

# Space Use by Forster's Terns Breeding in South San Francisco Bay

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**Abstract.**—Parental care behaviors often differ in dimorphic seabirds, leading to sex-specific differences in foraging behaviors. However, few studies have examined sex-specific foraging behaviors in monomorphic seabirds. Using radio-telemetry, we studied Forster's Terns (*Sterna forsteri*)—a monomorphic and socially monogamous seabird—breeding in the South San Francisco Bay, California. Space use did not differ between males and females. Instead, space use varied by breeding stage and colony affiliation. Forster's Terns were located farthest from the nest during pre-breeding and post-breeding time periods, and closest to the nest during incubation and chick-rearing. Home-range size and core-use areas decreased as the breeding season progressed and were most concentrated in the post-breeding stage. The results of this and other studies indicate that terns, unlike other monomorphic seabirds studied, do not exhibit sex-specific differences in space use. *Received 3 October 2007, Accepted 5 February 2008.*

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Birds are unique among vertebrates in that 90% of species are socially monogamous and males and females often differ in parental care behaviors (Lack 1968; Clutton-Brock 1991). Some breeding seabirds exhibit sex-specific parental care behaviors during incubation and chick-rearing (Bried and Jouvantin 2002), which may influence the foraging behaviors of the sexes (Weimerskirch *et al.* 1997; Gonzalez-Solis *et al.* 2000; Lewis *et al.* 2002, 2005). Most of these studies examined sexually size-dimorphic species (Lewis *et al.* 2002), indicating that differences in foraging between sexes are influenced by body size (Weimerskirch *et al.* 1997; Gonzalez-Solis *et al.* 2000; Lewis *et al.* 2005). However, sex-specific foraging behaviors among seabirds with negligible sexual size dimorphism (i.e., monomorphism) have been documented (Lewis *et al.* 2002; Adams *et al.* 2004; Peck and Congdon 2006), suggesting that differences reported in sexually dimorphic species are not mediated exclusively by differences in body size (Lewis *et al.* 2002).

Terns (Sterninae) are socially monogamous and monomorphic seabirds, and pa-

rental care behaviors vary between the sexes within the breeding season (Wiggins and Morris 1987; Quinn 1990; Fasola and Saino 1995). Male terns provision females during courtship (Nisbet 1973; Morris 1986), and contribute more toward chick provisioning in the form of larger, energetically richer prey delivered at a higher rate than females (Wiggins and Morris 1987; Quinn 1990; Fasola and Saino 1995). In contrast, female terns spend more time within the territory before and during courtship, perform most of the incubation and brooding, and provision chicks less than males (Nisbet 1973; Morris 1986; Wiggins and Morris 1987; Quinn 1990). Parental care behaviors vary over the breeding season and may alter foraging behaviors. For example, female Common Terns (*Sterna hirundo*) have less time to forage than males because of greater incubation duties (Wiggins and Morris 1987), and females lose mass during incubation at a greater rate than males (Wendeln 1997). Because of these energetic and time limitations, Wendeln (1997) found that some female Common Terns foraged in freshwater

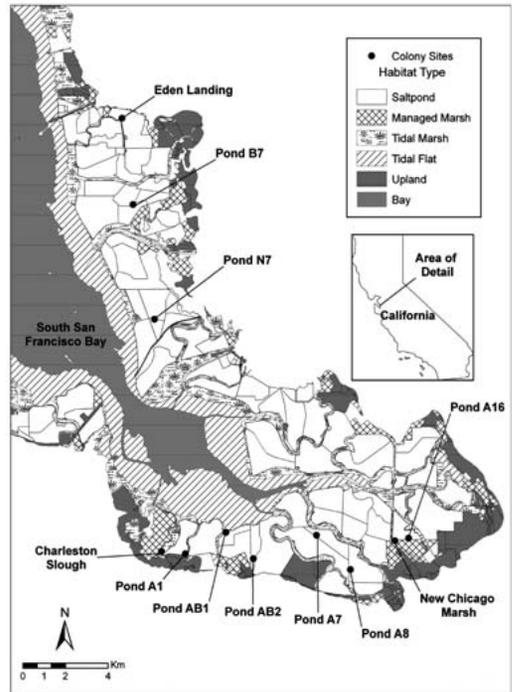
environments that were closer to the colony during incubation, and then switched to foraging in more distant marine environments when rearing chicks.

Sex-specific foraging behavior of terns has been indirectly documented by observed prey deliveries (Monaghan *et al.* 1989; Wagner and Safina 1989; Wendlen 1997), although recent analysis of radio-marked Caspian Terns (*Hydroprogne caspia*) did not find differences between the sexes in any space use measurement (Anderson *et al.* 2007). Therefore, to further examine sex-specific differences in space use of a tern species, we used radio-telemetry to investigate individual distance from nest, and home-range and core-use area size as measures of space use by male and female Forster's Terns (*S. forsteri*) breeding at several colonies in South San Francisco Bay, California. Forster's Terns have similar morphology and breeding biology to the more intensively studied Common Tern and Arctic Tern (*S. paradisaea*; McNicholl *et al.* 2001), and may also adopt sex-specific parental care behaviors. Furthermore, Forster's Terns show limited sexual size dimorphism: adult males are about 1 to 7% larger than females in bill and head measurements, but mass and wing length are similar between the sexes (Bluso *et al.* 2006). By examining distance from nest, foraging range, and home-range and core-use area size, we determined if sex, as well as breeding stage and colony affiliation, influenced space use in Forster's Terns.

## METHODS

### Study Area and Species

Forster's Terns are medium-sized terns whose annual range is limited to North America (McNicholl *et al.* 2001). About 30% of the Pacific Coast breeding population nests within San Francisco Bay, California (37.8°N, 122.3°W; McNicholl *et al.* 2001; Strong *et al.* 2004). The San Francisco Bay is the largest and most modified estuary on the west coast of the United States; 95% of its wetlands have been altered owing to urban development, agriculture, and salt production (San Francisco Bay Area Goals Project 1999). The South San Francisco Bay (hereafter South Bay; Fig. 1) has been heavily modified; 74% of the tidal marsh plain (10,975 ha) has been converted into salt evaporation ponds (San Francisco Bay Area Goals Project 1999). The levee system and dredge spoil islands associated with salt pond construction provide nesting habitat for Forster's Terns (Harvey *et al.*



**Figure 1.** Map of the South San Francisco Bay, California showing dominant habitat types and Forster's Tern colony sites in 2005 and 2006 (San Francisco Estuary Institute, San Francisco Bay EcoAtlas, version 1.5b, Oakland, California).

1990; Strong *et al.* 2004; U.S. Geological Survey, unpublished data).

### Tern Capture and Radio-telemetry

From 20 April-19 May 2005 and 19 April-19 May 2006, adult Forster's Terns were captured with remotely-detonated netlaunchers (Coda Enterprises, Mesa, AZ) at colonies prior to nest initiation. Pre-breeding capture sites included Eden Landing, A16, A8, A2E, A1 in 2005, and A16, A7, AB1, A1, Charleston Slough in 2006 (Fig. 1). From 10-19 June 2006, pairs of Forster's Terns were captured at the N7 colony (Fig. 1) with treadle-activated bow nets placed at three-egg nests that had been incubated 16-23 d. One egg was randomly removed from each nest as part of a study examining contaminant levels in San Francisco Bay birds (Ackerman *et al.* 2007). Blood was collected to determine sex via DNA genotyping (Zoogen Services, Inc., Davis, CA) and morphological features were measured (Bluso *et al.* 2006). Birds were held during processing in partitioned and shaded screen-lined poultry cages (model 5KTC, Murray McMurray Hatchery, Webster City, IA) until release (within 2.5 h).

Terns were marked with radio-transmitters (2005: Model A2470, 3.4 g, Advanced Telemetry Systems, Inc., Isanti, MN; 2006: Model A2440, 2.2 g, Advanced Telemetry Systems, Inc., Isanti, MN). Transmitters were fastened with epoxy to an aluminum band (2005: U.S. Geological Survey size 3A; 2006: U.S. Geological Survey size 3) and the band was attached to the tarsometatarsus of the tern (e.g., Plissner *et al.* 2000a). Including attach-

ment materials, radio-transmitters weighed  $\leq 3.6$  g in 2005 and  $\leq 2.3$  g in 2006 ( $< 3\%$  of a tern's body weight). Leg-mounted transmitters have been used successfully on male Common Terns with no effect on brood attendance or chick feeding of the radio-marked male or its mate (Morris and Burness 1992; Burness *et al.* 1994).

Following routes throughout the South Bay, radio-tagged individuals were tracked daily using a vehicle-mounted dual 4-element null-peak antenna system (AVM Instrument Company, Livermore, CA) beginning the day after capture until 1 August or their transmitter failed. To determine locations, two bearings were obtained on an individual within 10 min to minimize movement error. Using similar truck-mounted telemetry systems and location distances (e.g.,  $< 3$  km) within the South Bay salt pond complexes, average error rates of 1.5 degrees for bearings,  $58 \pm 35$  (SE) m for distances between true and calculated locations, and 1.1 ha for error-polygon size were reported by Warnock and Takekawa (1995). In the field, the bearings on the tern's position, and the truck's azimuth and location (obtained from a Global Positioning System with  $\pm 15$  m accuracy [GPS; GPSMAP 76, Garmin International, Inc., Olathe, KS]), were entered into the LOAS 3.0.1 program (Ecological Software Solutions, Urnäsch, Switzerland) to obtain Universal Transverse Mercator (UTM) coordinates of the tern's estimated location. Additionally, from 28 April-19 July 2005 and 26 April-17 August 2006, the entire San Francisco Bay was searched from an aircraft equipped with fixed-wing, left-right antenna system (Advanced Telemetry Systems Inc., Isanti, MN) every seven to 14 d. Search efforts were systematic with equal effort across all birds.

Nesting by radio-marked terns was confirmed using several criteria. Starting on 20 May (when 10% of Forster's Tern initiated nests [U.S. Geological Survey, unpublished data]), active colonies were observed two to four times a week for roosting radio-marked terns using both truck telemetry systems and visual observations. It was assumed that marked terns were nesting on the colony if they were found roosting on the same colony  $> 5$  times within a 10-d period. By visually identifying radio-marked terns flushing and returning to the same area, nests of radio-marked terns were located in an area of seven to twelve nests within a region of the colony (hereafter sub-colony, defined as an area of roughly  $25 \text{ m}^2$  on a colony site). In 2006, remote systems were also used to confirm initiation of nesting. Data-logging receivers (model R4500S, Advanced Telemetry Systems, Inc., Isanti, MN) linked to an H-antenna (AVM Instrument Company, Livermore, CA) or an omni-directional dipole antenna (Advanced Telemetry Systems Inc., Isanti, MN) and powered by 12-volt marine batteries (model 8A26 or 8A31, MK Battery, Anaheim, CA) were placed on six colonies. The receivers scanned for marked terns for 16 s every five to 13 min and stored the frequency, year, date, time of day, and number and strength of pulses detected. Reference transmitters were placed at each colony to ensure that the system functioned properly. Radio-marked terns were confirmed as breeding on these colonies by colony attendance records indicating breeding activities (e.g., incubation bouts; Fraser 1997).

Colonies or sub-colonies were entered to obtain nest ages using egg flotation (Hays and LeCroy 1971). For radio-marked terns nesting within a sub-colony, nest age was assigned based on the average nest age within the sub-colony. For all terns captured on nests, nest age was determined during the capture events. Forster's Terns

begin incubation after laying the first egg and incubate eggs for approximately 24 d (McNicholl *et al.* 2001). Therefore, the nest initiation and hatch dates were obtained by backdating and projecting nest age, respectively. For each tern, the breeding season was categorized into one of four stages. The pre-breeding stage was defined as the period prior to nest initiation. The incubation stage was defined as the period between nest initiation and the projected hatch date of the first chick. The chick-rearing stage began on the projected hatch date, and the presence of chicks on colony sites was confirmed by colony entry and observations of radio-marked terns defending colonies. Post-breeding status was assigned when chicks reached 30 d of age (approximate age of fledging; McNicholls *et al.* 2001), when nests failed due to nest depredation, flooding, or disturbance, or when colony attendance patterns indicated that a radio-marked tern had abandoned its nest. Each tern nest or sub-colony was assigned a UTM location from a GPS unit with  $\pm 15$  m accuracy (GPSMAP 76, Garmin International, Inc., Olathe, KS).

All research was conducted under the guidelines of the Humboldt State University Animal Care and Use Committee and the U.S. Geological Survey Western Ecological Research Center Animal Care and Use Committee. Forster's Terns were captured under California Department of Fish and Game permit SC-007250 and Fish and Wildlife Service permit MB102896-0.

#### Statistical Analyses

ArcGIS 9.1 (ESRI 2005) was used to map telemetry locations for Forster's Terns. For terns with five or more locations, the linear distance between a tern's locations and the UTM of the sub-colony or nest was calculated using Hawth's Tools for ArcGIS (Beyer 2004) and a foraging range value was assigned by calculating the 95<sup>th</sup> percent value of the data. This method was used instead of assigning the maximum distance value as the foraging range to avoid selecting an outlier. To avoid spatial autocorrelation of locations, observations obtained less than 90 min apart were randomly selected for inclusion in the analysis. In Forster's Terns, mean incubation duration is 69 min (Fraser 1997), and in Common Terns, a male provisioning two chicks averaged  $0.89 \pm 0.23$  prey deliveries/h or a prey delivery every 66 min (Wiggins 1989). Therefore, observations separated by 90 min were considered independent movements.

The fixed-kernel method was used to calculate home ranges and core-use areas, which were defined as the areas encompassing 95% and 50% of the utilization distribution, respectively. The fixed-kernel method was selected because it measures intensity of use (Kernohan *et al.* 2001), and likelihood-cross-validation (CVh) was used as the smoothing parameter (Worton 1989; Horne and Garton 2006). Likelihood-cross-validation generally produces home range estimates with better fit and less variability than other smoothing parameters, such as least-squares-cross-validation, for sample sizes  $\leq 50$  (Horne and Garton 2006). Animal Space Use 1.1 (Horne and Garton 2007) was used to calculate CVh and Home Range Tools for ArcGIS (Rodgers *et al.* 2005), with the CVh value as the smoothing parameter, was used to calculate home-range and core-use area size. Since home-range analyses can be sensitive to small sample sizes (Seaman *et al.* 1999), the effect of sample size on home-range and core-use area size was examined using random samples of observations of increasing sam-

ple size. The sample size where home-range size and core-use area of four terns stabilized was determined in each stage. Using these sample sizes as criteria, home ranges and core-use areas were estimated.

Differences in linear distances from the nest were tested with a three-factor repeated measures analysis of variance (ANOVA) using the mixed-effects model PROC MIXED in SAS (SAS Institute 1999). Foraging range, and home-range and core-use area size were examined with a three-factor ANOVA (PROC MIXED; SAS Institute 1999). The models included sex, stage, colony, and stage-by-sex and stage-by-colony interactions. The lack of independence between mated pairs was controlled for in the analyses, and Tukey-Kramer multiple comparison tests were used for pairwise comparisons among groups.

Because of the small number of marked terns at each colony, observations from A16, A8, and A7 (hereafter East Alviso) and A1 and Charleston Slough colonies (hereafter West Alviso) were pooled to examine the effect of colony site on space use of Forster's Terns; however, the small sample size at the West Alviso colony did not allow for comparisons between sex and site and the two terns nesting at that site were excluded from the analysis. The N7 colony was not pooled with any other colonies since it was distantly located (13.0-15.5 km) from the Alviso colonies. Pooling data was justified because the frequency distributions of colony members were similar among pooled colonies and the pooled colonies were located near each other (<3.6 km) compared to other colonies (6.8-15.5 km). Additionally, small sample sizes in 2005 did not permit comparisons between years, instead all terns from both years were pooled. Two terns re-nested after failed initial attempts, and their first or second incubation stage were randomly selected for inclusion in the analysis. For these individuals, pre-breeding distances were based on the first nest location and the chick-rearing and post breeding distances were based on the second nest location. When the breeding stage of radio-marked individuals could not be confirmed, those observations were excluded. Prior to analysis, all data were  $\log_{10}$ -transformed to meet assumptions of normality and all statistical tests were performed with  $\alpha = 0.05$ . Means  $\pm$  1 SE throughout are reported.

## RESULTS

Before nest initiation, 39 and 36 pre-breeding Forster's Terns were captured and radio-marked in 2005 and 2006, respectively, and ten incubating terns (5 pairs) were captured and radio-marked in 2006. Nest locations and breeding stages were confirmed for 3 female terns in 2005 and 20 terns (9 females, 11 males) in 2006. A total of 1,241 locations were collected and each tern was located an average of  $54.0 \pm 6.2$  times (range 8-121 locations). Terns captured in the pre-breeding stage were tracked for  $84.5 \pm 7.0$  d (range: 50-128 d) and terns captured in the incubation stage were tracked for  $43.9 \pm 5.1$

d (range: 17-65 d). Number of locations did not differ between females ( $49.8 \pm 9.2$ ) and males ( $58.5 \pm 8.5$ ;  $F_{1,21} = 1.21$ ,  $P = 0.50$ ).

### Distance from Nest and Foraging Range

Over all years and breeding stages, Forster's Terns were located an average linear distance of  $4.9 \pm 2.2$  km from the nest. Distances did not differ by sex or colony site (sex:  $F_{1,382} = 0.02$ ,  $P = 0.89$ ; colony:  $F_{1,12} = 0.21$ ,  $P = 0.65$ ), but differed by stage ( $F_{3,844} = 98.2$ ,  $P < 0.0001$ ; Table 1). The stage-by-sex interaction was significant ( $F_{3,874} = 4.06$ ,  $P < 0.01$ ), however, when males and females were compared within the same stage, the distances male and female terns were located from the nest did not differ ( $t \leq 1.96$ ,  $P \geq 0.51$ ; Table 1). The stage-by-colony interaction was significant ( $F_{3,844} = 45.59$ ,  $P < 0.0001$ ); N7 terns were located farther distances from the nest than East Alviso terns in post-breeding stage ( $t = 5.97$ ,  $P < 0.0001$ ), but not in pre-breeding, incubation, or chick-rearing stages ( $t \leq 2.29$ ,  $P \geq 0.30$ ; Table 1).

Over all years and breeding stages, the foraging range of Forster's Terns breeding in the South Bay averaged  $6.2 \pm 1.4$  km from the nest. The foraging range did not differ by sex ( $F_{1,16} = 0.47$ ,  $P = 0.50$ ), but differed by colony and stage (colony:  $F_{1,10} = 7.07$ ,  $P = 0.02$ ; stage:  $F_{3,27} = 4.57$ ,  $P = 0.01$ ; Table 1). The stage-by-sex interaction was not significant ( $F_{1,23} = 0.42$ ,  $P = 0.74$ ), but the stage-by-colony interaction was significant ( $F_{3,27} = 3.74$ ,  $P = 0.02$ ; Table 1). N7 terns ranged farther from the nest than East Alviso terns in the post-breeding stage ( $t = 4.49$ ,  $P < 0.01$ ), but not in any other stage ( $t \leq 1.89$ ,  $P \geq 0.57$ ; Table 1).

### Home-range and Core-use Area Size

Over all years and breeding stages, home-range size of Forster's Terns was  $5,775 \pm 1,184$  ha and average core-use area size was  $997 \pm 197$  ha. Home-range and core-use area size did not differ by sex (home range:  $F_{1,18} = 0.14$ ,  $P = 0.72$ ; core-use area:  $F_{1,9} = 0.50$ ,  $P = 0.50$ ) or colony site (home range:  $F_{1,10} = 4.21$ ,  $P = 0.07$ ; core-use area  $F_{1,9} = 1.92$ ,  $P = 0.20$ ).

**Table 1.** Factors affecting the mean ( $\pm$  SE) distance from nest and the mean ( $\pm$  SE) foraging range of Forster's Terns in the South San Francisco Bay, California, 2005 and 2006. Results are reported from ANOVA and Tukey-Kramer multiple comparisons tests. Data with same superscript letter are significantly different from each other ( $P < 0.05$ ). Data were  $\log_{10}$ -transformed prior to analysis.

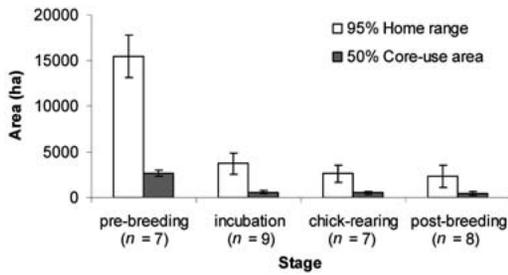
Term	Group	N	Distance from nest (km)	Foraging range (km)
Sex	Female	20	3.4 $\pm$ 0.97	5.7 $\pm$ 1.29
	Male	27	4.0 $\pm$ 0.99	7.1 $\pm$ 2.11
Stage	Pre-breeding	10	4.0 $\pm$ 0.92 <sup>AB</sup>	7.2 $\pm$ 1.97 <sup>EF</sup>
	Incubation	13	1.0 $\pm$ 0.25 <sup>BCD</sup>	3.1 $\pm$ 0.92 <sup>FG</sup>
	Chick-rearing	11	1.7 $\pm$ 0.56 <sup>AC</sup>	3.4 $\pm$ 1.23 <sup>EH</sup>
	Post-breeding	13	8.1 $\pm$ 1.86 <sup>AD</sup>	12.0 $\pm$ 3.99 <sup>GH</sup>
Site	East Alviso	27	1.6 $\pm$ 0.30	3.4 $\pm$ 0.80 <sup>I</sup>
	N7	20	6.6 $\pm$ 1.36	10.6 $\pm$ 2.68 <sup>I</sup>
Stage*sex	Pre-breeding, Female	4	2.7 $\pm$ 0.84	7.2 $\pm$ 4.50
	Pre-breeding, Male	6	4.8 $\pm$ 1.37	7.2 $\pm$ 1.87
	Incubation, Female	5	0.9 $\pm$ 0.31	2.8 $\pm$ 0.54
	Incubation, Male	8	1.0 $\pm$ 0.38	3.3 $\pm$ 1.50
	Chick-rearing, Female	5	1.4 $\pm$ 0.60	3.4 $\pm$ 2.04
	Chick-rearing, Male	6	1.8 $\pm$ 0.95	3.4 $\pm$ 1.64
	Post-breeding, Female	6	7.4 $\pm$ 2.50	8.9 $\pm$ 2.34
	Post-breeding, Male	7	8.6 $\pm$ 2.89	14.6 $\pm$ 7.25
Stage*colony	Pre-breeding, E. Alviso	7	3.5 $\pm$ 0.69	7.5 $\pm$ 2.48
	Pre-breeding, N7	2	6.9 $\pm$ 3.93	8.7 $\pm$ 5.32
	Incubation, E. Alviso	8	0.7 $\pm$ 0.17	2.2 $\pm$ 0.43
	Incubation, N7	5	1.4 $\pm$ 0.58	4.5 $\pm$ 2.29
	Chick-rearing, E. Alviso	5	0.7 $\pm$ 0.13	1.2 $\pm$ 0.12
	Chick-rearing, N7	6	2.4 $\pm$ 0.94	5.2 $\pm$ 2.03
	Post-breeding, E. Alviso	6	1.3 $\pm$ 0.32 <sup>J</sup>	2.5 $\pm$ 0.82 <sup>K</sup>
	Post-breeding, N7	13	13.8 $\pm$ 0.91 <sup>J</sup>	20.1 $\pm$ 5.88 <sup>K</sup>

Both home-range and core-use area size differed between stages (home range:  $F_{3,13} = 7.15$ ,  $P < 0.01$ ; core-use area:  $F_{3,18} = 5.67$ ,  $P < 0.01$ ; Fig. 2). Home-range size was larger in the pre-breeding stage than in incubation ( $t = 3.10$ ,  $P = 0.04$ ), chick-rearing ( $t = 3.51$ ,  $P = 0.02$ ), or post-breeding ( $t = 4.60$ ,  $P < 0.01$ ) stages. There was no difference in home-range size between any other stages ( $t \leq 2.32$ ,  $P \geq 0.15$ ; Fig. 2). Pre-breeding core-use areas were larger than incubation ( $t = 3.14$ ,  $P = 0.03$ ), chick-rearing ( $t = 2.85$ ,  $P = 0.05$ ), or post-breeding ( $t = 4.05$ ,  $P < 0.01$ ) stages. There was no difference in core-use area size between any other stages ( $t \leq 1.57$ ,  $P \geq 0.42$ ; Fig. 2). The stage-by-sex interaction was not significant for either analysis (home range:  $F_{3,10} = 0.42$ ,  $P = 0.74$ ; core-use area:  $F_{3,13} = 0.23$ ,  $P = 0.87$ ) and the stage-by-colony interaction was not significant (home range:  $F_{3,13} = 0.46$ ,  $P = 0.72$ ; core-use area:  $F_{3,18} = 2.13$ ,  $P = 0.13$ ).

## DISCUSSION

Ours is the first to examine space use in Forster's Terns and the first spatial study of any tern species over the entire breeding season. We found no support for sex-specific space use in Forster's Terns in South San Francisco Bay. Distance from the nest, foraging range, home-range size, and core-use area did not vary by sex (Table 1, Fig. 2). Additionally, distance from the nest, foraging range, home-range and core-use area size did not vary when females and males were compared within the same stage (Table 1, Fig. 2).

Our study of Forster's Terns supports the findings of Anderson *et al.* (2007), indicating that tern species do not exhibit sex-specific space use and providing the first evidence of monomorphic seabirds that do not follow these space use patterns. Sex-specific space



**Figure 2.** The mean ( $\pm$  SE) home-range and core-area size of Forster's Terns in South San Francisco Bay, California in relation to breeding stage during 2005 and 2006. Data were  $\log_{10}$ -transformed prior to analysis.

use has been documented only in a few monomorphic seabirds (i.e., Lewis *et al.* 2002; Adams *et al.* 2004; Peck and Congdon 2006); thus, it is unknown if the lack of sex-specific space use in terns contradict a general pattern among monomorphic seabirds. In Forster's Terns, parental care behaviors have not been documented, and it may be that Forster's Terns do not follow parental care patterns shown by other terns and gulls. If so, similarity in parental care behaviors between male and female Forster's Terns may promote similar space use. However, Caspian Terns follow specific parental care patterns (Quinn 1990) and the sexes do not differ in space use (Anderson *et al.* 2007). More likely, male and female Forster's Terns follow sex-specific parental care behaviors, yet do not differ in space use. If this is the case, the patterns of sex-specific space use documented in other monomorphic seabirds (e.g., Lewis *et al.* 2002; Adams *et al.* 2004; Peck and Congdon 2006) may not be mediated solely by differences in parental care behaviors. Instead, inter-sexual competition or differences in energy requirements (Lewis *et al.* 2002; Peck and Congdon 2006) may drive sex-specific space use in other monomorphic seabirds.

Despite the close proximity of the N7 and East Alviso colonies (13-15.5 km), terns from N7 were located farther from the nest and ranged farther in the post-breeding stage than East Alviso terns (Table 1). During incubation and chick-rearing stages, terns are constrained by the location of the colony site when foraging and can reduce overall energetic expense by foraging close to the nest.

For example, in Caspian Terns nesting in the Columbia River Estuary, individuals foraged on the closest available resources to their nesting colony, and colony affiliation influenced the distance individuals traveled to foraging locations (Lyons *et al.* 2005). However, in Forster's Terns in South Bay, distance from nest and foraging range were similar between colony members during incubation and chick-rearing stages, indicating that individuals from both colonies may incur similar energetic costs from their foraging activities during those time periods.

Forster's Terns were located closer to the nest during incubation and chick-rearing stages (Table 1) compared to the pre-breeding stage. In studies of Black-legged Kittiwakes (*Rissa tridactyla*), sex-specific differences or parental behaviors, rather than factors related to seasonal environments, were likely to be the cause of changes in space use between breeding stages (Humphreys *et al.* 2006). Likewise, seasonal variation in movements by Forster's Terns was likely due to prospecting colony sites and mates during the pre-breeding stage, greater attachment to the nest during incubation and chick-rearing stages, and emancipation from the nest during the post-breeding stage. In both Killdeer (*Charadrius vociferus*) and Common Ravens (*Corvus corax*), birds traveled shorter distances and reduced home-range size during incubation and chick-rearing, whereas distances from nest and home-range size increased during the post-breeding stage (Roth *et al.* 2004; Plissner *et al.* 2000b). In Forster's Terns, however, the mean distance and foraging range from the nest also increased during post-breeding, but home-range and core-area size decreased during the same stage. These data suggest that post-breeding terns were no longer attached to their nest site, but, unlike Killdeer and ravens, Forster's Terns concentrated their use at areas far from their nest. Similarly, Adams *et al.* (2004) found that post-breeding Cassin's Auklets (*Ptychoramphus aleuticus*) did not attend the colony and were located in foraging areas outside of their range during the breeding season. Although factors affecting post-breeding movements away from col-

ony sites are poorly understood, post-breeding movements of seabirds may reflect attempts by individuals to restore body condition after a breeding attempt (Weimerskirch *et al.* 2006). Since terns lose significant mass during incubation and chick rearing (Wendeln and Becker 1996), it is possible that the need to increase body condition by gaining mass and nutrients drives the post-breeding movements of Forster's Terns.

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