

POSTFLEDGING FORSTER'S TERN MOVEMENTS, HABITAT SELECTION, AND COLONY ATTENDANCE IN SAN FRANCISCO BAY

JOSHUA T. ACKERMAN^{1,4}, JILL D. BLUSO-DEMERS^{1,3}, AND JOHN Y. TAKEKAWA²

¹U.S. Geological Survey, Western Ecological Research Center, Davis Field Station, One Shields Avenue,
University of California, Davis, CA 95616

²U.S. Geological Survey, Western Ecological Research Center, San Francisco Bay Estuary Field Station,
505 Azuar Drive, Vallejo, CA 94592

Abstract. Relatively little is known about birds during the postfledging period when flighted chicks have left the nest and must learn to forage independently. We examined postfledging movements, habitat selection, and colony attendance of Forster's Terns (*Sterna forsteri*) radio-marked just before they fledged in San Francisco Bay, California. The proportion of the day spent at their natal colony declined as juveniles aged, from 65% at the time of fledging to <5% within two weeks of fledging. Accordingly, the distance postfledging terns were located from their colony increased as they aged, from <500 m within the first week of fledging to >5000 m by their fifth week. Time of day also influenced colony attendance, with older terns spending more time at the colony during nighttime hours (20:00 to 05:00) than during the day (06:00 to 19:00), when they were presumably foraging. Home ranges and core-use areas averaged 12.14 km² and 2.23 km², respectively. At each of four spatial scales of analysis, postfledging terns selected salt pond habitats strongly. No other habitat types were selected at any scale, but terns consistently avoided tidal flats and uplands. Terns also avoided open bay habitats at the two largest spatial scales, tidal marsh habitats at the two smallest scales, and sloughs and managed marshes at several scales. Within salt ponds, terns were located closer to salt-pond levees (58 m) than was expected (107 m). Our results indicate that tern chicks disperse from their natal colony within a few weeks of fledging, with older chicks using their natal colony primarily for roosting during the night, and that postfledging terns are highly dependent on salt ponds.

Key words: chick movements, colony attendance, Forster's Tern, home range, postfledging, *Sterna forsteri*, telemetry.

Movimientos, Selección de Hábitat y Presencia en las Colonias de *Sterna forsteri* Después del Emplumamiento

Resumen. Se conoce relativamente poco a cerca de las aves durante el período posterior al emplumamiento, cuando los pichones con capacidad de volar han abandonado el nido y deben aprender a forrajear independientemente. Examinamos los movimientos posteriores al abandono del nido, la selección de hábitat y la presencia en las colonias de individuos de la especie *Sterna forsteri* marcados con transmisores de radio justo antes del emplumamiento en la bahía de San Francisco, California. La proporción del día que las aves jóvenes pasaron en su colonia natal disminuyó a medida que su edad aumentó, desde el 65% al momento del emplumamiento hasta menos del 5% a las dos semanas de haber emplumado. De modo concordante, la distancia a su colonia a la que las aves fueron localizadas aumentó con su edad, de menos de 500 m durante la primera semana después de abandonar el nido a más de 5000 m para la quinta semana. La hora del día también influyó la presencia en la colonia: las aves de mayor edad pasaron más tiempo en la colonia durante las horas de la noche (20:00 a 05:00) que durante el día (06:00 a 19:00), cuando presumiblemente estaban forrajando. Los ámbitos hogareños y las áreas núcleo de uso promediaron 12.14 km² y 2.23 km², respectivamente. A cada una de cuatro escalas espaciales de análisis, las aves mostraron una preferencia marcada por los ambientes de estanques salinos. Los otros ambientes no fueron seleccionados a ninguna escala, pero las aves consistentemente evitaron las planicies mareales y las tierras altas. Éstas también evitaron los ambientes de bahías abiertas a las dos escalas espaciales más grandes, los pantanos mareales a las dos escalas más pequeñas y los barrizales y pantanos manejados a varias escalas. Dentro de los estanques salinos, las aves se encontraron más cerca de los diques (58 m) que lo que se esperaba (107 m). Nuestros resultados indican que los pichones de *S. forsteri* se dispersan desde su colonia natal antes de unas pocas semanas después de abandonar el nido, que los pichones de mayor edad usan su colonia natal principalmente para descansar durante la noche y que después del emplumamiento estas aves son altamente dependientes de los estanques salinos.

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³Current address: San Francisco Bay Bird Observatory, 524 Valley Way, Milpitas, CA 95035

⁴E-mail: jackerman@usgs.gov

INTRODUCTION

Although much research has examined habitat selection (Hall et al. 2007, Kesler and Haig 2007, Stolen et al. 2007) and colony attendance (Weimerskirch et al. 2001, Hedd and Gales 2005, Lyons et al. 2005, Anderson et al. 2007) by adult breeding birds, relatively few studies have investigated these characteristics once chicks have fledged (Baker 1993, White et al. 2005, King et al. 2006). Yet the postfledging stage can be a critical time period for exploration (Baker 1993), dispersal (Greenwood and Harvey 1982, Pärt 1990), growth (Stienen and Brenninkmeijer 2002, Schaubroth and Becker 2008), and survival (Bendel and Therres 1993, Keedwell 2003, Davies and Restani 2006), which can have important effects on population dynamics. Habitat selection of adults and juveniles may differ, and postfledging survival can be habitat dependent (King et al. 2006). Therefore, implementing conservation programs based on an understanding of habitat selection by breeding adults only does not necessarily translate successfully to their offspring.

San Francisco Bay is currently undergoing large-scale wetland restoration. Although it is the largest estuary on the west coast of North America, it has lost approximately 80% of its tidal marshes and 40% of its tidal flats (Goals Project 1999). Over 10 000 ha of former salt-evaporation ponds along San Francisco Bay's margins recently have been transferred to government ownership, with plans to convert 50 to 90% of these salt ponds into tidal marsh (Goals Project 1999). Whereas the conversion of salt ponds into tidal marsh will likely benefit birds dependent on tidal marshes, such as the endangered California Clapper Rail (*Rallus longirostris obsoletus*), the loss of salt-pond habitat could have negative effects on other waterbirds that currently use salt ponds heavily (Warnock et al. 2002, Takekawa et al. 2001, Takekawa et al. 2006). San Francisco Bay is a site of hemispheric importance to shorebirds and supports over one million waterbirds annually (Page et al. 1999, Stenzel et al. 2002). During peak spring migration numbers of shorebirds in a single salt pond have exceeded 200 000 (Stenzel and Page 1988). Of the locally breeding waterbirds, salt ponds might be especially important to Forster's Tern (*Sterna forsteri*). Approximately 30% of the population of Forster's Tern breeding along the Pacific coast nests within San Francisco Bay (McNicholl et al. 2001, Strong et al. 2004). Salt ponds currently provide nesting habitat for 80% of terns breeding in the estuary (Strong et al. 2004) and are the primary foraging area of adult terns (Ackerman et al. 2008a). Juvenile terns may also rely on these salt ponds, but their postfledging habitat use is currently unknown.

In order to broaden perspectives on wetland restoration in San Francisco Bay, we studied the postfledging ecology of Forster's Terns. Our objectives were to examine (1) colony attendance and movement patterns of fledged terns as they aged, (2) space use of terns during the postfledging period, and (3) habitat selection of postfledging terns at several spatial scales

by means of the hierarchical ordering process suggested by Johnson (1980). Specifically, we evaluated habitat selection by comparing individual locations within the study region (first order), core-use areas within the region (second order), core-use areas within the home range (third order), and individual locations within the home range (third order). Finally, we further evaluated habitat selection within salt ponds (third order) and examined whether postfledging terns used salt-pond levees and adjacent water as roosting sites and foraging areas, respectively.

METHODS

STUDY AREA

We assessed space use and habitat selection of postfledging Forster's Tern chicks in South San Francisco Bay, California, at the Don Edwards San Francisco Bay National Wildlife Refuge (37.4° N, 122.0° W). The northern limit of the South San Francisco Bay study area was defined by the San Mateo Bridge (Warnock and Takekawa 1995). The majority of Forster's Tern colonies in San Francisco Bay are on islands within former salt-evaporation ponds, and the number of colonies ranges from 4 to 14 depending on the year (Strong et al. 2004). We studied Forster's Terns at the largest San Francisco Bay colony in 2006 (>600 nests; J. Ackerman, unpubl. data), located on islands in Pond N7 within the Newark Salt Pond Complex.

RADIO-MARKING TERNS

We radio-marked Forster's Terns chicks just before they fledged at about 28 days of age. To do so, we monitored the Pond N7 tern colony weekly from nest initiation until fledging (May–August). At each visit, we hand-captured all chicks in the nesting colony, banded them with stainless steel U.S. Geological Survey leg bands, and measured them to estimate their age. We measured exposed culmen and short tarsus (diagonal length of the tarsometatarsus, measured along its outer edge; Dzubin and Cooch 1992) to the nearest 0.01 mm with Fowler electronic digital calipers (Newton, MA) and flattened wing to the nearest 1 mm with a wing board. We estimated each chick's age according to the following equation developed from our 2005 morphological data (mm) for South San Francisco Bay Forster's Terns that included chicks of known hatching date: chick age in days = $(0.11 \times \text{wing chord}) + (1.11 \times \text{culmen}) - (0.018 \times \text{culmen}^2) + (1.34 \times \text{tarsus}) - (0.035 \times \text{tarsus}^2) - 22.15$; $n = 472$, $R^2 = 0.98$ (J. T. Ackerman, unpublished data).

We radio-marked tern chicks that were between 23 and 29 days of age on either 5 or 12 July 2006, when most chicks at Pond N7 were fledging. Transmitters (model BD-2T, Holohil Systems, Ltd., Carp, Ontario, Canada [$n = 21$] and model A2410 modified, Advanced Telemetry Systems, Inc., Isanti, MN [$n = 9$]) were $\leq 1\%$ of chick body mass (≤ 1.1 g), ≤ 19 mm long \times ≤ 8 mm wide, and had a 12-cm external whip antenna. We attached radio transmitters to the midline of a chick's

mantle with sutures (Ethicon Vicryl FS-2, 3-0, Ethicon, Inc., Piscataway, NJ) through front and rear channels, and a third suture was tied in the middle and over the top of the transmitter. Each suture was secured with two or three knots and cyanoacrylic glue (Loctite 422, Henkel Corp., Rocky Hill, CT). We also collected a drop of blood from the brachial vein of each chick to determine its sex genetically (Zoogen Services, Inc., Davis, CA). Before attaching radio transmitters, we removed chicks from the nesting island to a processing station several hundred meters away, held them in shaded and screen-lined poultry cages (model 5KTC, Murray McMurray Hatchery, Webster City, IA), and then returned them to the specific region of the colony where they were found. Birds were captured and marked under California Department of Fish and Game scientific-collection (SC000009), U.S. Fish and Wildlife Service (MB102896), and U.S. Geological Survey Bird Banding Laboratory (22911) permits, and research was conducted under the guidelines of the U.S. Geological Survey, Western Ecological Research Center, Animal Care and Use Committee.

RADIO-TRACKING TERNS

We used trucks and fixed-wing aircraft equipped with dual four-element Yagi antenna systems (AVM Instrument Co., Colfax, CA) to track radio-marked terns. Trucks had null-peak systems to determine bearings accurately via triangulation (e.g., Takekawa et al. 2002, Ackerman et al. 2006), whereas aircraft had left–right systems to circle and pinpoint signals on either side of the plane (Gilmer et al. 1981). We used triangulation software (LOAS, version 3.0.1, Ecological Software Solutions, Urnäsch, Switzerland) to calculate Universal Transverse Mercator coordinates for each location. We located chicks daily by truck and twice weekly by aircraft until the estimated end of the transmitter's life (about 42 days). Chicks that were not detected were searched for each day until found or until the transmitter was determined to have quit working.

Using an automated system for logging telemetry data (e.g., Adams et al. 2004, Hedd and Gales 2005, Anderson et al. 2005, 2007, Lyons et al. 2005) we also monitored the presence or absence of radio-marked chicks at the Pond N7 tern colony continuously from 5 July to 4 August 2006. The system consisted of a data-logging telemetry receiver (model R4500S, Advanced Telemetry Systems, Inc., Isanti, MN) linked to an omni-directional dipole antenna (Advanced Telemetry Systems) and was powered by a 12-volt marine battery. The receiver system continuously scanned all 30 frequencies on a cycle of approximately 20 min, and, during normal system operation, we interpreted a lack of detection as an absence from the colony within the range of the receiving system (radius 150 m). We placed a reference transmitter at the colony to ensure that the receiving system functioned properly and manually confirmed correct function at least once every two weeks. We

detected the reference transmitter during >99% of the data-logging telemetry receiver's cycles. We also programmed four false frequencies that were not associated with actual radio transmitters, and we recorded only one false detection out of 1855 data-logger cycles. On one occasion, due to loss of battery power, the system failed to function properly for nearly three days; we omitted data from that period from our analyses. In addition, we excluded data recorded within 6 hr after observers entered and exited the colony. We included data in our analyses only when we knew a chick to be alive and excluded data after a chick was dead (Ackerman et al., 2008b) or permanently missing from the study area for the rest of the study period (e.g., not found by the logger, truck, or aircraft searches).

AUTOMATED DATA-LOGGER ANALYSES

We recorded data on colony-attendance patterns from 24 terns because, although we radio-marked 30 terns, only 24 had frequencies within our data-logger receiver's range. We analyzed patterns of chicks' colony attendance by examining presence/absence data at the Pond N7 colony at two temporal scales. First, to evaluate daily patterns of attendance, we calculated the proportion of each day that a chick attended the colony by dividing the number of data-logger cycles in which the chick was detected on a given day by the number of data-logger cycles completed that day. For this analysis, we used data only when records for the entire 24 hrs in a day were complete; that is, all 72 data-logger receiver cycles (20 min each) were functioning appropriately and there was no reason for data omission (e.g., due to observers entering the colony). We tested whether the proportion of the day spent at the colony was related to chick age by regression with JMP version 4.0.4 (Sall et al. 2001). Each radio-marked tern contributed one data point per day, unless it was censored, and we included data from age 25 to 55 days in this analysis because our sample size was ≥ 5 for each of these ages. For statistical analyses, we arcsin-square-root transformed proportion data and included the individual tern (transmitter frequency) as a random effect to control for the potential of autocorrelation among repeated measurements from the same tern.

Second, to investigate hourly patterns of attendance, we divided the data into 24 one-hour intervals for each chick. For each hour of the day, we considered a chick present (1) if it was detected at least once during that hour and absent (0) if it was not detected during that hour. We tested for differences in colony attendance (nominal: present or absent) by hour of day (circular continuous variable) and age (continuous from 24 to 56 days of age) with linear–circular logistic regression with JMP version 4.0.4 (Sall et al. 2001). To convert the hour of day (0–24) into a circular variable, we (1) divided the hour by 24 to scale the time value between 0 and 1, (2) multiplied this quantity by 2π to convert the values into radians, and (3) then calculated the sine and cosine of this value (Zar 1999). Both

of these sin-hour and cos-hour variables, along with chick age, were then entered into the logistic model as independent variables. We included the interactions between sin-hour \times chick age and cos-hour \times chick age, and the individual tern as a random effect. To reduce the influence of significant interactions between time and age (see Results), we categorized chicks into three age classes and re-ran the logistic models without including the fixed effect of chick age. In these revised models, we tested whether time significantly influenced colony attendance by comparing the full logistic models (which included hour and tern effects) to reduced models that contained only the tern effect by means of likelihood-ratio χ^2 tests. For each comparison, the difference in the negative log likelihoods (multiplied by 2 to estimate the χ^2 value) was compared to a χ^2 distribution with degrees of freedom (df) equal to the difference in the two-model df to estimate the P values.

ANALYSES OF SPACE USE

We used ArcGIS 9.2 (ESRI 2006) to map all truck- and aerial-telemetry locations. For the rare occasions when consecutive observations on an individual tern were obtained <60 min apart, we randomly selected only one observation to include in analyses. We also excluded any locations with error-polygon sizes >5 ha, which we calculated for each triangulation by assuming a constant variance (two standard deviations; LOAS, version 3.0.1). Using the fixed-kernel method (Seaman and Powell 1996), we calculated home ranges and core-use areas for each individual tern, which we defined as the areas encompassing 95% and 50% of the utilization distributions, respectively. We also used the fixed-kernel method to calculate the 99% utilization distribution for the entire population (Ackerman et al. 2006) for use in the distance analysis described below. We selected likelihood cross-validation (CVh) as the smoothing parameter because it generally produces home-range estimates with better fit and less variability with small sample sizes than do the other smoothing parameters, such as least-squares cross-validation (Horne and Garton 2006). We used Animal Space Use 1.2 (Horne and Garton 2007) to calculate CVh and Home Range Tools for ArcGIS (Rodgers et al. 2005), with the CVh value as the smoothing parameter, to calculate the sizes of home ranges and core-use areas for postfledging terns with ≥ 13 locations.

ANALYSES OF HABITAT AVAILABILITY

We used San Francisco Bay EcoAtlas habitat coverages (SFEI 1998) to categorize habitat types within our study area and to calculate the availability of each habitat. We categorized habitats as bay (deep water or shallow water), tidal flats (bay flats, shell beach, or sandy beaches), sloughs (major channels or channel flats), tidal marshes (high-, mid-, or low-elevation tidal marshes and muted tidal marshes), managed marshes (diked marshes or managed marshes), salt ponds (active or former salt-evaporation ponds), lagoons (lagoons, storage-treatment

ponds, or lakes), or uplands (developed or undeveloped fill; farmed, ruderal, and grazed baylands; willow groves; large islands; sand dunes; or urban uplands). We calculated the area of each habitat within the entire South San Francisco Bay (south of the San Mateo Bridge), and, by overlaying habitat coverages with telemetry locations and home-range maps, we assigned each telemetry location a habitat type and calculated the area of each habitat within individual home ranges and core-use areas.

ANALYSES OF HABITAT SELECTION

We evaluated habitat selection by postfledging terns at four spatial scales, adapted from those proposed by Johnson (1980), to reduce the potential for observer bias in defining what habitats are actually available to terns (Johnson 1980, Lopez et al. 2004). At each spatial scale, we calculated habitat-selection ratios (S) obtained by dividing observed use of a habitat by the expected use of that habitat (Aebischer et al. 1993, Manly et al. 2002, Lopez et al. 2004). At the largest spatial scale, we compared habitat use for each radio-marked tern using its specific telemetry locations to the availability of habitats in the entire South Bay. This is comparable to Johnson's (1980) definition of first-order selection (range selection), and we refer to it as the location-to-region scale. We calculated selection ratios for individual terns for each habitat type as $S = a/(bc)$, where a = the number of telemetry locations within a habitat for an individual, b = the total number of telemetry locations for that individual, and c = the proportion of that specific habitat within the entire South Bay. At the next largest scale, we compared the habitat contained within each tern's core-use area to the availability of habitats in the entire South Bay. This is similar to Johnson's (1980) definition of second-order selection (home-range selection within a region), and we refer to it as the core-use-area-to-region scale. Although many studies compare an animal's home range to the study region at the second-order scale (Johnson's 1980), we chose to use the animal's core-use area instead of its home range, as did Beasley et al. (2007) and McCleery et al. (2007), since our intent was to focus on areas where the terns' space use was most concentrated. Therefore, we calculated selection ratios for each tern as $S = d/c$, where d = the proportion of habitat within an individual's core-use area and c = the proportion of that specific habitat within the entire South Bay.

We evaluated habitat selection at a smaller spatial scale by means of two measures comparable to Johnson's (1980) definition of third-order selection (within home-range selection). First, we compared the habitat contained within each tern's core-use area to the availability of habitats in its home range. We refer to this as the core-use-area-to-home-range scale. We calculated selection ratios for each tern as $S = d/e$, where d = the portion of habitat within an individual's core-use area and e = the portion of that specific habitat within that individual's home range. Second, we compared habitat use for

each radio-marked tern using its specific telemetry locations to the availability of habitat in its home range. We refer to this as the location-to-home-range scale. At this scale, $S = f/(ge)$, where f = an individual's number of telemetry locations in a specific habitat within its home range, g = that individual's total number of telemetry locations inside its entire home range, and e = the proportion of each specific habitat within that individual's home range.

For each habitat within each scale of analysis, we calculated habitat-selection ratios for individual terns and then averaged those of all terns. We avoided zeros in the numerator or denominator when calculating S by adding 0.001 to both observed and expected values (Aebischer et al. 1993, Lopez et al. 2004). We tested whether \log_e -transformed S values differed by habitat type and sex by using analysis of variance with JMP version 4.0.4 (Sall et al. 2001). We then tested whether the average S for each habitat differed from a value of 1 by calculating upper and lower simultaneous 95% confidence limits, using the Bonferroni inequality to control for the potential for Type I error (Manly et al. 2002). Thus, for the habitat-selection analysis, we used the Bonferroni inequality with a confidence level of 99.375% for the eight individual tests with $\alpha = 0.05$ (Manly et al. 2002). Selection ratios significantly >1 indicated selection of a habitat (use of a habitat was proportionally greater than its availability), selection ratios significantly <1 indicated avoidance of a habitat (use of a habitat was proportionately less than its availability), and selection ratios no different from 1 indicated neither selection nor avoidance of a habitat (use of a habitat was proportionate to its availability; Neu et al. 1974, Beyers et al. 1984, Manly et al. 2002).

We further assessed habitat selection at the third-order scale (Johnson 1980) more closely by examining distances terns were located from the colony and salt-pond levees (both internal and external levees). Using Hawth's Tools for ArcGIS (Beyer 2004) we calculated the linear distance between each telemetry location and the center of the Pond N7 colony. Similarly, we used Hawth's Tools to calculate the linear distance between each telemetry location and the nearest salt-pond levee, which we identified from San Francisco Bay EcoAtlas habitat coverages (SFEI 1998). Because we recorded several locations for each individual tern per day, we used the average linear distance that birds were located from the colony (or the nearest salt-pond levee) for each bird on a specific day. Thus, only one averaged data point was used for each tern per day in the linear-distance analyses. All distance data were \log_e -transformed for statistical analyses, but we present untransformed data in figures to facilitate interpretation. We tested whether the distance terns were located from colonies, or the nearest salt-pond levee, increased as they aged by means of regression with JMP version 4.0.4 (Sall et al. 2001). For these analyses, we included the individual tern as a random effect to control for the potential of autocorrelation between repeated measurements from the same tern on subsequent days. Additionally, we

tested whether the terns' locations were closer to salt-pond levees than would be predicted by chance by first selecting 2000 random locations within an available area defined by the tern population's 99% utilization distribution (described above) and calculating their distances from the nearest-salt pond levee and, second, comparing these distances to terns' actual distances from the nearest salt-pond levee with resource-selection functions fitted by logistic-regression software (JMP version 4.0.4; Sall et al. 2001, Manly et al. 2002). For this analysis, the dependent variable was tern presence (1) or an available random location (0) and the independent variable was distance to the nearest salt-pond levee.

RESULTS

We radio-marked 30 Forster's Tern chicks (13 female and 17 male) just before they fledged at 25 ± 1.4 (SD) days of age. Using the automated telemetry-data-logger system, we tracked terns for up to 44 days after they fledged and recorded 1094 telemetry locations by truck (85%) and aircraft (15%) and 11 359 locations at the colony. The size (\pm SE) of home ranges and core-use areas did not differ by sex (ANOVA: home range: $F_{1,26} = 0.01$, $P = 0.91$; core area: $F_{1,26} = 0.07$, $P = 0.80$) and averaged 12.14 ± 2.14 km² and 2.23 ± 0.43 km², respectively.

POSTFLEDGING MOVEMENTS

The distance postfledging terns were located from their natal colony increased as they aged (regression with random intercepts: $n = 604$, $r^2 = 0.64$, age: $P < 0.0001$, tern: $P < 0.0001$; Fig. 1A). Terns also were more likely to be located close to salt-pond levees (geometric mean 58 m) than would be predicted by chance (geometric mean 107 m; resource-selection function: $n = 3041$, Wald $\chi^2 = 147.60$, $df = 1$, $P < 0.0001$). The distance terns were located from salt-pond levees also increased as they aged, although this relationship was weak (regression with random intercepts: $n = 602$, $r^2 = 0.08$, age: $P < 0.0001$, tern: $P = 0.60$; Fig. 1B).

COLONY ATTENDANCE

The proportion of time spent at the colony during the day (24 hr) declined as chicks aged (Fig. 2; regression with random intercepts: $n = 418$, $r^2 = 0.56$, age: $P < 0.0001$, tern: $P < 0.0001$). We also examined whether the time of day influenced colony presence or absence during 1-hr intervals. The full model that included interactions between sin-hour or cos-hour and chick age was better than a reduced model without the two interactions (likelihood ratio χ^2 test: $n = 10\ 935$, $\chi^2 = 174.76$, df difference = 4, $P < 0.0001$), indicating that colony attendance by 1-hr interval depended on age (Fig. 3).

To investigate the effect of time on colony attendance further, we re-ran the logistic model after separating the data into three age classes (24–31, 32–37, and 38–56 days of age) based on the similar amount of time they spent at the colony (Fig. 2).

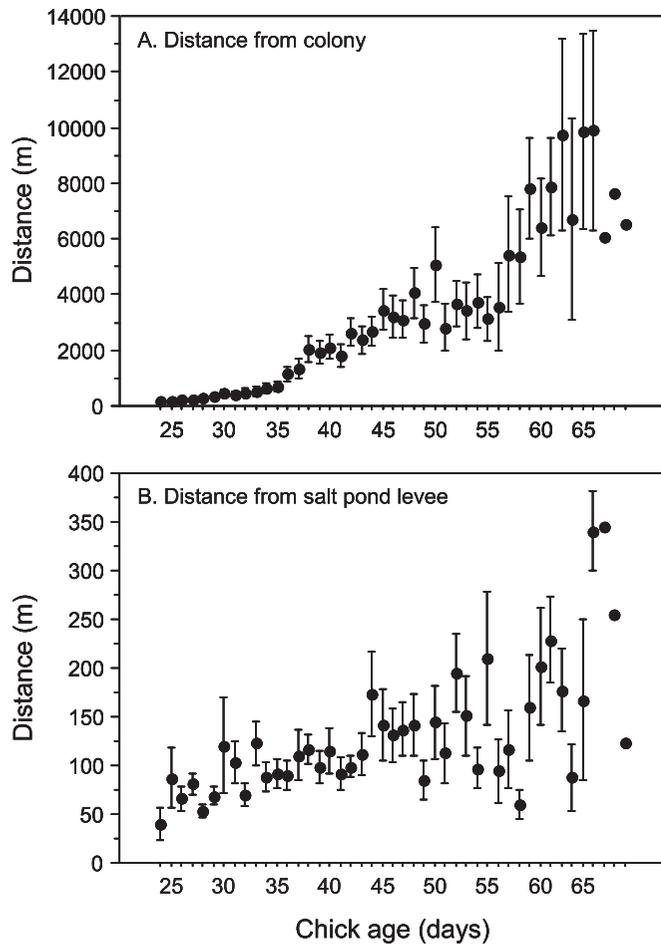


FIGURE 1. The distance postfledging Forster's Terns were located from (A) their natal colony and (B) salt pond levees in south San Francisco Bay, California, during 2006. Data were acquired by radio-marking 30 tern chicks just before they fledged and tracking them daily from trucks and twice weekly from aircraft until the end of the transmitter's estimated life. Each data point represents the mean (\pm SE) distance, and only one data point per tern per day was used in analyses.

We included the individual tern as a random effect and both the sin-hour and cos-hour as fixed effects for these revised models. For each of the age classes, the full models that included time as an explanatory variable were much better than the reduced models that included only the individual tern as a random effect (24–31 days of age, Fig. 3A: likelihood-ratio χ^2 test: $n = 2614$, $\chi^2 = 25.77$, df difference = 2, $P < 0.0001$; 32–37 days of age, Fig. 3B: likelihood-ratio χ^2 test: $n = 2738$, $\chi^2 = 36.60$, df difference = 2, $P < 0.0001$; 38–56 days of age, Fig. 3C: likelihood-ratio χ^2 test: $n = 5583$, $\chi^2 = 279.66$, df difference = 2, $P < 0.0001$). These data indicate that, in addition to chick age, time of day significantly influenced the amount of time terns spent at the colony. Older terns attended the colony mainly at night, whereas younger terns attended the colony more frequently during both the day and night (Fig. 3).

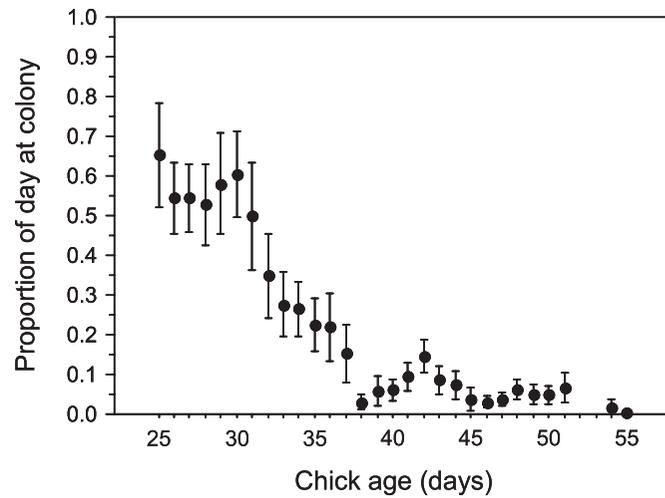


FIGURE 2. The proportion of the day postfledging Forster's Terns spent at their natal colony as they aged in south San Francisco Bay, California, during 2006. Data were acquired through an automated telemetry data-logger system placed at the Pond N7 tern colony from 24 tern chicks equipped with radios just before they fledged. Each data point represents the mean (\pm SE) colony attendance on the basis of 72 data-logger cycles per tern per day.

POSTFLEDGING HABITAT SELECTION

The study area was 889 km² consisting of bay (68%), salt ponds (13%), uplands (7%), tidal flats (5%), tidal marshes (4%), managed marshes (2%), sloughs (1%), and lagoons (1%). Postfledging terns ($n = 1050$) were most often located within salt ponds (94%), followed by tidal marsh (2%), lagoon (1%), managed marsh (1%), tidal flat (1%), slough (<1%), upland (<1%), and bay (<1%) (Fig. 4). In the first step of our habitat-selection analyses, we tested whether selection ratios (S) differed by habitat and sex. At all scales, S differed by habitat but not by sex, after the nonsignificant interactions (all $F_{7,208} \leq 0.96$ and $P \geq 0.46$) between habitat and sex were dropped (ANOVAs: location-to-region scale: habitat type: $F_{7,215} = 49.43$, $P < 0.0001$, sex: $F_{1,215} = 0.18$, $P = 0.67$; core-use-area-to-region scale: habitat type: $F_{7,215} = 73.49$, $P < 0.0001$, sex: $F_{1,215} = 2.18$, $P = 0.14$; core-use-area-to-home-range scale: habitat type: $F_{7,215} = 8.58$, $P < 0.0001$, sex: $F_{1,215} = 0.39$, $P = 0.54$; location-to-home-range-scale: habitat type: $F_{7,215} = 9.54$, $P < 0.0001$, sex: $F_{1,215} = 0.01$, $P = 0.99$). We therefore pooled data on both sexes to assess selection or avoidance of each habitat.

We then used simultaneous 95% confidence limits, using the Bonferroni inequality, to determine habitat selection or avoidance for each habitat type at each spatial scale (Fig. 5). At the largest spatial scale (first-order selection), the terns' locations in the context of regional habitat availability indicated that terns strongly selected salt ponds, avoided the bay, tidal flats, sloughs, and uplands, and used tidal marshes, managed marshes, and lagoons in proportion to their availability. At the next largest spatial scale (second-order selection), the terns' core-use areas in the context of regional habitat availability indicated a

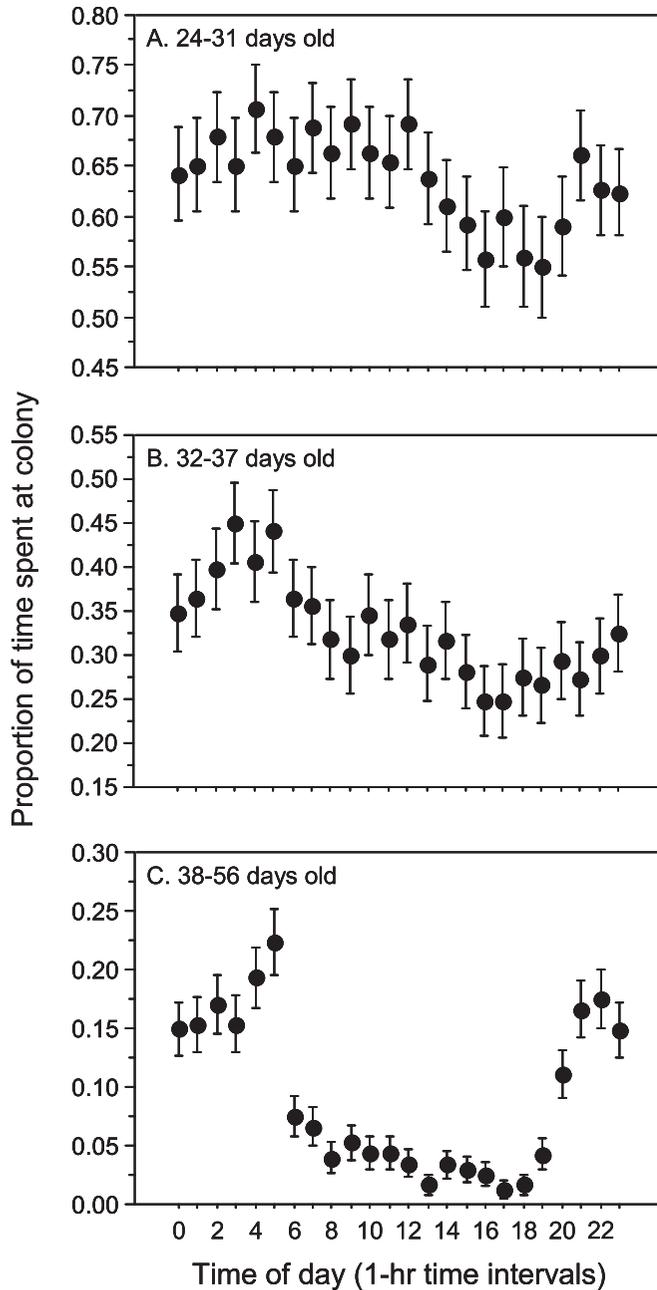


FIGURE 3. The proportion of time postfledging Forster's Terns spent at their natal colony by 1-hr intervals in south San Francisco Bay, California, during 2006. Data were split according to chick age: (A) 24-31 days of age ($n = 2614$), (B) 32-37 days of age ($n = 2738$), and (C) 38-56 days of age ($n = 5583$). Data were acquired through an automated telemetry data-logger system placed at the Pond N7 tern colony from 24 tern chicks equipped with radios just before they fledged. Each data point represents the mean (\pm SE) colony attendance among terns for each 1-hr interval for that age class.

similar pattern of strong selection for salt ponds, avoidance of the bay, tidal flats, sloughs, managed marshes, and uplands, and relatively proportional use of tidal marshes and lagoons. The main difference between our results at the two largest spatial

scales was that managed marshes became significantly avoided by terns at the core-use-area-to-region scale, whereas it was not statistically significant at the location-to-region scale.

At the two smaller spatial scales (third-order selection), terns still strongly selected salt ponds and avoided tidal flats and uplands available within their individual home ranges. At these scale, however, our results differed in that the bay and sloughs were used in proportions more similar to their availability at the smaller spatial scales, whereas they were avoided at the larger spatial scales. Also, tidal marsh habitat was avoided at the smaller spatial scales, whereas it was used in proportion to its availability at the larger spatial scales. Use of lagoons by terns remained proportional to its availability at all spatial scales. Finally, use of managed marshes available within individual terns' home ranges was inconsistent at the smaller spatial scales, as it was at the regional spatial scales. The terns' core-use areas in the context of their home ranges indicated that terns avoided managed marshes, whereas individual tern locations in the context of their home ranges indicated that they used managed marshes in proportion to their availability.

DISCUSSION

Colony attendance by postfledging Forster's Terns declined dramatically as chicks aged. Terns spent approximately 65% of the day at their natal colony near the time of fledging but spent <5% of the day at their natal colony within two weeks after fledging. Similarly, Schauroth and Becker (2008) found that Common Terns (*Sterna hirundo*) left the colony within 14 to 23 days after fledging. In addition to chick age, time of day also influenced the proportion of time terns spent at their natal colony. Postfledging terns spent more time at the colony at night (20:00–05:00) than during the day (06:00–19:00), when they were presumably foraging. This pattern of colony attendance was especially prominent for the oldest terns (38–56 days of age), which still returned to the colony at night after extended diurnal foraging trips, whereas younger terns attended the colony more frequently during both the day and night. We also found that during incubation and chick rearing colony attendance by adult Forster's Terns was highest at night and lower during the day in San Francisco Bay (authors, unpubl. data). Overall, colony attendance of adult Forster's Terns averaged 51% and 41% of the day during incubation and chick rearing, respectively (authors, unpubl. data). Similarly, Lyons et al. (2005) found that adult Caspian Terns breeding in the Columbia River estuary spent approximately 51% of the day at the colony, with colony attendance lowest during both the early morning and late afternoon.

Locations of radio-marked Forster's Terns also supported the colony-attendance patterns we observed. The distance radio-marked postfledging terns were located from their natal colony increased as they aged, from less than 500 m within the first week of fledging to >5000 m by their fifth week. These results indicate that newly fledged chicks are still highly

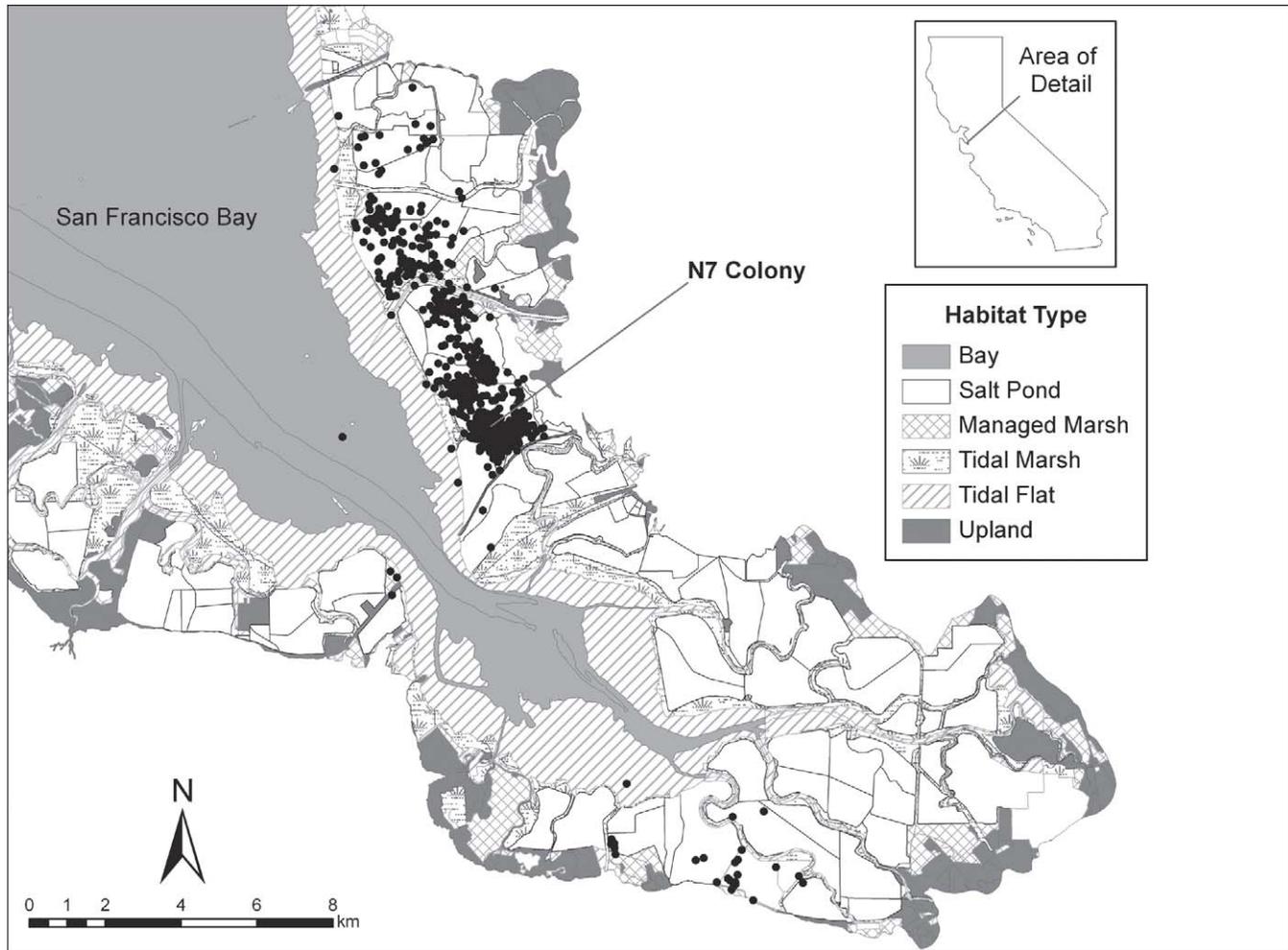


FIGURE 4. Telemetry locations of postfledging Forster’s Terns radio-marked at the Pond N7 colony in south San Francisco Bay, California, during 2006. Habitat types depicted include salt ponds, managed marshes, tidal marshes, tidal flats, uplands, and open bay (SFEI 1998).

dependent on their natal colony during the first week after fledging, but then, as they age, they use their natal colony primarily for roosting during the night. Although few studies have examined postfledging movements in seabirds, terrestrial birds rarely move farther than 5 km from their natal area for several weeks after fledging (Anders et al. 1998, Kershner et al. 2004, Davies and Restani 2006, Berkeley et al. 2007).

Postfledging Forster’s Terns strongly selected salt-pond habitats at all spatial scales. They selected no other habitat type at any scale but consistently avoided tidal flats and uplands. It is possible that the habitats we considered to be available at the largest spatial scales were not actually available to postfledging terns (e.g., the large amount of open bay we considered available within the region at the largest spatial scale). Instead, selection of locations and core-use areas within the South San Francisco Bay region (first- and second-order selection; Johnson 1980) may have been highly influenced by the location of the nest site (Orians and Wittenberger 1991),

which was selected previously by the parents. Accordingly, our results at the smallest spatial scale (third-order selection; Johnson 1980) assessing locations and core-use areas within an individual’s home range might be more predictive of postfledging terns’ actual habitat selection. Our results at the smallest spatial scales differed from those at the larger spatial scales mainly in that open bay habitat was used in proportion to its availability at the smallest spatial scales instead of being avoided at the largest spatial scales, and tidal marshes were avoided at the smallest spatial scales, instead of being used in proportion to their availability at the larger spatial scales. In general, however, differences among these spatial scales were minor, and trends were similar, but not always significant, at each spatial scale.

Although the home ranges of postfledging Forster’s Terns (12.1 km²) were much smaller than those of adult Forster’s Terns we simultaneously tracked in San Francisco Bay the same year (84.5 km²; Ackerman et al. 2008a, Bluso et al.

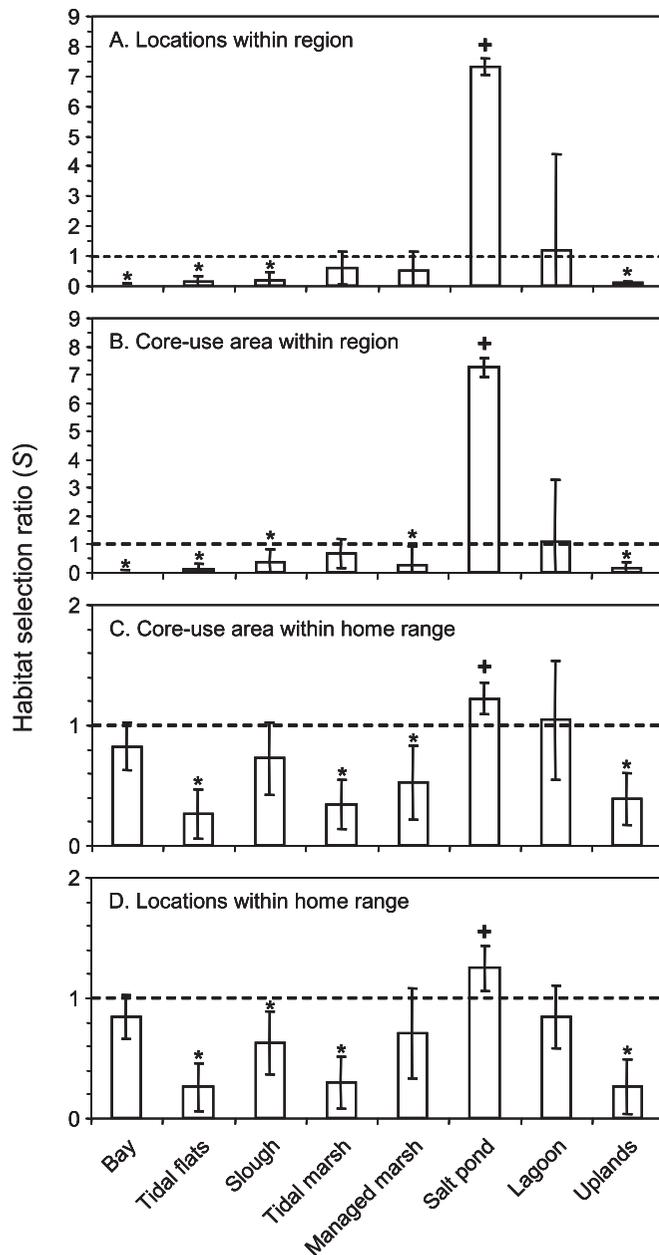


FIGURE 5. Habitat-selection ratios (S ; mean and simultaneous 95% confidence limits calculated with the Bonferroni inequality) of postfledging Forster's Terns radio-marked at the Pond N7 colony in south San Francisco Bay, California, during 2006. Habitat selection was assessed hierarchically at four spatial scales: (A) scale of locations within region; (B) scale of core-use area within region; (C) scale of core-use area within home range; (D) scale of locations within home range. The dashed line at $S = 1$ indicates the selection ratio where habitat was used in proportion to its availability; values >1 indicate habitat selection and <1 indicate habitat avoidance. Plus symbols (+) indicate significant selection of a habitat and asterisks (*) indicate significant avoidance of a habitat.

2008), habitat selection by postfledging terns was similar to that of adult terns during the breeding season. For example, adult terns strongly selected salt ponds and avoided open bay, tidal flat, and upland habitats (authors, unpubl. data). Adult Forster's Terns, however, tended to use tidal marshes, managed marshes, and sloughs in proportion to their availability (authors, unpubl. data), whereas postfledging terns avoided these habitats in at least two of the four spatial scales we assessed. Similarly, in Portugal, Little Terns (*Sternula albifrons*) use artificial salt-pans and coastal lagoons as foraging areas more often than the nearby sea (Paiva et al. 2008). Within San Francisco Bay, shorebirds also tend to select salt-pond habitats. For example, during winter, radio-marked Western Sandpipers (*Calidris mauri*) select salt ponds and avoid tidal marshes at multiple spatial and temporal scales (Warnock and Takekawa 1995). Similarly, radio-marked American Avocets and Black-necked Stilts use salt ponds more than any other habitat in San Francisco Bay (Ackerman et al. 2007).

Within salt ponds, postfledging Forster's Terns were located closer to salt-pond levees than would be predicted by chance, indicating either that they foraged near levees or that they used levees as roosting sites. We suspect, as have others (Ashmole and Tovar 1968, McNicholl et al. 2001), that postfledging terns are still being fed periodically by their parents and internal salt-pond levees may be used as roosting areas close to parental foraging sites. Similarly, Warnock and Takekawa (1995) found that Western Sandpipers select salt-pond levees as roosting sites, especially during high tides, throughout the winter in San Francisco Bay. We also found that both prebreeding and breeding Forster's Tern adults strongly select salt ponds, especially those of low salinity, indicating that these areas provide important foraging habitat (authors, unpubl. data).

Currently, to offset the loss of over 80% of San Francisco Bay's tidal marshes, large-scale restoration plans to convert 50–90% of the former salt-evaporation ponds into tidal marsh are being implemented (Goals Project 1999). Our results demonstrate the importance of salt-pond habitats for postfledging Forster's Terns and concur with several other studies assessing the value of salt ponds to wintering, migrating, and breeding waterbirds (Warnock et al. 2002, Takekawa et al. 2001, Takekawa et al. 2006). Not only are salt-pond habitats used extensively by Forster's Terns for foraging and roosting, but salt ponds currently provide nesting habitat for the vast majority of terns breeding in San Francisco Bay (Strong et al. 2004). Supporting similar numbers of foraging and breeding waterbirds with fewer salt ponds in San Francisco Bay will require a comprehensive understanding of waterbirds' habitat needs and an effective adaptive-management program for enhancing the remaining salt ponds. It is unknown what effect the loss of salt ponds will have on waterbirds in the estuary, so habitat restoration should proceed with caution and continued monitoring of waterbirds, especially locally breeding birds, is warranted.

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