



Space use by Black-Necked Stilts *Himantopus mexicanus* in the San Francisco Bay Estuary

Authors: Hickey, Catherine, Warnock, Nils, Takekawa, John Y., and Athearn, Nicole D.

Source: *Ardea*, 95(2) : 275-288

Published By: Netherlands Ornithologists' Union

URL: <https://doi.org/10.5253/078.095.0210>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Space use by Black-necked Stilts *Himantopus mexicanus* in the San Francisco Bay estuary

Catherine Hickey¹, Nils Warnock¹, John Y. Takekawa^{2,*} & Nicole D. Athearn²

Hickey C., Warnock N., Takekawa J.Y. & Athearn N.D. 2007. Space use by Black-necked Stilts *Himantopus mexicanus* in the San Francisco Bay estuary. *Ardea* 95(2): 275–288.



We examined space use by Black-necked Stilts *Himantopus mexicanus* in the San Francisco Bay estuary, USA, to better understand how shorebirds use their Pacific Flyway landscape. These efforts are particularly important in the San Francisco Bay estuary where ongoing large-scale restoration projects are rapidly changing the mosaic of wetland habitats. We radio-marked 59 stilts and tracked individuals for up to four months and found no difference in home range size by sex or between North and South Bay subregions. We did find differences in home range size by capture site. Mean home range was 283.5 ha and movement from capture sites was 4.5 km. We used cluster analysis to calculate number of focal areas for individuals and found that overall space requirements were larger for stilts with multiple centres of activity. Birds with multiple use areas were often those that bred in vegetated marshes and moved into salt ponds when their nests failed or after chicks hatched. In the South Bay subregion, salt pond use was greater than availability in core use home range areas despite comprising the largest proportion of available habitat. Tidal salt marsh restoration from former salt ponds may reduce available habitat of invertebrate prey species that depend on hypersaline habitats; retention of some shallow, mid-salinity managed ponds may mitigate this loss. A better understanding of the space use and habitat requirements of stilts will provide for more specific habitat and management recommendations in areas targeted for wetland restoration, contributing to better conservation of shorebird populations along the Pacific Flyway.

Key words: *Himantopus mexicanus*, home range, space use, movements, San Francisco Bay, shorebirds, waders, wetlands

¹PRBO Conservation Science, 3820 Cypress Drive #11, Petaluma, CA 94954, USA; ²U.S. Geological Survey, Western Ecological Research Center, San Francisco Bay Estuary Field Station, 505 Azuar Drive, Vallejo, CA 94592, USA;

*corresponding author (john_takekawa@usgs.gov)

INTRODUCTION

Understanding how birds select, use, and move among habitats is necessary to identify landscape elements critical to a bird's life cycle (Cody 1985, Wiens 1994, 1996, Walters 1998). Increasingly,

patterns of space and habitat use by shorebirds are being elucidated by satellite and radio technology (Warnock & Takekawa 2003); these data provide information needed to manage species, identify biologically important habitats, and restore habitats in regions of rapid change.

During the past two centuries, the San Francisco Bay estuary (Fig. 1) has been altered by loss of 79% of its tidal salt marshes, 42% of its tidal flats, and construction of >13 000 ha of artificial salt evaporation ponds (Goals Project 1999). The transfer of 6111 ha of South Bay salt ponds to government ownership in 2003 marked the implementation of a management plan to convert salt ponds to tidal marsh and managed pond habitat (Steere & Schaefer 2001, Siegel & Bachand 2002, Life Science 2003). Similar efforts are underway for 4567 ha of former commercial salt ponds in the North Bay subregion (COE 2003). Recent studies characterize baseline ecological conditions (Takekawa *et al.* 2006, unpubl.), but limited information is available to predict how habitat changes will affect birds in the estuary (but see Stralberg *et al.* 2005). Detailed information about space and habitat use by representative bird species will be a key factor guiding management decisions as restoration projects are undertaken.

The Black-necked Stilt *Himantopus mexicanus mexicanus* breeds from western and southern North America to northern South America and winters throughout its southern breeding range, including the San Francisco Bay estuary (Robinson *et al.* 1999). Stilts may have responded positively to past changes in the estuary, particularly the construction of salt ponds (Harvey *et al.* 1992, Masero & Hurtado 2001, Masero 2003). Few breeding or wintering stilts were present prior to the early 1970s (Grinnell & Wythe 1927, Sibley unpubl.), when they were first considered common (Gill 1977, Rigney & Rigney 1981). By May 2001, 1184 Black-necked Stilts were counted in south San Francisco Bay, of which at least 270 were known to be breeding (Rintoul *et al.* 2003). The estuary is now considered as a priority area under the U.S. Shorebird Conservation Plan (Brown *et al.* 2001) for maintaining and potentially increasing breeding stilts in the Southern Pacific Region (Hickey *et al.* 2003). However, future habitat changes may threaten stilts, as they are as vulnerable to habitat loss and alteration as other western North American shorebirds (Page & Gill 1994).

In an attempt to better understand space use by shorebirds along the Pacific Flyway and to address the potential effects of wetland conversion in the San Francisco Bay estuary, we studied the ecology of stilts in the San Francisco Bay during the summer and fall of 1999. Spatial requirements for breeding and post-breeding Black-necked Stilts have not previously been quantified (but see Reed *et al.* 1994, 1998). Thus, we used radio-telemetry to examine space use and position patterns by stilts breeding in the estuary and quantified home-range size, position patterns, and degree of clustered activity.

METHODS

Study Area

We studied stilts in the North and South Bay subregions of the San Francisco Bay (Fig. 1). The major wetland habitat types surrounding the North Bay were tidal marsh (6615 ha), diked wetland (15 351 ha), tidal flats (3690 ha), and salt ponds (3276 ha). The South Bay primarily was surrounded by salt ponds (11 594 ha), diked wetland (2907 ha), tidal flats (6070 ha), and small fragments of tidal marsh (3807 ha, Goals Project 1999).

Radio-marking

We captured breeding stilts from brackish marshes and salt ponds in the North Bay (4 sites; $n = 26$) and South Bay (5 sites; $n = 33$) subregions from 6–29 June 1999 (Table 1, Fig. 1). We used spring-loaded bow traps (placed over stilt nests or over chicks captured by hand and held in a small cage) to mark 9 males and 17 females in the North Bay and 20 males and 13 females in the South Bay (Table 1). We used radio telemetry to facilitate location of marked birds and to remove sighting bias and observer error that could result from visibility-limiting cover. Additionally, we marked all adults with a unique colour-band combination to allow identification of individuals through resighting, should a transmitter become lost or cease to function, as well as a U.S. Fish and Wildlife Service band.

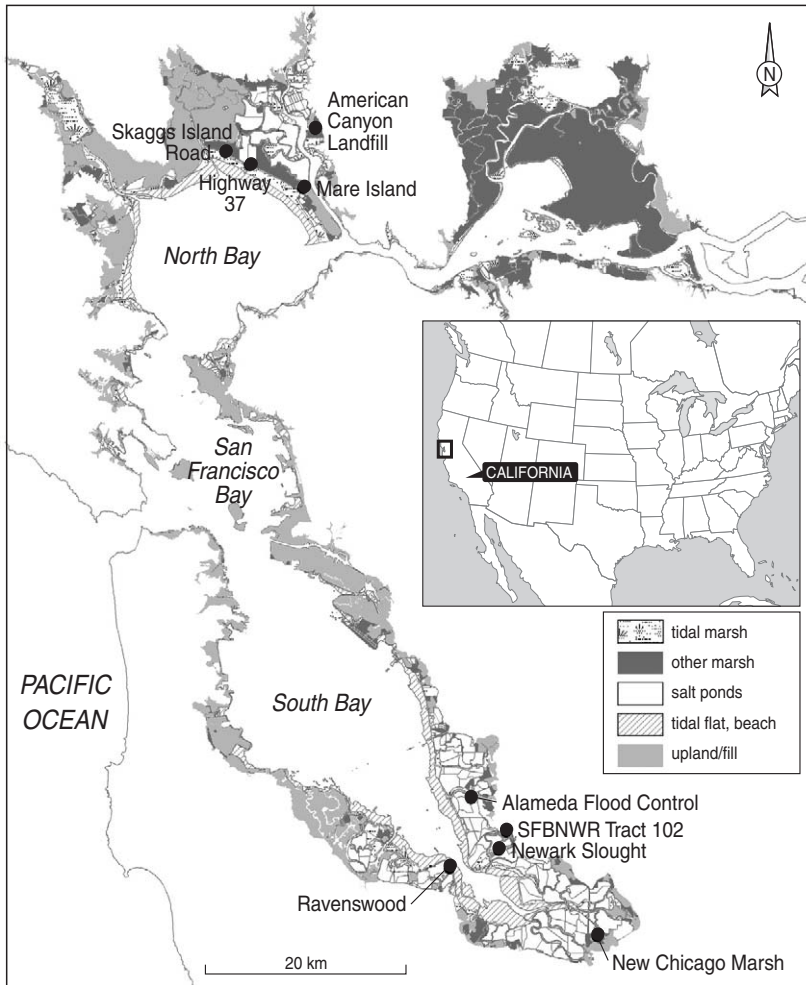


Figure 1. San Francisco Bay estuary, California, USA. North Bay and South Bay Black-necked Stilt capture sites indicated.

Transmitters had a four-month life expectancy. Each transmitter (2.5 g; model PD-2, Holohil Systems Ltd, Woodlawn, ON) was attached to a metal band and placed on the stilt's upper left tibia (Plissner *et al.* 2000a). The metal bands used for radio attachment were one size greater than normal to accommodate the transmitters.

We tracked stilts twice daily on low and high tides through mid-September. We followed individual stilts until 1) the radio ceased transmitting; 2) we were unable to locate the bird after multiple

attempts; 3) the bird was reported dead; or 4) the study period ended. We used trucks with null-peak telemetry systems to obtain stilt locations: we estimated each location by taking two bearings of the bird's position from the truck, then recording the truck's location and azimuth. Universal Transverse Mercator (UTM) coordinates of bird locations were generated using a modified version of the XYLOG and UTMEL programs (Dodge *et al.* 1986, Dodge & Steiner 1986). We estimated the accuracy of truck locations as 60 m using results from a study

Table 1. Number of male and female Black-necked Stilts radio-marked by subregion and capture location. Habitat lists the general wetland type of the capture location.

Location	Male	Female	Habitat
North Bay			
American Canyon	8	11	brackish marsh
Mare Island	0	2	freshwater marsh
Skaggs Island	0	4	brackish marsh
Highway 37	1	0	brackish marsh
Subtotal	9	17	
South Bay			
Ravenswood	2	2	brackish marsh
Newark Slough	7	5	brackish marsh and salt pond
New Chicago Marsh	9	4	brackish marsh
SFBNWR Tract 102	2	1	brackish marsh and salt pond
Alameda Flood Control	0	1	brackish marsh and salt pond
Subtotal	20	13	
Total	29	30	

with similar telemetry systems and transmitters (Warnock & Takekawa 1995). We conducted an aerial survey to attempt to locate stilts that had not been detected for more than two weeks.

We omitted observations from the first three days after marking to allow for behavioural adjustments to the radios (Warnock & Warnock 1993, Warnock & Bishop 1998). We made no attempt to reduce autocorrelation of our observations because 1) our observations were separated by long intervals – generally >12 h; 2) our home range estimator was robust to autocorrelation (Swihart & Slade 1997, De Solla *et al.* 1999); and 3) restricting space use inferences to a defined time frame obviates concern over autocorrelation (Otis & White 1999).

Statistical analyses

Sample sizes at most capture sites were small; we included capture sites in the analyses where ≥ 4 birds were captured. We used several approaches to quantify space use by stilts. In order to detect behavioural changes associated with shifts from the end of the breeding period to post-breeding,

we estimated daily distance travelled by stilts through the study period. We calculated the straight-line distance travelled among locations on consecutive days. For cases where two or more locations were obtained for an individual in one day, we randomly selected which location to include. Thirty-one percent of observations were omitted for these analyses, either because they were same-day observations or because there was no observation on a day prior to or after another observation. The data were normalized after log transformation (Zar 1999), and we used generalized estimating equations (GEE) with step-down variable selection to test for effects on daily distance travelled by sex, subregion, month of observation, and interactions among these terms (Diggle *et al.* 1994).

We estimated home range size with the Animal Movement Extension (Hooge & Eichenlaub 1997) for Spatial Analyst in ArcView 3.1 (Environmental Systems Research Institute, Redlands, CA, USA). Although Horne & Garton (2006) found some inconsistencies between home range sizes calculated with this and other methods, all home ranges for

this study were calculated using the same method and are directly comparable. We tested location data for each stilt for goodness-of-fit to a bivariate normal distribution using the Cramer-von Mises test with ArcView Spatial Analyst. Because our location data were not bivariate-normally distributed and 86% of the individuals had multiple centres of activity, we chose the kernel method, a non-parametric utilization distribution (UD) estimator of home range size (Worton 1989). We used the fixed-kernel method with least-squares-cross-validation (LSCV) for smoothing parameter selection (Worton 1995, Seaman & Powell 1996, Seaman *et al.* 1999); kernel home range estimates were normalized following log transformation.

We calculated both 50% and 95% UD for stilts with ≥ 30 observations (Seaman *et al.* 1999). These two estimates of home range size represent the core area of activity for each stilt (50% UD), and the larger home range area (95% UD: Hooze *et al.* 2001). We tested for effects of sex, subregion, and capture site on home range size. To determine the effects of breeding status on home range size, we compared home range sizes of 6 stilts known to have abandoned their nests or lost their chicks within 7 days of capture and 6 stilts observed with chicks at least 30 days after capture. We used cluster analysis to quantify the degree to which stilts concentrated their activity in one or more sites. Where stilts had ≥ 30 observations, we used Ranges V (Kenward & Hodder 1996) to calculate the number of nuclei in each bird's 95% home range; we then tested for differences in number of nuclei for sex and subregion. We also used simple regression analysis to test for correlation between number of nuclei and home range size.

To examine space use by habitat, we overlaid home range polygons with Bay Area EcoAtlas coverages (v. 1.50b, SFEI 1998) that quantified areas of tidal marsh, diked wetland, tidal flats, salt ponds, and other habitats contained within 50% and 95% UD polygons for each stilt (ArcGIS 9.1, Environmental Systems Research Institute, Redlands, CA, USA). We examined second-order selection use of habitats within home ranges compared to available habitat (Johnson 1980, Warnock &

Takekawa 1995). Available habitat was determined by the proportion of each habitat type contained within each subregion. Habitat usage was estimated by determining the proportion of each habitat type contained within home ranges and was then compared to available habitat by chi-square analysis within subregions. We also calculated selectivity indices by dividing the proportion of habitat type within each individual's home range by the proportion available in the subregion. Selectivity indices >1 indicated a greater proportion of that habitat type than expected, whereas indices <1 indicated a smaller proportion. We qualitatively compared habitat proportions contained within core use home ranges of birds with and without chicks, and used *t*-tests to compare home range size among birds with and without chicks during the study period.

Statistical analyses were performed with SAS (SAS Institute Inc. 1999) and NCSS 2000 (Hintze 1998). We examined the data for departures from normality and homogeneity and normalized the data with standard transformations (Zar 1999). When data met parametric assumptions, we used ANOVA to investigate differences between means of main effects and interaction terms. If we found insignificant effects with multiple main factors, we ran one-way ANOVAs for each factor. When a main effect was found to be significant overall, we ran Bonferroni Multiple Comparison tests to determine between-group differences. If data were non-normal, we used the Kruskal-Wallis test for differences. Significance was set at $P = 0.05$. When necessary, we used GEE to test for significance of main effects and interaction terms; GEE adjusted for correlation within same-subject observations (Diggle *et al.* 1994). To obtain final models with GEE, we used a step-down selection method with $P = 0.05$ criteria for removal of interaction terms and main effects. We reported arithmetic means, except for area estimates where we reported geometric means, and 95% confidence intervals. Where necessary to facilitate interpretation of results, we used the Delta method (Christensen 1997) to back-transform standard errors of log-transformed data.

RESULTS

We obtained 1943 total locations for the 59 radio-marked stilts, 965 locations for stilts captured in the North Bay, and 978 locations for stilts in the South Bay. The average number of locations per stilt was 34 ± 3.1 . Of the 59 stilts, 29 had ≥ 30 locations ($\bar{x} = 48.9 \pm 3.8$) and were included in home range and cluster analyses.

Comparing the subsamples where we documented birds were with or without chicks, we were unable to detect differences among 50% UD core use areas ($t = 0.094, P = 0.46$) and 95% UD home range areas ($t = -0.124, P = 0.45$).

Daily movements and dispersal

Only 3 stilts moved from the North to South Bay, and they travelled 66.0–71.8 km to their post-breeding locations; since this was a rare occurrence that skewed local-scale results, we omitted the regional movement data from analyses. Testing for sex, capture subregion, month, and interaction terms on the distance stilts travelled daily, we found a significant interaction between capture subregion and month of observation (GEE test,

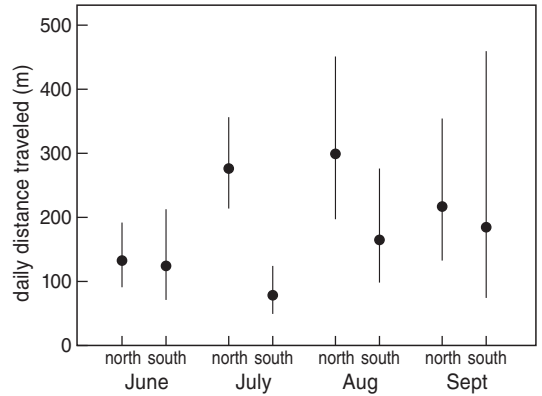


Figure 2. Daily distance travelled through the study period for Black-necked Stilts captured in the North and South San Francisco Bay estuary. Means and 95% confidence intervals presented.

$\chi^2_3 = 9.7, n = 54$ stilts, $P = 0.02$). Daily distance travelled was similar for stilts captured in the North and South Bays in all months except for July when stilts in the North Bay moved greater distances on a daily basis (Fig. 2).

Table 2. Home range size for male and female Black-necked Stilts determined with the fixed kernel method for 95% and 50% Utilization Distribution (UD) areas (ha). North and South Bay subregions include locations with $n \geq 4$ captured stilts. CI = 95% confidence interval.

Parameter	95% UD					50% UD				
	<i>n</i>	\bar{x}	CI	<i>F</i>	<i>P</i>	<i>n</i>	\bar{x}	CI	<i>F</i>	<i>P</i>
All birds	29	283.5	196–667				44.8	36.1–118		
Sex				$F_{1,27} = 0.90$	0.3				$F_{1,27} = 1.7$	0.2
Male	16	209	109–718			16	28.9	18.5–118		
Female	13	423	213–1150			13	83.5	46.9–208		
Subregion				$F_{1,27} = 0.05$	0.8				$F_{1,27} = 0.11$	0.7
North Bay	13	288	146–767			13	48.5	26.9–128		
American Canyon	9	233	89.8–836							
South Bay	16	280	146–1020			16	42.1	27.6–183		
Ravenswood	4	2080	585–7890							
New Chicago	8	112	38.2–557							
Capture site	21			$F_{2,18} = 4.8$	0.02					

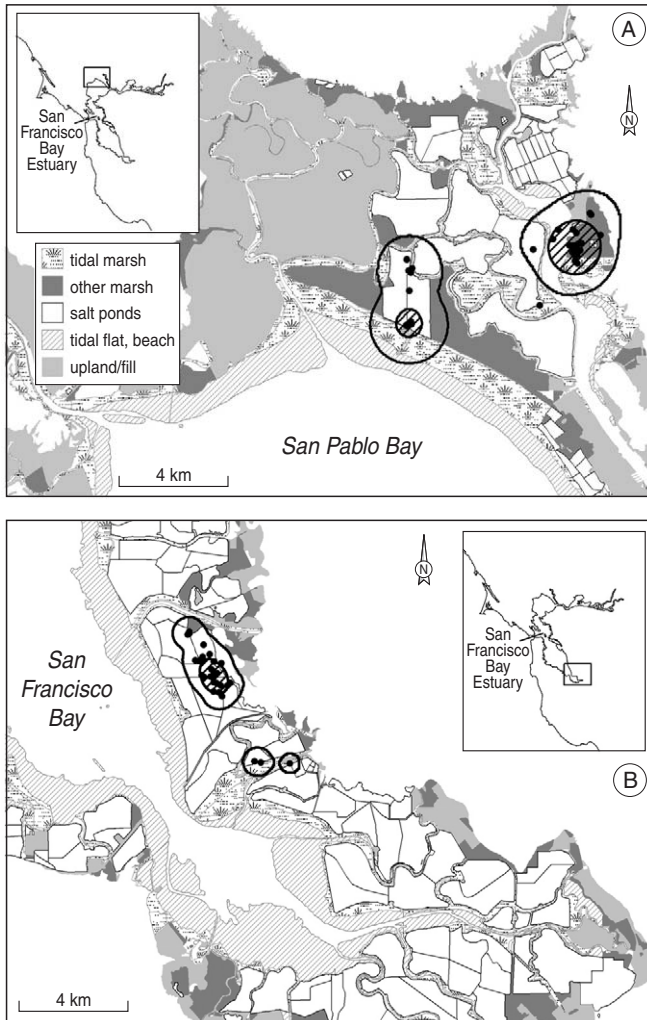


Figure 3. Example Black-necked Stilt home ranges in the San Francisco Bay estuary. Black dots = individual locations. (A) Fixed kernel estimates for bird 5257 with two centres of activity in the North Bay; 95% UD = 2090 ha (within bold outline), 50% UD = 370 ha (cross-hatched within bold outline). (B) Fixed kernel estimates for bird 5948 with three centres of activity in the South Bay; 95% UD = 639 ha (within bold outline), 50% UD = 98.1 ha (cross-hatched within bold outline).

Home range size

Mean home range sizes based on 95% and 50% UD were 283.5 and 44.8 ha, respectively (Table 2). We found no difference between males and females in 95% UD home range size or in 50% UD home range size. Similarly, we found no difference between stilts captured in the North Bay (Fig. 3A) and South Bay (Fig. 3B) in 95% UD home range size or in 50% UD home range size (Table 2).

However, home range size did vary by capture site. Stilts captured at Ravenswood Marsh had larger home ranges than stilts captured in New

Chicago Marsh, but home range size for stilts in these two South Bay sites were not different from stilts captured at American Canyon Landfill in the North Bay (Table 2).

Centres of activity and subregional movements

Most stilts (86%) had >1 centre of activity, with a mean of 2.6 ± 0.2 ($n = 29$). All 4 stilts with only 1 centre of activity were captured in the North Bay and centred their activity at American Canyon Landfill; 3 were also captured at that site. Overall, there was no difference between the number of

Table 3. Proportion of habitat types available, average proportion selected, and selectivity indices (SI) within North Bay (NB) and South Bay (SB) subregions.

Available Habitat	% of region		50% UD (core use area)				95% UD (home range area)			
	NB	SB	North Bay		South Bay		North Bay		South Bay	
			% Use ± SE	SI ± SE	% Use ± SE	SI ± SE	% Use ± SE	SI ± SE	% Use ± SE	SI ± SE
Diked wetland	47.5	9.5	72.5 ± 9.3	1.5 ± 0.2	19.6 ± 5.0	2.1 ± 0.5	58.1 ± 6.5	1.2 ± 0.1	21.6 ± 4.6	2.3 ± 0.5
Tidal flat	11.4	20	-	0 ± 0	5.7 ± 3.9	0.3 ± 0.2	1.2 ± 0.6	0.1 ± 0.1	4.9 ± 2.1	1.1 ± 0.2
Salt ponds	10.1	38.3	6.6 ± 4.2	0.6 ± 0.4	57 ± 6.5	1.5 ± 0.2	6 ± 2.7	0.6 ± 0.3	49.9 ± 4.6	0.6 ± 0.1
Tidal marsh	20.4	12.6	9 ± 5.0	0.4 ± 0.2	11.9 ± 4.7	0.9 ± 0.4	13.9 ± 2.8	0.7 ± 0.1	12.2 ± 3.6	1.7 ± 0.4
Other	10.6	19.6	11.9 ± 4.3	1.1 ± 0.4	5.8 ± 2.1	0.3 ± 0.1	20.8 ± 2.9	2 ± 0.3	11.4 ± 2.3	1.1 ± 0.2

nuclei for male and female stilts ($\chi^2_1 = 1.5, P > 0.3$), nor for stilts captured in the North and South Bays ($\chi^2_1 = 0.80, P > 0.4$). There was a relationship between number of nuclei and home range size ($F_{1,27} = 6.4, P = 0.02$), indicating larger overall space requirements for stilts that used multiple sites. Alternatively, birds that had a large home range may have been more able to use multiple sites.

Twenty-three of the 26 stilts captured in the North Bay stayed in that subregion for the duration of their individual tracking periods (3 moved to the South Bay within several weeks after capture). Most stilts captured at American Canyon Landfill stayed there consistently through the end of their tracking periods. No stilts that bred at Mare Island or Skaggs Island remained in the marsh after capture; most moved between salt ponds and brackish marshes.

All stilts captured in the South Bay stayed in that subregion for the duration of their tracking periods. Stilts in 3 of the 4 South Bay breeding areas heavily used salt ponds at Don Edwards San Francisco Bay National Wildlife Refuge. All of the 4 stilts captured in Ravenswood, the brackish marsh on the southwest shore of the Bay, stayed there less than 3 weeks after the beginning of their tracking periods; 3 of those stilts crossed to the Bay's east shore. Stilts captured in New Chicago Marsh, the brackish marsh at the southern end of the Bay, moved into nearby salt ponds and stayed in the southern portion of the Bay for their entire tracking periods.

Habitat selection

Diked wetland was the primary habitat type comprising calculated home range areas in the North Bay, comprising 58–72% of home range areas; selectivity indices were >1, indicating greater use than expected from availability (Table 3). Tidal flat comprised >11% of available habitat in the North Bay, but was nearly absent from home range areas. Salt ponds and tidal marsh habitats were represented by proportions in home ranges closer to those available in the North Bay subregion and had selectivity indices close to 1 (Table 3).

Salt ponds comprised the largest proportion of available habitat in the South Bay subregion. Even so, the proportion of salt pond habitat within home range areas was greater than expected from availability, at least for 50% UD core use areas (Table 3). Diked wetland, generally adjacent to salt ponds, was also represented proportionately more than was available in stilt home ranges, with mean selectivity indices >2 (Table 3). Tidal marsh represented a similar proportion of core home range areas as expected by chance. Tidal flats comprised a larger proportion of available habitat (20%) and of stilt home range areas in the South Bay than in the North Bay, but was still the least represented habitat in core use areas (selectivity index 0.3 ± 0.2 ; Table 3).

DISCUSSION

Movements

Along the Pacific Flyway, shorebird species often respond to rapid changes in habitat and prey availability over wide spatial scales. Wintering Dunlin *Calidris alpina* and Long-billed Dowitchers *Limnodromus scolopaceus* move hundreds of kilometers between coastal, including San Francisco Bay, and interior sites in a matter of days, where they exploit new habitat and prey brought forth by seasonal flooding (Warnock *et al.* 1995, Sanzenbacher & Haig 2002, Takekawa *et al.* 2002). Post-breeding American Avocets *Recurvirostra americana* disperse hundreds of kilometers to a few alkali lakes in the Great Basin (Plissner *et al.* 1999, 2000a), where they feed on superabundant prey resources (Boula unpubl.) before migrating to mainly coastal sites (Robinson & Oring 1996, Robinson *et al.* 1999).

We detected small daily movements by stilts. All stilts were captured at nesting sites and had eggs or chicks at the beginning of the study period, but not all birds retained chicks throughout the tracking period. Breeding status was not documented for all individuals throughout the tracking period, because habitat cover or distance often precluded visual observation of stilts when locations were obtained through telemetry, and

because parentage of chicks in groups could not be easily determined. Although breeding status is a potentially confounding factor in space use analyses, data from the subset of birds where we documented breeding status suggested that home range size and habitat composition among stilts with and without chicks did not differ. This is not surprising because the birds in our study were in a late stage of incubation or had already hatched chicks prior to capture, and precocial stilt chicks may not severely constrain the movements of adults. However, recent work suggests that pre-breeding and early-breeding stilts may have space use differences from stilts later in the season (JYT, unpubl. data). We concluded that the presence of chicks did not significantly affect home range or habitat use of adults during the late-breeding and post-breeding season following incubation.

Daily distance travelled was similar for stilts captured in the North and South Bay subregions in all months except for July (Fig. 2). In July, stilts in the North Bay moved greater distances on a daily basis than South Bay stilts. Although this study did not reveal differences in other months, our recent work (2004–2005) suggests that microclimate in the South Bay subregion is distinct from the North Bay, and that South Bay has an earlier and longer chronology (JYT, unpubl. data); at any rate, habitat composition differs between the two subregions (Table 3). These studies suggest that North Bay habitats may change at a different rate and that stilts may need to move greater distances earlier in the season to obtain adequate resources than in the South Bay subregion.

Within San Francisco Bay, the relatively short intra-estuary movements by breeding and post-breeding stilts and the $\geq 23\%$ of individuals resident in the estuary (PRBO unpubl. data) suggest that resources within diked wetlands, marshes, and salt ponds were adequate at North and South Bay sites for breeding and post-breeding activities. High densities of invertebrates that stilts may prey on, including brine shrimp (*Artemia franciscana*, often called *A. salina*, Larsson 2000) and brine flies (*Ephydra* spp. and *Lipochaeta slossonae*; Carpelan 1957, Larsson 2000, Maffei 2000)

predictably occurred in salt ponds where stilts brought their young to feed and where post-breeding stilts aggregated (Hamilton 1975). A potential negative effect of this high breeding and post-breeding fidelity of stilts in the Bay is that such relatively small local use areas have been suggested to increase contaminant risks to shorebirds of this urbanized estuary (Hui *et al.* 2001), and stilts have been reported to be vulnerable to contaminants in other western wetlands (Ohlendorf *et al.* 1989, Williams *et al.* 1989). Recent work has found that 17% of pre-breeding adult stilts in San Francisco Bay were at or above high risk to mercury contamination (Ackerman *et al.* unpubl. data). Although the lowest observable adverse effects level for stilts is not yet known, this level has been shown to cause impaired reproduction in Common Loons *Gavia immer* (Evers *et al.* 2004).

Space use and movement patterns of shorebirds have been observed to vary by sex (e.g. Myers 1981, McCloskey & Thompson 2000). Robinson & Oring (1996) suggest sexual differences exist in migratory behaviour of stilts, which exhibit some gender differences in wing chord and tarsus length (Robinson *et al.* 1999). Such differences may only apply to longer distance migratory movements, as male and female stilts in the San Francisco Bay estuary exhibited similar behaviour for each space use measure investigated.

Home range

Comparisons of our stilt home range size with other shorebirds are constrained due to varying estimation methods and different life-history stages investigated (Hudgins *et al.* 1985, Høglund & Robertson 1990, Keppie & Whiting 1994, Warnock & Takekawa 1995, Drake *et al.* 2001, Sanzenbacher & Haig 2002). Two home range estimates for breeding and post-breeding Killdeer *Charadrius vociferous* in the western Great Basin are most comparable to our stilt home range estimates. Both Killdeer studies used variations of the kernel method for estimating home range sizes (Powers unpubl., Plissner *et al.* 2000b), as we did, and both Killdeer and stilts are monogamous, biparental caregivers, that feed on many of the same

prey items (Robinson *et al.* 1999, Jackson & Jackson 2000). Killdeer mean home ranges varied from approximately 3–6 ha, orders of magnitude smaller than those for Black-necked Stilts in the San Francisco Bay estuary. One difference may be that many of the stilts in the Bay we marked had multiple core-use areas (e.g. Figs. 3A and B), reflecting the varying habitat needs of the stilts. Stilts in the estuary frequently breed in vegetated marshes (over 20% of nests in the South Bay, PRBO unpubl. data), but when their nests failed or after the chicks hatched, most of the birds moved into the salt ponds (PRBO unpubl. data, Warnock *et al.* 2002). This was supported especially in the South Bay, where salt ponds comprised about 60% of core use habitat areas for South Bay stilts regardless of breeding status.

Within the San Francisco Bay estuary, comparable home range data are only available for a few shorebird species. Warnock & Takekawa (1995) found an average home range size of 2200 ha in the South Bay for wintering Western Sandpipers *Calidris mauri*, an area 7-times larger than the stilts' range. Similarly, Takekawa *et al.* (2002) found an average home range size of 1700 ha for wintering Long-billed Dowitchers in the North Bay, 5–6 times larger than the stilt's home range. For breeding Snowy Plovers *Charadrius alexandrinus*, based on observations of marked birds, Feeney (1991) estimated that the average home range in South San Francisco Bay salt ponds was about 1.6 ha. Although due in part to different area estimation methods, the large home range differences among shorebirds within the Bay partially reflect varying use of wetlands by the species. Western Sandpipers and, to some degree, dowitchers, travel on a daily basis from high tide sites to the edge of the tidal flat at lower tides (Warnock & Takekawa 1996, Takekawa *et al.* 2002). Stilts were more highly dependent on diked wetlands and salt ponds throughout the tidal cycle, and they rarely used the tidal mudflats, which comprised small portions of their home range areas relative to availability (Hamilton 1975, Rintoul *et al.* 2003).

Preliminary comparisons and observations indicated that high and low tide locations for indi-

vidual birds overlapped and that groupings of locations from individual birds in tidally influenced areas were obtained approximately equally from low and high tide surveys. Tidally influenced habitat (tidal marsh and tidal flat) comprised similar proportions of home range areas to those available in each region, so stilts had no apparent preference for tidal habitat and there was no apparent influence of tide on habitat selection. In this regard, stilts are more similar to Long-billed Dowitchers in the North Bay that used marshes with ponded water in vegetated areas and made infrequent use of tidal flats (Takekawa *et al.* 2002).

Home range size did not differ by subregion in this study despite the marked difference in the proportions of various wetland types between the North and South Bays, but differing home range size by capture site indicates that stilts are responding to habitats on a finer scale. Wetland habitat over the whole estuary is generally stable through the breeding and post-breeding period. However, within subregions, changes can be rapid as water levels are actively managed, flooding or drying in a short period of time, forcing some stilts to move. The large home ranges for stilts at Ravenswood undoubtedly were a product of water management at that site. The site dried up soon after stilts were captured there; those stilts then travelled to other wetlands in the South Bay in search of post-breeding habitat. Relatively consistent water levels in New Chicago Marsh, combined with nearby salt ponds, likely contributed to significantly smaller home ranges for stilts captured there.

Recent habitat management in the San Francisco Bay estuary has been directed toward restoring over 40 000 hectares of tidal marsh around San Francisco Bay, mostly at the expense of salt pond habitat (Goals Project 1999, Steere & Schaefer 2001, Siegel & Bachand 2002). Breeding and post-breeding stilts in this study used a variety of habitat types including salt ponds and tidal marsh. However, stilts in the South Bay seemed to prefer salt ponds, and studies of stilts wintering in the South Bay indicate that the majority of stilts are found in salt pond habitats (Warnock *et al.* 2002).

The effect of conversion of salt ponds to tidal marsh on the stilt population in the estuary or to the overall North American population is still unknown, but initial management changes directed at salinity reduction may reduce available habitat of invertebrate prey species that depend on hypersaline habitats, such as brine flies and perhaps brine shrimp (Takekawa *et al.* 2006, unpubl.). Maintenance of some shallow, mid-salinity managed ponds, especially during breeding periods near known nesting sites, should mitigate this loss.

Additionally, habitat conversion may reduce availability of breeding habitat, particularly at South Bay salt pond complexes. Stilts may face increasing nest site competition from California Gulls *Larus californicus*, which have increased exponentially since the early 1980s (Strong *et al.* 2004). Linking space use data with demographic data to better understand potential source and sink habitats (e.g., Pulliam & Danielson 1991) should be a critical next step towards conserving stilts in the region. The information provided in this study, combined with an understanding of stilt habitat preferences and site fidelity will aid land managers and planners in providing sufficient resources to continue to support the breeding and wintering stilt populations in the estuary.

ACKNOWLEDGEMENTS

We would like to thank T. Foin, G. Page, M. Johnson, and S. Wainwright-De La Cruz for their critical review of the manuscript. We also thank P. Capitolo and B. Sauer for tracking the stilts, and S. Wainwright-De La Cruz, D. Whitworth, C. Lu, G. Page, and C. Marn for assistance in catching stilts on the nest. We also thank J. Albertson, C. Morris, and the San Francisco Bay National Wildlife Refuge Complex staff, as well as L. Wyckoff at the California Department of Fish and Game, and the City of Vallejo for providing access and logistical support. J. Yee provided statistical advice and D. Stralberg assisted with GIS analyses and map figures. Funding for the project was provided by the USGS Western Ecological Research Center, the USGS Priority Ecosystem Science initiative for San Francisco Bay, the Gabilan Foundation, and the Rintels Charitable Trust. The use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by PRBO Conservation Science or the U.S. Government.

REFERENCES

- Brown S., Hickey C., Harrington B. & Gill R. (eds) 2001. The U.S. Shorebird Conservation Plan. Manomet Center for Conservation Sciences, Manomet, MA.
- Carpelan L.H. 1957. Hydrobiology of the Alviso Salt Ponds. *Ecology* 38: 375–390.
- Christensen R. 1997. Log-linear models and logistic regression. Springer-Verlag, New York.
- Cody M.L. 1985. An introduction to habitat selection in birds. In: Cody M.L. (ed.) *Habitat selection in birds*. Academic Press Inc., San Diego, CA.
- COE. 2003. Napa River salt marsh restoration project: feasibility report. Army Corps of Engineers.
- De Solla S.R., Bonduriansky R. & Brooks R.J. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. *J. Anim. Ecol.* 68: 221–234.
- Diggle P.J., Liang K.Y. & Zeger S.L. 1994. *Analysis of longitudinal data*. Clarendon Press, Oxford.
- Dodge W.E. & Steiner A.J. 1986. XYLOG: A Computer Program for Field Processing Locations of Radio-tagged Wildlife. USFWS, Technical Report No. 4, Washington, DC.
- Dodge W.E., Wilkie D.S. & Steiner A.J. 1986. UTMEL: A laptop computer program for location of telemetry “finds” using Loran-C. Massachusetts Cooperative Research Unit, USFWS, Amherst, MA.
- Drake K.R., Thompson J.E., Drake K.L. & Zonick C. 2001. Movements, habitat use, and survival of nonbreeding Piping Plovers. *Condor* 103: 259–267.
- Evers D.C., Lane O.P., Savoy L. & Goodale W. 2004. Assessing the impacts of methylmercury on piscivorous wildlife using a wildlife criterion value based on the Common Loon, 1998–2003. Gorman (ME): Biodiversity Research Institute. Report no. BRI 2004–05.
- Feeney L.R. 1991. Snowy Plovers and their habitat at the Baumberg area and Oliver salt ponds Hayward, California, March 1989 through May 1990. Report prepared for the City of Hayward.
- Gill, R.E., Jr. 1977. Breeding avifauna of the south San Francisco Bay estuary. *Western Birds* 8: 1–12.
- Goals Project. 1999. Baylands ecosystem habitat goals. A report of habitat recommendations prepared by the San Francisco Bay Area Wetlands Ecosystem Goals Project. USEPA, San Francisco and San Francisco Bay Regional Water Quality Control Board, Oakland, CA.
- Grinnell J. & Wythe M.W. 1927. Directory to the bird-life of the San Francisco Bay region. *Pacific Coast Avifauna* 18.
- Hamilton R.B. 1975. Comparative behavior of the American Avocet and the Black-necked Stilt (Recurvirostridae). *Ornithol. Monogr.* 17.
- Harvey T.E., Miller K.J., Hothem R.L., Rauzon M.J., Page G.W. & Keck R.A. 1992. Status and trends report on wildlife of the San Francisco Estuary. USFWS report for the San Francisco Estuary Project. USEPA, San Francisco, CA.
- Hickey C., Shuford W.D., Page G.W. & Warnock S. 2003. The Southern Pacific Shorebird Conservation Plan: A strategy for supporting California's Central Valley and coastal shorebird populations. PRBO Conservation Science, Stinson Beach, CA.
- Hintze J.L. 1998. NCSS 2000. NCSS, Kaysville, Utah.
- Hoglund J. & Robertson J.G.M. 1990. Spacing of leks in relation to female home ranges, habitat requirements and male attractiveness in the great snipe (*Gallinago media*). *Behav. Ecol. Sociobiol.* 26: 173–180.
- Hooge P.N. & Eichenlaub B. 1997. Animal movement extension to arcview. ver. 1.1. Alaska Science Center – Biological Science Office, USGS, Anchorage, AK.
- Hooge P.N., Eichenlaub W.M. & Solomon E.K. 2001. Using GIS to analyze animal movements in the marine environment. In: Kruse G.H., Bez N., Booth A., Dorn M.W., Hills S., Lipcius R.N., Pelletier D., Roy C., Smith S.J. & Witherell D. (eds) *Spatial Processes and Management of Marine Populations*. Alaska Sea Grant College Program, Anchorage, AK.
- Horne J.S. & Garton E.O. 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. *J. Wildl. Manage.* 70: 641–648.
- Hudgins J.E., Storm G.L. & Wakeley J.S. 1985. Local movements and diurnal habitat selection by male American Woodcock in Pennsylvania. *J. Wildl. Manage.* 49: 614–619.
- Hui C.A., Takekawa J.Y. & Warnock S.E. 2001. Contaminant profiles of two species of shorebirds foraging together at two neighboring sites in south San Francisco Bay, California. *Environ. Monit. Assess.* 71: 107–121.
- Jackson B.J.S. & Jackson J.A. 2000. Killdeer (*Charadrius vociferus*). In: Poole A. & Gill F. (eds) *The birds of North America*, No. 517. Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- Johnson D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65–71.
- Kenward R.E. & Hodder K.H. 1996. Ranges V: An analysis system for biological location data.
- Keppie D.M. & Whiting R.M. 1994. American Woodcock (*Scolopax minor*). In: Poole A. & Gill F. (eds) *The birds of North America*, No. 100. Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- Larsson B.C. 2000. Invertebrates: Franciscan Brine Shrimp. In: Olofson P. (ed.) *Baylands ecosystem species and community profiles: life histories and environmental requirements of key plants, fish and*

- wildlife. Prepared by the San Francisco Bay Area Wetlands Ecosystem Goals Project. San Francisco Bay Regional Water Quality Control Board, Oakland, CA.
- Life Science Inc. 2003. South Bay Salt Ponds Initial Stewardship Plan. Woodland, CA.
- Maffei W.A. 2000. Invertebrates: Brine flies. In: Olofson P. (ed.) Baylands ecosystem species and community profiles: life histories and environmental requirements of key plants, fish and wildlife. Prepared by the San Francisco Bay Area Wetlands Ecosystem Goals Project. San Francisco Bay Regional Water Quality Control Board, Oakland, CA.
- Masero J.A. & 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.
- Masero J.A. 2003. Assessing alternative anthropogenic habitats for conserving waterbirds: salinas as buffer areas against the impact of natural habitat loss for shorebirds. *Biodivers. Conserv.* 12: 1157–1173.
- McCloskey J.T. & Thompson J.E. 2000. Sex-related differences in migration chronology and winter habitat use of Common Snipe. *Wilson Bull.* 112: 143–148.
- Myers J.P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Can. J. Zool.* 59: 1527–1534.
- Ohlendorf H.M., Hothem R.L. & Welsh D. 1989. Nest success, cause-specific nest failure, and hatchability of aquatic birds at selenium-contaminated Kesterson Reservoir and a reference site. *Condor* 91: 787–796.
- Otis D.L. & White G.C. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *J. Wildl. Manage.* 63: 1039–1044.
- Page G.W. & Gill R.E., Jr. 1994. Shorebirds in western North America: late 1800s to late 1900s. *Studies Avian Biol.* 15: 147–160.
- Plissner J.H., Haig S.M. & Oring L.W. 1999. Within- and between-year dispersal of American Avocets among multiple western Great Basin wetlands. *Wilson Bull.* 111: 314–320.
- Plissner J.H., Haig S.M. & Oring L.W. 2000a. Post-breeding movements of American Avocets and implications for wetland connectivity in the western Great Basin. *Auk* 117: 290–298.
- Plissner J.H., Oring L.W. & Haig S.M. 2000b. Space use of Killdeer at a Great Basin breeding area. *J. Wildl. Manage.* 64: 421–429.
- Pulliam H.R. & Danielson B.J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am. Nat.* 137: S50–S66.
- Reed J.M., Elphick C.S. & Oring L.W. 1998. Life-history and viability analysis of the endangered Hawaiian Stilt. *Biol. Conserv.* 84: 35–45.
- Reed J.M., Oring L.W. & Silbernagle M. 1994. Meta-population dynamics and conservation of the endangered Hawaiian Stilt (*Himantopus mexicanus knudseni*). *Trans. Western Section Wildl. Soc.* 30: 7–14.
- Rigney, M. & Rigney T. 1981. A breeding bird survey of the south San Francisco Bay salt pond levee system 1981. Report by members of the South Bay Institute of Avian Studies for the San Francisco Bay National Wildlife Refuge, Newark, CA.
- Rintoul C., Warnock N., Page G.W. & Hanson J.T. 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. & Oring L.W. 1996. Long-distance movements by American Avocets and Black-necked Stilts. *J. Field Ornithol.* 67: 307–320.
- Robinson J.A., Reed J.M., Skorupa J.P. & Oring L.W. 1999. Black-necked Stilt (*Himantopus mexicanus*). In: Poole A. & Gill F. (eds) *The birds of North America*, No. 449. The Birds of North America, Inc., Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- Sanzenbacher P.M. & Haig S.M. 2002. Residency and movement patterns of wintering Dunlin in the Willamette Valley of Oregon. *Condor* 104: 271–280.
- SAS Institute Inc. 1999. SAS OnlineDoc Version 8. SAS Institute Inc., Cary, NC.
- Seaman D.E., Millsbaugh J.J., Kernohan B.J., Brundige G.C., Raedeke K.J. & Gitzen R.A. 1999. Effects of sample size on kernel home range estimates. *J. Wildl. Manage.* 63: 739–747.
- Seaman D.E. & Powell R.A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77: 2075–2085.
- SFEI. 1998. Bay Area EcoAtlas Narrative Documentation, EcoAtlas beta release, version 1.5b4. San Francisco Estuary Institute, Oakland, CA.
- Siegel S.W. & Bachand P.A.M. 2002. Feasibility analysis of South Bay salt pond restoration, San Francisco Estuary, California. *Wetlands and Water Resources*, San Rafael, CA.
- Steere J.T. & Schaefer N. 2001. Restoring the Estuary: Implementation Strategy of the San Francisco Bay Joint Venture. San Francisco Bay Joint Venture, Oakland, CA.
- Stralberg D., Warnock N., Nur N., Spautz H. & Page G.W. 2005. Building a habitat conversion model for San Francisco bay wetlands: a multi-species approach for integrating GIS and field data. USDA Forest Service Gen. Tech. Rep. PSW-GTR-191.
- Strong C.M., Spear L.B., Ryan T.P. & Dakin R.E. 2004. Forster's Tern, Caspian Tern, and California Gull colonies in the San Francisco Bay: habitat use, numbers, and trends, 1982–2003. *Waterbirds* 27: 411–423.

- Swihart R.K. & Slade N.A. 1997. On testing for independence of animal movements. *J. Agric. Biol. Environ. Stat.* 2: 48–63.
- Takekawa J.Y., Warnock N., Martinelli G.M., Miles A.K. & Tsao D.C. 2002. Waterbird use of bayland wetlands in the San Francisco Bay Estuary: movements of Long-billed Dowitchers (*Limnodromus scolopaceus*) during the winter. *Waterbirds* 25: 93–105.
- Takekawa J.Y., Miles A.K., Schoellhamer D.H., Athearn N.D., Saiki M.K., Duffy W.D., Kleinschmidt S., Shellenbarger G.G. & Jannusch C.A. 2006. Trophic structure and avian communities across a salinity gradient in evaporation ponds of the San Francisco Bay estuary. *Hydrobiologia* 567: 307–327.
- Walters J.R. 1998. The ecological basis of avian sensitivity to habitat fragmentation. In: Marzaluff J.M. & Sallabanks R. (eds) *Avian conservation*. Island Press, Washington, DC.
- Warnock N. & Bishop M.A. 1998. Spring stopover ecology of migrant Western Sandpipers. *Condor* 100: 456–467.
- Warnock N. & Takekawa J.Y. 2003. Use of radio telemetry in studies of shorebirds: past contributions and future directions. *Wader Study Group Bull.* 100: 138–150.
- Warnock N. & Warnock S.E. 1993. Attachment of radio-transmitters to sandpipers: review and methods. *Wader Study Group Bull.* 70: 28–30.
- Warnock N., Page G.W., Ruhlen T.D., Nur N., Takekawa J.Y. & 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: 75–92.
- Warnock N., Page G.W. & Stenzel L.E. 1995. Non-migratory movements of Dunlins on their California wintering grounds. *Wilson Bull.* 107: 131–139.
- Warnock S.E., and Takekawa J.Y. 1995. Habitat preferences of wintering shorebirds in a temporally changing environment: Western Sandpipers in the San Francisco Bay Estuary. *Auk* 112: 920–930.
- Warnock S.E. & 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.
- Wiens J.A. 1994. Habitat fragmentation: island v landscape perspectives on bird conservation. *Ibis* 137: S97–S104.
- Wiens J.A. 1996. Wildlife in patchy environments: metapopulations, mosaics & management. In: McCullough D.R. (ed.) *Metapopulations and Wildlife Conservation*: 53–84. Island Press, Washington DC.
- Williams M.L., Hothem R.L. & Ohlendorf H.M. 1989. Recruitment failure in American Avocets and Black-necked Stilts nesting at Kesterson Reservoir, California, 1984–1985. *Condor* 91: 797–802.
- Worton B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168.
- Worton B.J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *J. Wildl. Manage.* 59: 794–800.
- Zar J.H. 1999. *Biostatistical analysis*. Fourth ed. Prentice Hall, Upper Saddle River, NJ.

SAMENVATTING

Om te onderzoeken hoe de Amerikaanse Steltkluit *Himantopus mexicanus* het snel veranderende landschap van de Baai van San Francisco (VS) gebruikt werden 59 vogels van een kleine radiozender voorzien en gedurende vier maanden gevolgd. De gemiddelde home range bedroeg 283,5 ha, zonder verschil tussen de seksen of tussen het noordelijke en zuidelijke deel van de baai. Gedurende de studieperiode verplaatsten de vogels zich gemiddeld 4,5 km. Individuen hielden zich meestal op in een of meerdere kerngebieden. De totale omvang van de home range nam toe met het aantal benutte kerngebieden. Vogels die meerdere kerngebieden benutten bleken overwegend te broeden op sterk begroeide kwelders om na het uitkomen van de eieren, of het mislukken van het nest, te verhuizen naar zoutpannen. Uit vergelijking tussen het aanbod van habitattypes en de tijdsbesteding van de steltkluten bleek een sterke voorkeur voor zoutpannen te bestaan. De oorzaak voor deze voorkeur is mogelijk een lager aanbod aan ongewervelde prooien in de meer natuurlijke getijdengebieden. De auteurs bevelen daarom enige terughoudendheid aan in de omvorming van zoutpannen tot getijdengebied, een beheersmaatregel waar tegenwoordig veel aandacht naar uitgaat. Steltkluten, en mogelijk andere steltlopers zouden kunnen profiteren van het behoud van ondiepe zoutpannen waarin de waterdiepte goed kan worden geregeld. (YIV)

Corresponding editor: Yvonne I. Verkuil

Received 2 February 2006; accepted 15 September 2006