SPACE USE, MIGRATORY CONNECTIVITY, AND POPULATION SEGREGATION AMONG WILLETS BREEDING IN THE WESTERN GREAT BASIN

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Abstract. Western Willets (Catoptrophorus semipalmatus inornatus) were banded (n = 146 breeding adults and chicks) and radio-marked (n = 68 adults) at three western Great Basin wetland complexes to determine inter- and intraseasonal space use and movement patterns (primarily in 1998 and 1999). Birds were then tracked to overwintering sites where migratory connectivity and local movements were documented. Willets arrived synchronously at breeding sites during mid-April and spent less than 12 weeks in the Great Basin. There were no movements to other sites in the Great Basin during the breeding or post-breeding season. However, most breeding birds moved locally on a daily basis from upland nest sites to wetland foraging sites. The mean distance breeding birds were detected from nests did not differ between sexes or between members of a pair, although these distances were greater among postbreeding than breeding birds. Home-range estimates did not differ significantly between paired males and females during breeding or postbreeding. However, female home ranges were larger following breeding than during breeding. Shortly after chicks fledged, adult Willets left the Great Basin for locations primarily at coastal and estuarine sites in the San Francisco Bay area. Limited data revealed little among-site movements once Willets arrived at the coast, and birds appeared to be site faithful in subsequent winters. Winter sites of western Great Basin Willets differed from those used by birds from other areas in the subspecies' range, suggesting another subspecies or distinct population segment may exist. This study illustrates the importance of understanding movements and space use throughout the annual cycle in conservation planning.

Key words: annual cycle, Catoptrophorus semipalmatus inornatus, connectivity, dispersal, Great Basin, home range, Willet.

Uso del Espacio, Conectividad Migratoria y Segregación Poblacional entre Catoptrophorus semipalmatus que se Reproducen en el Great Basin Occidental

Resumen. Un total de 146 individuos reproductivos y polluelos de Catoptrophorus semipalmatus inornatus fueron anillados y 68 marcados con radio transmisores en tres complejos de humedales del Great Basin occidental para determinar patrones inter- e intraestacionales en el uso del espacio y los movimientos, principalmente en 1998 y 1999. Las aves fueron seguidas mediante radio telemetría hasta sus áreas de invernada, donde se documentaron la conectividad migratoria y los movimientos locales. Las aves arribaron sincrónicamente a sus sitios reproductivos a mediados de abril, donde permanecieron menos de 12 semanas. No hubo movimientos hacia otros sitios del Great Basin durante la estación reproductiva o post-reproductiva. Sin embargo, muchas aves se movieron a diario localmente desde sitios de anidación en zonas altas hasta sitios de forrajeo en humedales. La distancia media entre las aves y sus nidos no difirió entre sexos ni entre miembros de una pareja, aunque estas distancias fueron mayores entre aves post-reproductivas que entre aves que estaban reproductándose. Los rangos de hogar no difirieron significativamente entre machos y hembras de una misma pareja durante o después de la reproducción, pero los de las hembras fueron mayores luego del período reproductivo. Poco después de que los polluelos emplumaron, los adultos abandonaron el Great Basin principalmente hacia sitios costeros o estuaires de la Bahía de San Francisco. Una vez que las aves llegaron a la costa, se movieron poco entre sitios, y los individuos parecieron ser fieles a sus sitios en invernios subsiguientes. Los sitios de invernio de C. s. inornatus en el Great Basin occidental difirieron de aquellos usados por aves de otras áreas del rango de esta subespecie, sugiriendo que otra subespecie o una sección poblacional distinta podría existir. Este estudio ilustra la impor-
INTRODUCTION
The study of avian movement is deceptively challenging. In actuality, much of the avian literature pertaining to movement describes site fidelity. That is, returns of chicks and adults are recorded but often ornithologists do not search additional areas to determine where birds have moved within or between seasons or years. Constraints to studying avian movement are numerous and restrict the utility of even the most recent technology (Webster et al. 2002). For example, satellite transmitters, the most effective means of tracking movements, are only available for birds weighing more than 450 g. Further, the scope of study needed to track even the simplest movements can be prohibitive (Haig et al. 1998).

Documenting seasonal and annual movements and space use by individual birds is imperative for understanding temporal and spatial habitat connectivity (Coulter and Frederick 1997, Haig et al. 1998). In migratory birds, connectivity includes the extent to which individuals from the same breeding area migrate to the same non-breeding area and the reverse (Webster et al. 2002). Even similar species may use local, regional, and continental sites and habitats in very different ways (Naugle et al. 1999). Thus, it is important to understand species-specific patterns of habitat use over time prior to identifying sites of conservation importance for a species or devising comprehensive conservation plans covering a regional avifauna.

The Great Basin of North America is a region characterized by desert habitats with few, but significant, wetlands. Correspondingly, hundreds of thousands of waterbirds use these wetlands during breeding and migration (Warnock et al. 1998, Oring et al. 2000). Species cope with the changes in water availability and quality that occur within and among seasons in various ways. American Avocets (Recurvirostra americana) breed primarily at freshwater or brackish ponds, yet move hundreds of kilometers to oligosaline or hypersaline postbreeding foraging sites, functionally connecting discrete sites within a large landscape (Plissner et al. 1999, Plissner, Haig and Oring 2000). In contrast, Killdeer (Charadrius vociferus) remain in local areas (<1 km²) adjacent to freshwater for much of the annual cycle (Plissner, Oring, and Haig 2000). The western Willet (Catoptrophorus semipalmatus inornatus) is another common shorebird that breeds near Great Basin and prairie wetlands (Lowther et al. 2001). In comparison to eastern Willets (C. s. semipalmatus), there are few life history data on Great Basin Willets (although see Mendenhall 1970) or western Willets in general, as they can be difficult to observe, nests are cryptic, and adults are difficult to trap. They are socially monogamous, biparental, territorial breeders that nest at upland sites adjacent to wetlands (Lowther et al. 2001).

In this study, we examined space use and movements among breeding, postbreeding, and wintering Willets that bred in the western Great Basin and wintered on the Pacific Coast of North America. Our objectives were to investigate the scale of local space use and patterns of migratory connectivity among western Great Basin-breeding Willets. We sought to identify land resources that may limit Willet populations and will be useful in regional conservation planning.

METHODS
STUDY AREAS
Breeding Willets were opportunistically banded in 1996–1997 and intensively studied in 1998 and 1999 in the western Great Basin, an arid region characterized by high desert habitats with dispersed saline and freshwater wetlands (Reed et al. 1997). Annual precipitation in this area is low but variable (averaging 10–30 cm per year; Engilis and Reid 1997). Consequently, high rates of evapotranspiration and agricultural demands for water from lakes and stream inflows result in large annual and within-year fluctuation of water levels (Neel and Henry 1997). During the 1998 breeding season, Willets were observed at three wetland complexes in the western Great Basin (Fig. 1). Areas used by Willets at Summer Lake (42°54’N, 120°47’W; Lake Co., Oregon), Goose Lake (42°9’N, 120°24’W; Lake Co., Oregon), and Honey Lake (40°8’N, 120°14’W; Lassen Co., California) were all characterized by small freshwater ponds and stream inflows (e.g., Summer Lake Wildlife Area, Lake County airport, and J. Dow Sr. Wetlands, respectively) ad-
adjacent to large brackish to saline lakes. In summer 1999, breeding-ground observations were restricted to the Goose Lake area. Postbreeding areas were searched along the entire California coast from southern Oregon to Mexico in 1998.

**breeding season**

Weekly censuses of Willets were carried out from 10 April–15 July 1998 at wetland complexes surrounding and including Summer Lake, Goose Lake, and Honey Lake. In 1999, similar weekly censuses were carried out in the Goose Lake area. The number of adults was recorded to provide data on population size, arrival and departure dates, and phenology of breeding. Cryptic nests, often hidden at the base of sagebrush (Artemisia spp.) or rabbitbrush (Chrysothamnus spp.), were identified via ground searches using a drag rope and observations of incubation exchanges. Observers verified hatching date and nest success based on periodic nest visits, flotation stage of eggs, and the presence of eggshell fragments in empty nests. Adult Willets were captured for individual identification by dropping mist nets over them as they incubated. Attempts were made to capture breeding pairs, but in some cases only one individual at a nest was marked. Chicks were captured opportunistically by hand and banded. Following guidelines approved by the American Ornithologists’ Union (Gaunt and Oring 1997), adults were sexed using blood samples (0.2 mL) collected from the brachial vein with a 27 gauge needle. Blood was stored in a cryogenic tube containing a buffer solution (100 mM Tris HCl pH 8.0, 100 mM EDTA pH 8.0, 10 mM NaCl, 0.5% SDS) until shipment to Celera AgGen (Davis, CA) for molecular sexing.

All trapped birds were given unique combinations of UV-stable Darvic color bands and a U.S. Fish and Wildlife Service aluminum leg band placed on the tibiotarsus. Adults were fitted with radio-transmitters (model PD-2sp, 16–24 week lifespan, 4.5 g; Holohil Systems Ltd., Ontario, Canada) attached with epoxy to aluminum bands and coated in a colored plastic that identified the banding site. Various options for safe placement of radios on large shorebirds were tested at the University of Nevada Shorebird Facility and in the field prior to attachment. Observations of color-marked birds, including those whose radios no longer functioned, were recorded during weekly censuses, nest searches, and general observations.

In 1998, the study focused on broad-scale movement patterns in the western Great Basin. Thus, radio-marked birds were tracked at Summer Lake, Goose Lake, and Honey Lake from 1 May–20 July. Telemetry surveys were conducted 2–3 times daily for the period that birds remained in the region. Surveys occurred at all times of day, with most observations collected during daylight hours. Ground telemetry, using a handheld Yagi antenna, was carried out from multiple vantage points chosen to maximize coverage of each site to determine the presence or absence of radio-marked individuals. Weekly flights were conducted at the three focal sites in 1998. Using a Piper Super Cub with wing-mounted Yagi antennae, the presence of radio signals was checked at each breeding site, along the path between breeding wetlands, and at other major wetlands in the region, such as Lake Abert, Oregon; Surprise Valley, California; Carson Lake, Nevada; and Klamath Lake, Oregon and California. Flight paths included the entire perimeter of each lake as well as adjacent wetlands.

In 1999, the study examined local movements for the dense nesting assemblage of Willets at the Lake County airport adjacent to the north end of Goose Lake. Observers determined locations of radio-marked birds based on signal bearings from two or more sites collected from radio-tracking trucks. Geographic coordinates of locations were later derived with software program LOAS (Ecological Software Solutions 2001). Consecutive observations of an individual were separated by a minimum of 1 hr and most (96%, 1445 of 1506) observations were separated by $\geq$3 hr (median = 5.9 hr, mean = 13.5 hr). During incubation, the time between most observations was greater (median = 7.7 hr, mean = 13.4 hr). In tracking individuals over time there is an inherent degree of autocorrelation of observations (De Solla et al. 1999, Otis and White 1999). In our study, the potential for autocorrelation was greatest in cases when the duration of an incubation bout was greater than the time between consecutive locations of an individual. However, the fact that our tracking efforts were systematic with equal effort across all birds alleviated this potential bias.
WINTER SEASON
In 1998, weekly flights to identify locations of postbreeding birds were carried out in the San Francisco Bay area (north to Tomales Bay, Marin Co., California) from mid-July through August, and on 26 November. Two flights in late July and early August were also flown from Goose Lake directly west to the Oregon-California border and then south along the coast (including Humboldt Bay, Humboldt Co., California) to San Francisco Bay. In early October, a 2-day flight was conducted from Goose Lake directly west to the Pacific Coast and south to San Diego. Weekly ground telemetry surveys of radio-marked birds were also carried out in the San Francisco Bay National Wildlife Refuge area from 30 September through 1 December.

Postbreeding aerial surveys in 1999 included a 14 July flight from Goose Lake to Humboldt Bay via the Klamath Basin and weekly flights of the San Francisco Bay area from mid-July through mid-October. Three additional flights were carried out from San Francisco Bay to Humboldt Bay in mid-September through early October. Throughout the study, other biologists and local birdwatchers were contacted in the Great Basin and along the Pacific coast for information regarding marked birds.

STATISTICAL ANALYSES
Breeding-season data were partitioned into two periods: the breeding period was defined as the time from clutch initiation to hatching (approximately 24 days). The period following hatching or nest failure, but prior to migration, was designated postbreeding. All comparisons were of adults where both members of a breeding pair were monitored. We calculated the mean and maximum distances that individuals were detected from nest sites. The mean ± SD number of locations recorded per individual used in distance analyses was 25.9 ± 13.1. Because such variation may influence estimates of movement, we examined potential bias due to sample size differences by plotting and regressing movement data (mean, maximum distance) on number of locations per individual. Slopes were not significant for any mean or maximum distance estimate. Thus, we included data for all individuals, regardless of sample size.

Home-range estimates from Goose Lake were calculated using a fixed kernel method (Worton 1989). Previous studies have established that fixed kernel estimators provide reliable results with less bias than other home-range procedures (Seamann and Powell 1996, Swihart and Slade 1997). We calculated home-range size with KERNELHR software (Seamann et al. 1998) using the least-squares cross-validation method to determine smoothing parameters (bandwidth) and automatic selection of grid cell size (Worton 1995). Home-range estimates described the 95% utilization distribution for each individual. In certain cases, the distribution of observations (e.g., highly clumped locations) can result in erroneous estimates of home-range size with the kernel method. Thus, based on evaluation of the home-range volume parameter, we eliminated from further analyses birds whose volume differed from 1 by more than 0.02 (15% of birds sampled). Assessment of scatterplots and regression analyses indicated that sample size biases were avoided by inclusion of birds with at least 10 locations for a given sampling period. The mean number of locations recorded per individual used in home-range analyses was 27.9 ± 11.7.

Paired t-tests were used to examine differences in mean and maximum distance from nest site and home-range size among individuals within a breeding pair. Separate tests were conducted for breeding and postbreeding periods. Maximum distance from nest and home-range data required log transformation to meet assumptions of normality.

Repeated measures ANOVA was used to compare movements and space-use patterns between sexes across breeding periods for all paired birds. We conducted separate tests for each response variable (i.e., mean and maximum distance from nest, home-range size), with sex, breeding period, and the interaction term (sex × breeding period) included in each analysis. This approach required omission of individuals lacking data for breeding or postbreeding periods. In addition, we removed all locations within 100 m of the nest site during the breeding period to calculate mean distances birds were detected from nest sites. This accounted for all cases in which an individual was potentially incubating, eliminating bias in comparisons between breeding and postbreeding periods. All data were log transformed prior to repeated measures ANOVA to meet assumptions of normality. Summary data are presented as means ± SD, with a P-value ≤ 0.05 considered significant.
FIGURE 1. Wetland systems where breeding Willets were banded and monitored in the western Great Basin, and winter locations of resightings. Filled symbols represent breeding sites where Willets were marked \( n = 146 \), primarily Summer Lake, Goose Lake, and Honey Lake; unfilled symbols identify banding origin of birds resighted on wintering grounds \( n = 40 \) individuals.

RESULTS

BREEDING SEASON

Return patterns. Overall, 146 Willets (68 radio-marked adults, 1 additional banded adult, and 77 chicks) were marked during this study. Of these, six adults and 62 juveniles were marked in the pilot study years of 1996 and 1997 at the three focal areas and Lake Abert (Fig. 1). The sex ratio among 50 of 68 adults radio-tagged, banded, and bled in 1998 and 1999 was 26:24 (males: females). All breeding birds resighted \( n = 16 \) during the breeding season in subsequent years were seen in the breeding area in which they had been banded, despite searches among other Willet breeding sites in the region. Breeding site fidelity varied among study sites: five of six adults (83%) banded at Honey Lake in 1998 returned the following year to breed, and 5 of 15 (33%) 1998 birds returned to Goose Lake in 1999. Three of four adults (75%) banded at Summer Lake in 1997 returned in 1998, and 3 of 15 (20%) adults banded in 1998 were resighted in 1999, although resight efforts were minimal at Summer Lake in 1999. Among all western Great Basin adults resighted, five were males, one was a female, and 10 were not sexed. Four juveniles were resighted at natal sites two years after hatching, even though none were resighted one year after hatching.

Phenology. Exact spring arrival dates were not possible to attain without attaching radios to birds at winter sites. However, survey data from all three breeding sites indicated most Willets arrived in the Great Basin in mid-April. For example, the first Willet was observed at Honey Lake on 14 April 1998 and 13 April 1999, and at Goose Lake on 15 April 1998. Often a single or few birds were observed on one or two days in mid-April and then numbers increased dramatically over the next few days. Nest initiation dates were fairly synchronous among sites and most often occurred in mid-May (Table 1). Both males and females incubated nests, although the periodicity of incubation exchange and relative time investment by each sex remains unknown. Hatching occurred on average 24.0 \( \pm \) 3.5 days \( n = 34 \) nests) after the fourth egg was laid. Overall, 44% (37 of 84) of nests hatched chicks and 1.6 \( \pm \) 1.9 chicks hatched per four-egg clutch laid (Table 1). Among nests where one or more chicks hatched, mean number of chicks hatched per nest was 3.7 \( \pm \) 0.7. Willet within-year tenure in the Great Basin varied by sex and whether chicks hatched (Table 2). In general, females de-

<table>
<thead>
<tr>
<th>Location/year</th>
<th>Nests</th>
<th>Nest initiation date</th>
<th>% clutches hatched</th>
<th>Chicks hatched per nest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer Lake 1998</td>
<td>27</td>
<td>12 May ± 11</td>
<td>41</td>
<td>1.5 ± 1.8</td>
</tr>
<tr>
<td>Honey Lake 1998</td>
<td>9</td>
<td>10 May ± 8</td>
<td>22</td>
<td>0.9 ± 1.8</td>
</tr>
<tr>
<td>Goose Lake 1998</td>
<td>22</td>
<td>11 May ± 9</td>
<td>50</td>
<td>2.0 ± 2.0</td>
</tr>
<tr>
<td>Goose Lake 1999</td>
<td>26</td>
<td>14 May ± 5</td>
<td>50</td>
<td>1.7 ± 1.9</td>
</tr>
</tbody>
</table>
parted the Great Basin prior to males, and birds with chicks remained in the Great Basin longer than those whose nests had failed.

*Within-season movements.* Despite intensive ground and air searches throughout the western Great Basin, Willets were only observed in the wetland complexes in which they bred (Fig. 2). At Goose Lake in 1999, birds moved from upland nests to wetland foraging sites up to 13 km away during incubation recesses, although most movements were within 5 km. The average distance paired breeders were observed from nest sites during the breeding period was 713 ± 356 m for females and 665 ± 342 m for males. In comparison, during the postbreeding period females averaged 1562 ± 470 m and males 1696 ± 742 m from nest sites. There were no differences in distances moved among mates during the breeding (n = 14 pairs, t = 0.6, P = 0.6) or postbreeding periods (n = 13 pairs, t = -0.4, P = 0.7). Analyses of Willets with data across both breeding periods also indicated sexes did not differ in the mean distance observed from nest sites (Table 3). However, breeding period was a significant factor, as Willets remained closer to nests during the breeding period (mean distance from nest = 689 ± 344 m) than the postbreeding period (1609 ± 609 m; Table 3).

The maximum distance that paired birds were detected from nest sites during the breeding period averaged 4362 ± 3675 m for females and 3677 ± 3221 m for males; postbreeding females averaged 4605 ± 2818 m and postbreeding males 5192 ± 5252 m. There were no differences between mates for either the breeding (n = 14 pairs, t = 0.5, P

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**TABLE 2.** Mean (± SD in days) departure dates, and the number of days after chicks hatched (successful nests) or nests failed (failed nests) that radio-tagged Willets departed Goose and Summer Lakes, Oregon, in 1998 and 1999. Departure dates include birds whose chicks may have been lost after hatching.

<table>
<thead>
<tr>
<th>Lake</th>
<th>1998 Successful nests</th>
<th>1999 Successful nests</th>
<th>1999 Failed nests</th>
<th>1999 Failed nests</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Days</td>
<td>n</td>
<td>Days</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Departure</td>
<td>Departure</td>
</tr>
<tr>
<td>Summer Lake</td>
<td>2</td>
<td>7 July ± 17</td>
<td>5</td>
<td>18 ± 8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10 July ± 17</td>
<td>7</td>
<td>31 ± 9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4 July ± 14</td>
<td>15</td>
<td>29 ± 8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Overall*</td>
<td>Overall*</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>23</td>
<td>31 ± 9</td>
<td>15</td>
</tr>
</tbody>
</table>
|               |                        |                        | Includes unmarked radio-tagged birds.

FIGURE 2. Distances observed (mean ± SD) from nest sites within breeding (n = 14 pairs) and postbreeding (n = 13 pairs) seasons for paired male and female Willets at Goose Lake, Lake Co., Oregon, in 1999.
TABLE 3. Factors affecting estimates of mean and maximum distance from nest and home-range size of breeding Willets in 1999 at Goose Lake, Lake County, Oregon. Results reported are from repeated measures ANOVAs (using log-transformed data).

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Term</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean distance from nest (m)</td>
<td>Sex</td>
<td>1, 26</td>
<td>0.6</td>
<td>&gt;0.5</td>
</tr>
<tr>
<td></td>
<td>Breeding period</td>
<td>1, 26</td>
<td>28.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Sex X Breeding period</td>
<td>1, 26</td>
<td>0.7</td>
<td>&gt;0.4</td>
</tr>
<tr>
<td>Maximum distance from nest (m)</td>
<td>Sex</td>
<td>1, 26</td>
<td>0.6</td>
<td>&gt;0.2</td>
</tr>
<tr>
<td></td>
<td>Breeding period</td>
<td>1, 26</td>
<td>1.9</td>
<td>&gt;0.4</td>
</tr>
<tr>
<td></td>
<td>Sex X Breeding period</td>
<td>1, 26</td>
<td>0.1</td>
<td>&gt;0.8</td>
</tr>
<tr>
<td>Home range (ha)</td>
<td>Sex</td>
<td>1, 8</td>
<td>0.3</td>
<td>&gt;0.6</td>
</tr>
<tr>
<td></td>
<td>Breeding period</td>
<td>1, 8</td>
<td>0.6</td>
<td>&gt;0.4</td>
</tr>
<tr>
<td></td>
<td>Sex X Breeding period</td>
<td>1, 8</td>
<td>6.7</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

For paired birds with data in both breeding periods, there was no effect of sex or breeding period on the maximum distance birds were detected from nest sites (Table 3).

**Breeding home range.** Overall home-range size of Willets at Goose Lake during the 1999 breeding season averaged $167 \pm 145$ ha. The mean home-range size of breeding females and males was $112 \pm 66$ ha and $162 \pm 208$ ha respectively. During the postbreeding period, mean home-range size was $242 \pm 129$ ha for females and $153 \pm 134$ ha for males. There were no differences between mates during either breeding ($n = 9$ pairs, $t = -0.1, P = 0.9$) or postbreeding periods ($n = 9$ pairs, $t = 1.9, P = 0.1$). For paired birds with data across periods, there were no differences in home-range size between sexes or breeding periods (Table 3); however, female home ranges were significantly larger during postbreeding ($232 \pm 140$ ha) than breeding ($125 \pm 78$ ha; Table 3).

**Winter season.** Telemetry and resighting data suggested that Willets move from breeding sites in the western Great Basin to sites along the Pacific Coast without stopping at intermediate locations in the Great Basin, as no birds were recorded at sites other than breeding and coastal areas. During postbreeding periods in 1996–2001, 127 observations (83 telemetry, 44 visual) of 40 marked birds indicated that western Great Basin Willets spent the winter in coastal and estuarine habitats along the Pacific Coast south of the Oregon border (Fig. 1). Despite extensive searches along the Pacific coast, most birds (32 of 40) were found within 50 km of San Francisco Bay. Within one annual cycle, 34 breeding adults and 4 juveniles were observed on both breeding or natal sites and winter sites. These birds were not segregated at winter sites according to breeding site, sex, or age (postfledging vs. adult). In two separate cases, paired birds were observed in the same winter. In one case, the male wintered at Morro Bay and the female in San Francisco Bay (approximately 280 km apart). In a second case, both wintered in the San Francisco Bay area within several km of each other. Following arrival at winter sites, there was no movement out of a general area (e.g., San Francisco Bay) in a given year among any birds for which we had multiple observations ($n = 26$). Further, 80% (55 of 69) of movements occurred less than 10 km from the winter site where an individual was first observed. Among birds that moved, the mean distance observed from the initial winter site to other winter sites was $9.6 \pm 13.6$ birds ($n = 25$ birds), although four birds moved between 25 and 72 km after being at a single site for more than a month.

Willets were philopatric in subsequent winter seasons. Six adults were seen in the same winter locations for 2–3 years. Only one bird, a female, changed winter sites: she was observed at Tomales Bay in 1998 and Bodega Bay in 2000 (approximately 50 km apart). Of three juveniles later seen at winter sites, one bird from Lake Abert was seen in Santa Barbara from 1997–2000, a 1997 juvenile from Honey Lake was seen in San Francisco Bay in winter 2001 and fall 2001, and a 1998 Goose Lake juvenile was seen in Bodega Bay in May and September of 1999.

**Discussion.**

**Breeding space use.** Lack of movement among sites during the breeding and late-summer postbreeding season.
suggested that Willets did not connect habitats across a large scale as exhibited by other Great Basin shorebirds such as American Avocets (Plissner et al. 1999, Plissner, Haig, and Oring 2000). However, on a smaller scale, their daily movements connected upland sites with nearby wetlands. Killdeer home-range estimates from Honey Lake ranged from 1.5–7 ha (Plissner, Oring, and Haig 2000). Thus, space used by breeding Willets fell in the mid-range of that used by other shorebirds breeding in the Great Basin. Across the arid West, Willet home ranges were most similar to those found for Mountain Plovers (C. montanus) in Colorado, where Knopf and Ruppert (1996) found home ranges averaged 56.6 ha.

At each of three focal areas, Willets utilized separate feeding and nesting areas, although some foraging took place close to nest sites. A similar pattern was observed in Willets nesting in Alberta (Lowther et al. 2001) and Virginia (Howe 1982). However, Willets in North Dakota defended multipurpose territories (Ryan and Renken 1987). The distribution of nesting territories varied among sites in the western Great Basin. Nests were widely dispersed (i.e., hundreds to thousands of meters apart) at Summer Lake and Honey Lake; most nests at Goose Lake were found within a 65-ha area at the airport. Often these nests were close (some within 25 m of each other) and birds participated in joint alarm calling. Howe (1982) describes a similar situation in Virginia where he considered Willets to be semicolonial.

Patterns of within-season space use indicate conservation strategies for Willets should protect both nesting and foraging sites. Further, their sometimes semicolonial breeding suggests nearby resources are not limiting but may be clustered throughout the landscape. Lack of movement to other postbreeding, premigratory sites further points to a dependence on the few breeding sites used. Thus, these specific sites warrant protection.

Home-range and distance estimates indicated that female Willets ranged farther than males once chicks hatched. Their early departure also suggested that males provided more parental care than females, at least after chicks hatched. Similarly, in eastern Willets, breeding females deserted broods two to three weeks after they hatched (Howe 1982) and in Alberta males remained with broods longer than females in 87% of cases (n = 52, Lowther et al. 2001). This pattern has been demonstrated in other monogamous shorebirds where there was a tendency toward greater male parental care (Oring 1982). Female emancipation from some chick-rearing duties provides time to prospect for new mates or territories for the subsequent breeding season (Reed et al. 1999) or depart early for the wintering grounds.

MIGRATORY CONNECTIVITY

Western Willets exhibit varying patterns of migratory connectivity depending on the scale examined. Following the paradigm proposed by Webster et al. (2002), there is weak connectivity between breeding and winter sites at the subspecies scale: western Great Basin Willets appear to winter on the California coast, whereas Willets breeding in Alberta are reported farther south in Mexico and Costa Rica (Lowther et al. 2001, C. L. Gratto-Trevor, pers. comm.). On their northward migration, western Willets move up the Mississippi Valley where they may be joined by birds that winter on the Atlantic coast (Lowther et al. 2001). However, it is clear that western Great Basin birds do not follow this pathway. Given these differences and the high site fidelity exhibited by Willets in breeding and winter seasons, there may be more than two subspecies or distinct population segments. Future genetic investigations will resolve this issue.

Seasonal movement data suggest weak migratory connectivity among birds from individual western Great Basin sites and the San Francisco Bay area because birds from different breeding sites mix during the nonbreeding season. However, on a regional scale, there is strong connectivity between the western Great Basin and San Francisco Bay. That is, most individuals from the region move to the same nonbreeding area. This strong connection illustrates the importance of San Francisco Bay to western Great Basin Willets and points to the vulnerability of Great Basin Willets to current threats facing shorebird habitat in San Francisco Bay. This vulnerability may be buffered by birds that winter in other areas in California and by pairs not remaining together in winter. Regardless, it is clear that continued habitat loss or degradation along the California coast poses a serious threat to the viability of western Great Basin Willets.

Wintering Willets are site faithful to San Francisco Bay within and among years. Kelly and
Cogswell (1979) found that most Willets stayed in a localized (1000 m or less) part of San Francisco Bay for seven to nine months of the year. In this area, they moved from roost sites to feeding areas in response to tide, although Myers et al. (1979) found some Willets at Bodega Bay defended multipurpose territories. A few birds moved farther south along the coast as the winter progressed. Willets wintering in Florida also used foraging and roosting sites and were site faithful in winter (Gabbard et al. 2001).

Phenologically, Willets stay briefly at a breeding site and then migrate directly over the mountains to the Pacific Coast, primarily northern California, where they remain in the same area until spring migration. A previous winter Willet study corroborated this: marked individuals were absent from San Francisco Bay for a mean of only 91 days during spring and summer (Kelly and Cogswell 1979). Thus, Willets breeding in the western Great Basin are a primarily marine-associated population.

Given a relatively brief stay on Great Basin breeding grounds, an issue of interest is why the entire breeding population leaves the coastal wintering sites where they spend approximately nine months per year. Despite the fact that coastal marshes were at one time widely distributed along the California coast, there are no breeding records of Willets on or near the coast or in the Central Valley of California (D. Shuford, pers. comm.). Thus, the absence of western Willets breeding in coastal marshes directly contrasts with eastern Willets, which breed primarily in coastal marshes (Tomkins 1965, Howe 1982).

Explanations for the evolution of the breeding distribution of West Coast-wintering Willets fall into two categories: (1) migratory Western Willets from farther northeast in the subspecies' distribution colonized the Great Basin and continued their southwest migratory trajectory, wintering on the coast where the birds did not develop a sedentary life with coastal breeding; or (2) colonizers from the Great Basin attempted to breed at coastal and inland sites. Inland breeders were more successful and a genetic or cultural tendency to migrate to inland breeding sites dominated coastal breeders. Numerous factors may have contributed to greater success of inland breeders: lower levels of nest predation, reduced salt stress for chicks, or greater availability of food resources for chicks.

The key for some species to remain in the Great Basin for an extended period may be availability of food for which they have adapted foraging strategies. There is extremely high seasonal productivity of small invertebrates in Great Basin wetlands (Oring et al. 2000), a fact likely to foster high chick survival in much the same manner that high productivity in arctic environments fosters success of many migratory shorebird species. American Avocets spend months at hypersaline western Great Basin post-breeding feeding areas (e.g., Lake Abert, Mono Lake) foraging on abundant brine flies (adults, larvae, pupae; *Ephydra* spp.) and other small invertebrates (Boula 1985, Mahoney and Jehl 1985). Killdeer and some Long-billed Curlews (*Numenius americanus*) remain near wetlands to forage on terrestrial invertebrates (Plissner, Oring, and Haig 2000, L. W. Oring, unpubl. data). In contrast, Willets are not adapted to exploit aquatic invertebrates as avocets can and, while they forage on some terrestrial invertebrates, they are better adapted for generalist foraging (Lowther et al. 2001). Thus, adults may always have better foraging opportunities in coastal areas but must remain inland because of resources needed by chicks: freshwater and small invertebrates. Further, in a situation that may pertain to adult Willets, Leeman et al. (2001) suggest that early-returning Long-billed Curlews to Humboldt Bay forage on large prey with less disturbance from conspecifics and kleptoparasitism from gulls than later-arriving migrants. Chicks may remain in the Great Basin only until their bills have developed and they can forage more successfully at coastal sites that have a higher density and diversity of larger prey items than would be encountered in the Great Basin.

In this study, data collected throughout the annual cycle provide a multiscale perspective that illustrates relative inflexibility in Willet use of space and specific sites. This renders Willets vulnerable to changes in these resources. Comparative data from similar species (American Avocets and Killdeer) breeding in the same ecosystem provide another dimension that will be useful in conservation planning. In developing reasonable ecosystem conservation plans, benefits of acquiring detailed data for known individuals in multiple species will far outweigh difficulties in their collection.
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LITERATURE CITED


