

Breeding Stage Influences Space Use of Female American Avocets in San Francisco Bay, California

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Abstract.—Female American Avocets (*Recurvirostra americana*) were radio-marked (N = 15) and tracked in the South San Francisco Bay, California, to determine if space use varied by breeding stage. Visual observations were used to determine breeding stage (pre-incubation, incubation, brood-rearing, post-breeding) of marked avocets. Space use measurements (linear movements, home ranges, core areas, and average distance from nest) varied significantly among breeding stages. Space use was greatest for the post-breeding stage, followed by pre-incubation, incubation, and brood-rearing. Most avocet nests (93%) were located within their pre-incubation core area boundaries, whereas only 36% of nests were within post-breeding core areas. Distance between daily location and future nest sites decreased significantly as the number of days prior to incubation decreased, suggesting that avocets prospected future nest sites several weeks prior to nesting. These data indicate that breeding stage influences space use of female American Avocets and illustrates the importance of delineating breeding stages to better understand space use of avian species. *Received 7 September 2007, Accepted 15 February 2008.*

Key words.—American Avocet, breeding stage, home range, movements, *Recurvirostra americana*, San Francisco Bay, shorebird, space use, telemetry.

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Investigating factors that influence space use of avian species is valuable to understand how they use habitats, when those areas are important to their survival, and when populations may be at risk. Recent studies have demonstrated that breeding stages influence space use of avian species. Roth *et al.* (2004) found that Common Ravens (*Corvus corax*) remained closer to the nest during the incubation and nestling stages than in the pre-incubation period, and core areas were centered around nest sites and food sources. Home ranges and movements of Golden Eagles (*Aquila chrysaetos*) were larger during the non-breeding than breeding season (Marzluff *et al.* 1997). Willets (*Tringa semiplamata*) and Killdeer (*Charadrius vociferus*) remained closer to their nesting areas while breeding than in the post-breeding stage (Plissner *et al.* 2000a; Haig *et al.* 2002). Killdeer also moved greater distances during the non-breeding stages than during the nesting stage (Plissner *et al.* 2000a).

Previous studies of breeding stage and space use in shorebirds (Plissner *et al.* 2000a; Haig *et al.* 2002) grouped the brood-rearing and the post-breeding stages, leading to the assumption that there is no difference in space use between these distinct stages. Since shorebird species care for precocial chicks after hatching (Lack 1968), space use during brood-rearing may be different and should be treated as a distinct stage. To our knowledge, no study has examined space use within four breeding stages (pre-incubation, incubation, brood-rearing, and post-breeding), likely due to the logistical difficulties of capturing non-breeding birds and obtaining visual confirmation of each stage.

Wetland species, like the American Avocet (*Recurvirostra americana*), are often considered priorities for conservation and management due to their susceptibility to habitat degradation and loss (Frayser *et al.* 1983; Dahl 1990; Catallo 1993; Plissner *et al.* 2000a). The San Francisco Bay estuary, California is an

important region for wintering and breeding avocets (Rintoul *et al.* 2003). However, avocet populations in this estuary may be at risk due to environmental contaminants, exponential increases in potentially predaceous California Gull (*Larus californicus*) populations, and habitat conversion. In light of these changes to the San Francisco Bay, understanding space-use patterns would be beneficial in determining which areas avocets use and when they are most at risk during the annual cycle. Therefore, this study examined how space use of American Avocets varies across four stages of the annual cycle: pre-incubation, incubation, brood-rearing, and post-breeding.

STUDY AREA

San Francisco Bay (Fig. 1) is one of the largest estuaries on the Pacific coast of North America (Conomos 1979; Monroe and Kelly 1992). This study was conducted in the South San Francisco Bay, which is defined here as the region south of the San Mateo Bridge. Habitats in this region include tidal flats, sloughs, tidal marshes, salt evaporation ponds, and other wetlands (sewage and water treatment ponds, small seasonal wetlands). American Avocets were captured in two salt ponds (Ponds A8 and A16) and a tidal flat (Coyote Creek Lagoon; Fig. 1). Avocet populations in the San Francisco Bay estuary have been estimated at 23,200 and 4,300 individuals in the winter and spring, respectively (Stenzel *et al.* 2002). South Bay spring avocet numbers have been estimated at 2,800 (Rintoul *et al.* 2003).

METHODS

Capture and Radio Telemetry

Between 15-30 March 2005 and 16 February-16 March 2006, American Avocets were captured with rocket-nets (Dill and Thornberry 1950; Hill and Frederick 1997) and net launchers (Coda Enterprises, Mesa, Arizona) at two former salt ponds (A8 and A16) and a tidal lagoon (Coyote Creek Lagoon; Fig. 1). Female avocets were radio-marked as part of a larger study examining contaminant levels of birds in the San Francisco Bay (Ackerman *et al.* 2007a). The sex of avocets was determined from dimorphic bill characteristics (Hamilton 1975). Female avocets were fitted with radio-transmitters (Advanced Telemetry Systems, model A2470, Isanti, Minnesota) and UV-resistant Darvic™ color bands (A. C. Hughes LTD, Hampton Hill, UK). Transmitters were attached to U.S. Geological Survey leg bands with epoxy, and placed on each bird's tibiotarsus as described by Plissner *et al.* (2000b) and Haig *et al.* (2002). Total mass of the transmitter and bands was <4 g, or approximately 2% of the bird's mass (mean = 340 ± 2.2 g).

Avocets were tracked from truck-mounted null-peak telemetry systems (AVM Instrument Company, Livermore, CA). Ground-tracking routes were established

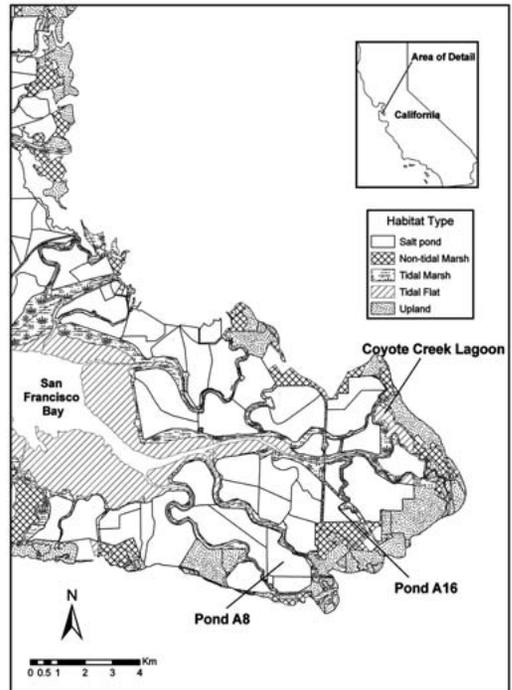


Figure 1. South San Francisco Bay, California, showing dominant habitat types and American Avocet capture locations in 2005 and 2006. Avocets were captured at two salt ponds (Ponds A8 and A16) and a tidal flat (Coyote Creek Lagoon).

throughout the study area, with equal effort across all birds to eliminate bias in tracking effort (e.g., Haig *et al.* 2002). Exceptions to the tracking schedule included inclement weather, adverse road conditions, and levee or road maintenance. Avocets were tracked during morning (the three h after sunrise), day (three h after sunrise to three h before sunset), evening (the three h before sunset), and night (all hours after sunset and before sunrise) intervals, as avocets are active both day and night (Dodd and Colwell 1998; Johnson *et al.* 2003; Koestcke and Smith 2003). Approximately 48% of observations were obtained during the day, 19% in the morning, 19% in the evening, and 14% at night.

Avocet locations were obtained with at least two azimuths from telemetry-mounted trucks with known Universal Transverse Mercator (UTM) coordinates. Locations were estimated with LOAS 3.0.1 (Ecological Software Solutions, Urnash, Switzerland), unless recorded directly on maps from visual re-sightings (28%, 471 of 1,667 locations). Locations were recorded as UTM coordinates, as well as the date and time of all truck azimuths. The azimuths were taken within 15 min of each other to minimize error due to potential bird movement. To minimize autocorrelation of spatial data, consecutive locations were at least one h apart and most (92%, 1,535 of 1,667) observations were separated by >3 h (e.g., Haig *et al.* 2002). In a study with similar transmitters and truck systems in the San Francisco Bay, average telemetry location error was reported at 58 m, with error polygons of 1.1 ha (Warnock and Takekawa 1995).

Locations with large error polygons (>3 ha) were excluded from analyses.

For each radio-marked avocet, daily visual observations were used to categorize individuals into one of four breeding stages. If necessary, egg flotation (Alberico 1995) was used to back-calculate nest-initiation dates. The pre-incubation stage was defined as the time of capture in late winter through the day prior to incubation. Since avocets begin incubation with the laying of the third egg (Robinson *et al.* 1997), the incubation period commenced with the laying of the penultimate egg and ended when either the eggs hatched or failed. The brood-rearing stage began when eggs hatched and ended when either chicks fledged or disappeared. The post-breeding stage started after the last day of brood-rearing, or after the nest failed or was depredated.

Data Summary and Analysis

Hawth's Tools for ArcGIS (Beyer 2004) was used in a geographic information system (ArcGIS 9.1, ESRI, Inc., Redlands, California) to calculate the linear distance between consecutive locations (hereafter: linear movements) for radio-marked avocets. Because observations often were obtained more than once a day, potential bias of multiple daily observations on movements was examined by consecutively removing locations less than one, two, four, eight, and 16 h apart from analyses (Demers 2007). These removals did not significantly alter average distance calculations; therefore all locations >1 h apart were used for analyses.

Home ranges and core areas were estimated using Home Range Tools for ArcGIS in ArcGIS 9.1 (Rodgers *et al.* 2005). Home ranges and core areas were defined as the area encompassing the 95% and 50% utilization distribution, respectively. The fixed-kernel method, with likelihood cross-validation (CVh) for smoothing parameter, was used to estimate home range and core area sizes (Horne and Garton 2006). Kernel methods provide the most accurate measures of space use, are generally superior to the minimum convex polygon and harmonic-mean methods (Worton 1995; Kernohan *et al.* 2001), and exclude large areas that are not used by the animal (White and Garrott 1990). Likelihood cross-validation tends to outperform least squares cross-validation, producing estimates with better fit and less variability, and is especially useful with sample sizes <50 (Horne and Garton 2006). Likelihood cross-validation parameters were calculated with Animal Space Use 1.1 (Horne and Garton 2007).

Hawth's Tools for ArcGIS (Beyer 2004) in ArcGIS 9.1 was used to calculate linear distances of avocets from nest locations (hereafter: average distance from nest). To examine the extent to which avocets prospected for future nest sites, nest locations were overlaid with pre-incubation core areas and distances to nest sites were calculated and regressed against the number of days prior to incubation. To calculate average distances, one distance was included for each bird during each day. If multiple observations were obtained on a bird for a day, an average distance from the nest was calculated.

Single-factor Generalized Linear Models (GLM) analysis of variance was used to compare linear movements, home range, core area and average distances from nests across breeding stages for radio-marked avocets. Tukey-Kramer multiple-comparison tests were used to test for differences between breeding stages. Linear movement, home range, and core area data were

\log_{10} transformed to meet the assumptions of normality. To control for effects of individual variation in avocet space use and to allow direct comparisons between stages, additional home range and linear movement analyses were conducted on standardized scores (Afifi *et al.* 2004) for the four avocets with data during each breeding stage. Linear regression was used to test for relationships between distances from nests and number of days prior to incubation. Individual avocets were the unit of analysis; sample sizes varied by stage because of a high rate of radio failure in 2006. Data are presented as means \pm SE.

RESULTS

In 2005 and 2006, 116 female American Avocets were radio-marked, but only a small proportion of them were resident breeders. A total of 15 radio-marked avocets were confirmed resident breeders, the majority of marked birds were wintering migrants when captured. Data collected on migrant avocets were used as part of separate studies. A total of 1,667 locations were collected by observers and the mean number of locations obtained for an individual's breeding stage was 34.0 ± 2.4 . The mean number of d for each breeding stage was: pre-breeding, 50.3 ± 4.8 ; incubation, 19.9 ± 0.9 ; brood-rearing, 23.0 ± 7.3 ; post-breeding, 30.3 ± 3.6 . Of the 15 avocets, four lost their eggs to predators prior to hatching, seven lost or abandoned their chicks immediately following hatching, and four tended chicks during a brood-rearing stage.

Linear movements varied ($F_{3,40} = 8.84$, $P < 0.001$) among stages (Table 1). Pre-incubation distances were larger than incubation and brood-rearing distances (both $P < 0.001$). Movements were greater during post-breeding than incubation and brood-rearing stages ($P < 0.001$, $P = 0.03$). Post-breeding movements were larger than pre-incubation ($P = 0.04$), but incubation and brood-rearing distances did not differ ($P = 0.53$). These patterns were supported by analysis of standardized linear movements ($F_{3,12} = 34.02$, $P < 0.001$) for the four avocets followed throughout each breeding stage (Fig. 2). Post-breeding scores were significantly different from pre-incubation, incubation, and brood-rearing stages (all $P < 0.001$). Pre-incubation, incubation, and brood-rearing scores were not significantly different (all $P > 0.05$).

Table 1. Linear movements, home ranges, core areas, and average distance from nest of American Avocets in South San Francisco Bay, California, 2005-06. Data are presented as means \pm SE.

Breeding stage	N	Linear movements (m)	Home range (95% kernel; ha)	Core area (50% Kernel; ha)	Distance from nest (m)
Pre-incubation	15	985 \pm 114	1,310 \pm 310	220 \pm 44	1,756 \pm 240
Incubation	14	523 \pm 69	383 \pm 125	56 \pm 18	578 \pm 189
Brood-rearing	4	437 \pm 66	174 \pm 13	38 \pm 26	440 \pm 25
Post-breeding	11	1,576 \pm 275	3,397 \pm 755	665 \pm 168	4,288 \pm 736

Home ranges ($F_{3,40} = 20.24$, $P < 0.001$) and core areas ($F_{3,40} = 21.41$, $P < 0.001$) differed among breeding stages (Table 1, Fig. 3). Pre-incubation home ranges and core areas were larger than incubation and brood-rearing stages (all $P < 0.001$). Post-breeding home ranges and core areas were significantly larger than pre-incubation, incubation, and brood-rearing stages (all $P < 0.001$). In-

cubation home ranges and core areas did not differ from brood-rearing home ranges ($P = 0.61$) and core areas ($P = 0.96$). Standardized home ranges differed significantly among stages ($F_{3,12} = 16.97$, $P < 0.001$) for the four focal avocets (Fig. 2). The post-breeding scores were significantly different from pre-incubation ($P = 0.01$), incubation ($P < 0.001$), and brood-rearing stages ($P < 0.001$);

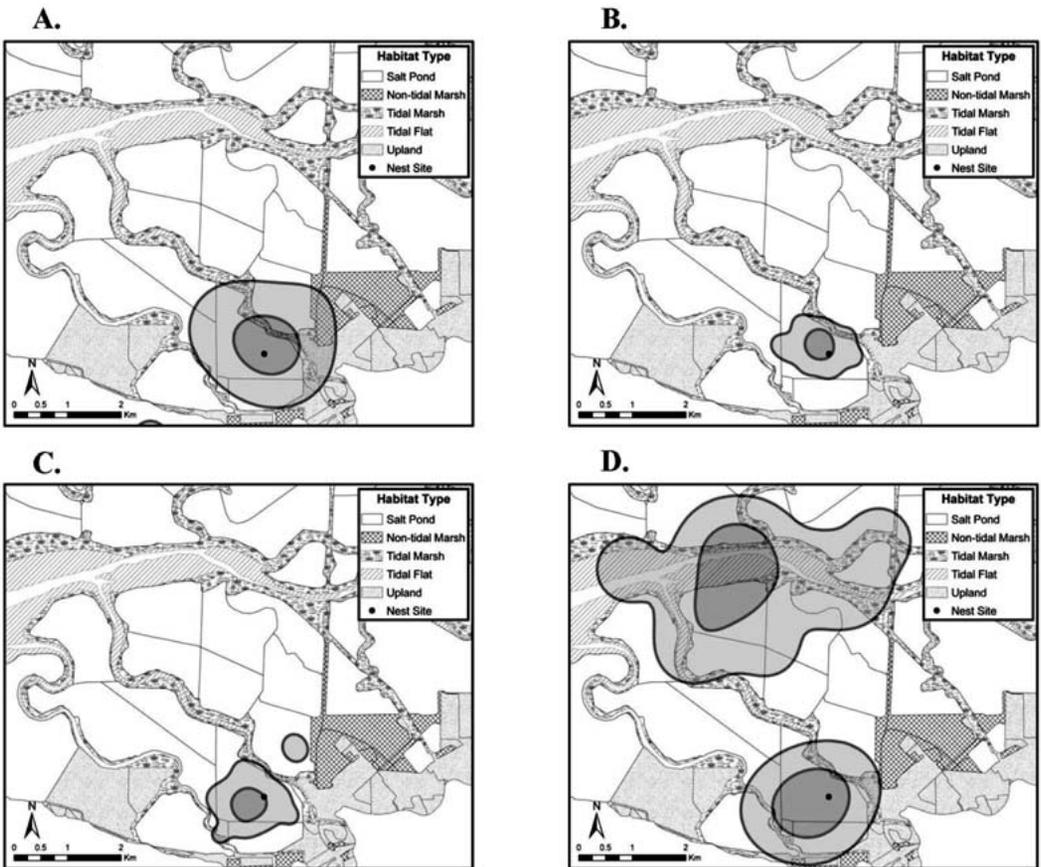


Figure 2. Home-range and core-area size fluctuations of a representative American Avocet during four breeding stages (A. pre-incubation, B. incubation, C. brood-rearing, D. post-breeding) in the South San Francisco Bay, California. The nest site, represented by the dark point, was located in Pond A8. Home range (95% fixed kernel) is represented by the light outer contour and core area (50% fixed kernel) is represented by the dark interior contour area.

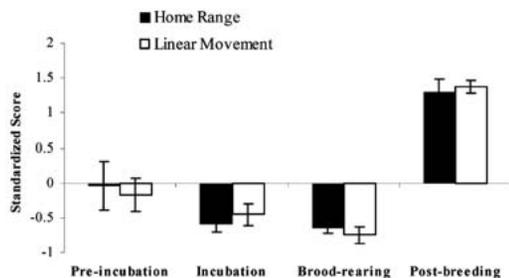


Figure 3. Mean (\pm SE) home range size and linear movements of four American Avocets sampled in each breeding stage in South San Francisco Bay, California, 2005-06. Standardized scores were calculated based on individual mean values across the four stages.

pre-incubation, incubation, and brood-rearing scores were not significantly different (all $P > 0.05$).

The average distance from nest ($F_{3,40} = 38.78$, $P < 0.001$) varied among stages (Table 1). Pre-incubation distances were greater than incubation ($P < 0.001$) and brood-rearing stages ($P = 0.003$). Post-breeding distances were significantly greater than during pre-incubation ($P = 0.001$), as well as incubation and brood-rearing (both $P < 0.001$). Average distance from nest did not differ during the incubation and brood-rearing stages ($P = 0.94$).

Fourteen of the 15 avocet nest locations (93%) were within the pre-incubation core area boundaries, whereas four of 11 (36%) nests were within post-breeding core areas ($P = 0.003$, Fisher's exact test). The distance between future nest sites and daily location decreased ($R^2 = 0.69$, $P < 0.001$) with the number of days prior to incubation (Fig. 4). Post-breeding distances from nest locations increased ($R^2 = 0.16$, $P < 0.03$) with number of days after breeding.

DISCUSSION

Space use of female American Avocets in South San Francisco Bay varied significantly among stages. Linear movements, home ranges, core areas, and distances from nest were greater in the post-breeding and pre-incubation stages than during the incubation and brood-rearing stages. Several other studies of avian species have found a seasonal re-

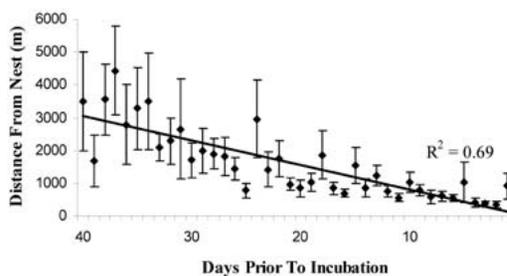


Figure 4. Relationship between mean (\pm SE) distance from nest and days prior to incubation during the pre-incubation stage for American Avocets in South San Francisco Bay, California, 2005-06.

duction in space use during nesting stages (Grahn 1990; Marzluff *et al.* 1997; Plissner *et al.* 2000a; Roth *et al.* 2004), but none has demonstrated significant differences between pre-incubation and post-breeding stages. Pre-incubation home ranges were 61% smaller and core area sizes were 66% smaller than in the post-breeding stage (Table 1). There was more variation in average distance from nest earlier in the pre-incubation stage and more variation in home range, linear movements, and distance from nest in the post-breeding stage than during pre-incubation.

Differences in space use between the pre-incubation and post-breeding stages indicate that pre-incubation space use of female avocets was influenced by breeding activities. Pre-incubation core areas contained the future nest sites for all but one of the radio-marked avocets, demonstrating female avocets spent a substantial period of time at their future nest site prior to nesting. The average distances from nest during the pre-incubation stage (Fig. 4) suggests that avocets were prospecting future nest sites, or engaged in pair-bonding behaviors prior to nesting. Additionally, visual observations of radio-marked avocets during the pre-breeding stage indicate that a substantial number of nest scrapes can be made by the pair, sometimes at multiple colony sites, prior to the final nest placement (Demers, pers. obs.). Similarly, research on other avocet populations indicates that nest prospecting occurs in the weeks prior to nesting, not in

the post-breeding period of the previous year (Robinson and Oring 1997; Plissner *et al.* 1999). Since the San Francisco Bay is characterized by a Mediterranean climate receiving nearly all rainfall during the cooler winter months, it is likely that avocets visit nesting sites in the late winter as water levels drop and temperatures increase.

We found that avocet space use differed substantially between the brood-rearing and post-breeding stages. Post-breeding home ranges, core areas, and average distances from nest were approximately 90% larger than in the brood-rearing stage. This suggests that avocets move less, encounter fewer habitats, and stay much closer to their nesting colonies while brood-rearing than in the post-breeding stage. These differences demonstrate that the brood-rearing stage is a distinct stage from post-breeding; however, obtaining data on brood-rearing avocets was difficult since avocet chicks often did not survive long and observing families with broods was difficult. In our study, only two females fledged chicks and two others raised chicks long enough to collect space-use data.

There is evidence that behavioral differences exist between avocet sexes, which may influence space use patterns during the annual cycle. Male avocets have been observed spending more time foraging while swimming than females (Dinsmore 1977); and they tend to use plunging foraging methods (head and upper breast enter the water to capture food) more often than females (Hamilton 1975). These observations suggest that males will forage in slightly deeper water than females, which could contribute to sex differences in space use. Since only female avocets were radio-marked for this study, sex differences in space use of American Avocets in the San Francisco Bay have yet to be determined.

However, differences in roles of males and females may influence space use during nest prospecting and site selection. Pairing occurs when a female persistently associates with a male until she is accepted as a mate (Hamilton 1975). Also, Robinson and Oring (1997) suggest that nest-site selection of avo-

cets breeding in northeastern California is likely determined by social factors associated with breeding colonies and the individual experience of males; therefore it is possible that females in our study follow males during the pre-incubation period and males play a larger role in nest prospecting.

Our study showed that breeding stage influences the space use patterns of female avocets in South San Francisco Bay. Understanding shifts in space use may help managers elucidate which regions or habitats are critical for avocets at different stages in the annual cycle. Also, it is possible to assess what risks avocets are exposed to at different times of the year. For instance, radio-telemetry location data, can determine where and when avocets are exposed to mercury and other environmental contaminants (Ackerman *et al.* 2007b). Perhaps most importantly, refuge managers in the San Francisco Bay can manipulate wetland conditions during the nest prospecting period of the pre-incubation stage to improve breeding conditions for avocets. By raising water to unsuitable levels in areas of high risk and creating more optimal breeding conditions in other wetlands, managers can mitigate risk of environmental contaminants and California gull depredation.

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