USFWS and CDFG [online]. 2007. South Bay Salt Ponds Restoration Project final environmental impact statement/report. Prepared by EDAW, Philip Williams and Associates, Ltd., H. T. Harvey & Associates, Brown and Caldwell, and Geomatrix. <http://www.southbayrestoration.org/EIR/> (11 February 2009).

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

Warnock, N., G. W. Page, T. D. Ruhlen, N. Nur, J. Y. Takekawa, and J. T. Hanson. 2002. Management and conservation of San Francisco Bay salt ponds: effects of pond salinity, area, tide, and season on Pacific Flyway waterbirds. Waterbirds 25 Special Publication 2:79–92.

Warnock, S. E., and J. Y. Takekawa. 1995. Habitat preferences of wintering shorebirds in a temporally changing environment: Western Sandpipers in the San Francisco Bay estuary. Auk 112:920–930.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego.

With, K. A. 1994. Using fractal analysis to assess how species perceive landscape structure. Landscape Ecology 9:25–36.

Worton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794–800.